AN ABSTRACT OF THE THESIS OF

Joel Bartholemew Hagen for the degree of Doctor of Philosophy

in General Science (Biological Science) presented on 31 July 1981

Title: Experimental Taxonomy, 1930-1950: The Impact of Cytology,

Ecology, and Genetics on Ideas of Biological Classification

Redacted for privacy

Abstract approved: ______________________________

Paul Lawrence Farber

During the years between 1930 and 1950 a number of attempts were made to introduce techniques and ideas from cytology, ecology, and genetics into the field of taxonomy. Advocates of this "experimental taxonomy" believed that cytological, ecological, and genetic techniques would provide a rigorous, objective methodology to replace the traditional descriptive methods of taxonomy. Between 1930 and 1950 a number of impressive experimental taxonomic research programs were instituted. Despite the enthusiastic activity in experimental taxonomy, the introduction of cytological, ecological, and genetic methods into taxonomy was problematic. Taxonomists who borrowed from other biological fields were not taking methods and ideas from fully "mature" sciences. Cytology, ecology, and genetics were themselves going through

major theoretical and methodological changes. The integration of methods and ideas from a number of complex, semi-autonomous biological disciplines was difficult. Experimental taxonomists, themselves, disagreed on the form this integration should take. Finally, although experimental taxonomy proved to be a viable and fruitful line of research, it did not constitute a complete reform of general taxonomic theory and practice. By 1950 most taxonomists realized that experimental taxonomy was a valuable, but limited, area of research within the more comprehensive discipline of general systematics.

Experimental Taxonomy, 1930-1950: The Impact of Cytology, Ecology, and Genetics on Ideas of Biological Classification

by

Joel Bartholemew Hagen

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Commencement June 1982

APPROVED

Redacted for privacy

Associate Professor of History of Science in charge of major

Redacted for privacy

Chairman of Department of General Science

Redacted for privacy

Dean of Graduate School

Date thesis is presented July 31, 1981

Typed by Jean Kreitlow for Joel Bartholemew Hagen

ACKNOWLEDGMENTS

At the completion of such a long project it is a pleasure to acknowledge the help that so many people have given me along the way. In particular I owe a debt of gratitude to my adviser, Paul Farber. As teacher, critic, and friend he has been instrumental in bringing this work to a successful conclusion. Without his patience and optimistic encouragement throughout the years this project would certainly never have been completed. I am also grateful to the other members of my dissertation committee. Peter Dawson, Brookes Spencer, and Charles Warren have all been extremely generous with their time and have provided keen insights and criticism. Lawrence Small was generous enough to serve as graduate school representative on very short notice.

I owe much to both formal and informal teachers at Oregon State University. In particular, Paul Farber, Dan Jones, Jim Morris, and Brookes Spencer have contributed toward the development of my interest in history of science. I have learned much history of biology in a very enjoyable manner through the "Dinner and Reading Club" consisting of Marshall Allen, Keith Benson, David Chapin, and Paul Farber. I have benefited greatly from long discussions on the nature of modern science with Marshall Allen and Walter Hellmann.

To my friends and co-workers in the General Science Department at Oregon State University I am grateful for support and encouragement throughout the years. Many friends have helped to buoy my spirits during this project. In particular I would like to thank Kit Chesla, Margaret Coleman, Debbie Goldenberg, Diane Bunting, Finn Pond, and Jean Kreitlow. Jean Kreitlow was generous enough to type this work during a rather hectic spring.

Much of the preliminary work on this project was completed during a year as Scholar-in-Residence at Cornell College. I am thankful to the faculty, students, and administration of Cornell for a most enjoyable period of unimpeded study.

My family has been extremely supportive and encouraging throughout this project. A special thanks goes to my wife, Susan. She enthusiastically undertook the thankless tasks of filing bibliography cards and proof-reading drafts. Most of all I am grateful for her constant encouragement throughout the completion of this project.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

EXPERIMENTAL TAXONOMY, 1930-1950: THE IMPACT OF CYTOLOGY, ECOLOGY, AND GENETICS ON IDEAS OF BIOLOGICAL CLASSIFICATION

INTRODUCTION

Much recent research in the history of modern biology has been directed at a limited number of biological episodes. The rise of genetics has received a lion's share of historians' attention.[1] The fusion of genetics and natural selection theory into the neo-Darwinian or "synthetic theory" of evolution has been another major focus of historical research. The introduction of experimentalism via experimental embryology and experimental physiology has been a third area of active historical inquiry. While no historian would claim that these episodes constitute all that is important in the development of modern biology, historians have drawn heavily on these episodes for their characterizations of twentieth century biology.

Perhaps the best example of this type of characterization is presented in Garland Allen's *Life Science in the Twentieth Century*. According to Allen, "The chief goal of this book is to show how biology as it was practiced in the nineteenth century—in natural history, descriptive and speculative; in physiology, largely mechanistic—was transformed into its twentieth-century mold: experimental, analytically rigorous, and integrative."[2] Allen explicitly disclaims any pretense to writing a comprehensive history of biology. Nonetheless, he portrays developments in genetics, embryology, and physiology as characteristic of the modern biological enterprise as a whole.[3]

Among other themes that Allen stresses in his historical account is the influence of experimentalism on the practice of modern biology. The rise of experimentalism is portrayed as coming at the expense of descriptive natural history. This change, Allen rather graphically terms the "revolt from morphology."[4] Although at least one historian has criticized Allen's emphasis on the antagonism between experimentalism and descriptive biology, the "naturalist—experimentalist dichotomy" appears to be a widely held historical generalization.[5]

In a recently published article, John Dean has analyzed an episode in twentieth century plant taxonomy in terms of the naturalist—experimentalist dichotomy.[6] The aspect of taxonomy that Dean has chosen, experimental taxonomy, is particularly intriguing because it entails the introduction of experimental methods into what is generally considered a descriptive science. In contrast to Garland Allen, who argues that the experimentalists effectively won the day early in the 1900s, Dean argues that the conflict between experimentalists and descriptive biologists, at least in taxonomy, is very much alive today.[7] In fact, according to Dean, no easy resolution of this conflict is likely to occur in the near future.

Experimental taxonomy is an interesting aspect of the history of systematics for a number of reasons. The problematic relationship between experimental and descriptive methods is only one point of historical interest. The new methods, borrowed largely from cytology, ecology, and genetics, were introduced into systematics primarily after 1920. This was a period of intense ferment in systematics, hence the popularity of the term "new systematics." The developments which surrounded experimental taxonomy and the new systematics closely coincided with the rise of neo-Darwinian evolutionary theory. A number of taxonomists who view the new systematics very differently agree in their close identification of the new systematics with the synthetic theory of evolution.[8]

The purpose of this dissertation is to examine the introduction of cytological, ecological, and genetic methods into taxonomy and to analyze the impact that these methods had on ideas about the science of classification. In contrast to the analysis of John Dean, I place relatively little emphasis on the conflict between experimental taxonomists and "orthodox" taxonomists. This is not to claim that conflicts over taxonomic theory and practice did not occur during the period of the new systematics. Nonetheless, I contend that the distinction between experimental taxonomists and orthodox taxonomists is highly artificial. A number of important figures in taxonomy during the period 1930-1950 cannot be accurately characterized by either of these terms. To force such figures onto the Procrustean bed of the naturalist—experimentalist dichotomy tends to distort rather than clarify our understanding of experimental taxonomy.

Rather than stress distinctions between types of taxonomists, I have emphasized the tentative nature of experimental taxonomic research itself. Those who attempted to incorporate methods from cytology, ecology, and genetics into taxonomic research were not borrowing from fully "mature" sciences. During the period between 1920 to 1950 the disciplines of cytology, ecology, and genetics were themselves going through fundamental changes in theory and methodology. While a number of taxonomists eagerly borrowed from these fields, there was no agreed upon formula for the proper procedure of experimental taxonomy.

I have used the term "experimental taxonomy" because it was widely applied during the period under study, and not because I believe that it is a particularly descriptive term. A second theme in this dissertation is the broad scope of research methods that can be characterized as part of experimental taxonomy. Not all of the methods advocated by experimental taxonomists were experimental. As some taxonomists of the period noted many cytological and ecological methods, and even some genetic methods, were basically descriptive.

Finally, in placing experimental taxonomy within the larger context of the new systematics I have tried to emphasize the interest which a number of taxonomists showed in broadening the scope of their discipline. These taxonomists not only incorporated the methods of cytology, ecology, and genetics into taxonomy, but also supported cooperation with biologists in other fields. This cooperation took the form not only of joint research ventures, but also discussions and symposia on the relationships between taxonomy and other biological disciplines. Even some critics of certain experimental taxonomic research projects took part in this aspect of the "expansion of taxonomy."[9] In short, I have presented experimental taxonomy, not so much as a unified school of thought, but rather as a more amorphous tendency to explore the limits of taxonomy and to "experiment" with the science of classification itself.

NOTES

INTRODUCTION

1. For an extensive annotated bibliography of historical works on genetics, see: Garland Allen, *Life Science in the Twentieth Century* (New York: John Wiley & Sons, Inc., 1975), pp. 236-241.

2. Ibid., p. xv.

3. Ibid., pp. xi-xii.

4. Ibid., p. 19.

5. Ernst Mayr has recently presented a discussion of the conflicts between experimental geneticists and naturalists as a major hindrance to the development of the synthetic theory of evolution. Other contributors to the conference at which Mayr presented his analysis also mentioned the conflict. See: Ernst Mayr, "Prologue: Some Thoughts on the History of the Evolutionary Synthesis;" and Ernst Mayr, "The Role of Systematics in the Evolutionary Synthesis;" both in: Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge: Harvard University Press, 1980). For a critical appraisal of the naturalist—experimentalist dichotomy as applied to turn of the century morphology, see: Keith R. Benson, "Problems of Indvidual Development: Descriptive Embryological Development at the Turn of the Century," *Journal of the History of Biology* 14 (1981): 133-146.

6. John Dean, "Controversy Over Classification: A Case Study from the History of Botany," in: Barry Barnes and Steven Shapin, eds., *Natural Order: Historical Studies of Scientific Culture* (Beverly Hills, California: Sage Publications, 1979).

7. Ibid., pp. 224-227.

8. For example, compare: Ernst Mayr, *Systematics and the Origin of Species* (Columbia University Press, 1942), pp. 6-8; George G. Simpson, *Principles of Animal Taxonomy* (New York: Columbia University Press, 1961), pp. 63-66; Richard E. Blackwelder, *Taxonomy* (New York: John Wiley & Sons, Inc., 1967), pp. 341-350; P.H.A. Sneath and R.R. Sokal, *Numerical Taxonomy* (San Francisco: W.H. Freeman & Co., 1973), pp. 16-17.

9. The term "expansion of taxonomy" was apparently coined by W.B. Turrill. See: W.B. Turrill, "The Expansion of Taxonomy with Special Reference to Spermatophyta," *Biological Review* 13 (1938): 342-373.

Chapter One: The New Systematics and the Modern Synthesis

The early decades of the twentieth century witnessed major changes in biology. A number of fields, notably ecology and genetics, became recognizable as distinct disciplines.[1] Biological disciplines such as cytology that were already well-established went through major methodological and theoretical changes.[2] Historians have also described more general changes in the entire enterprise of biology during the early twentieth century. Darwinism, which had been embattled during the late nineteenth and early twentieth centuries, became widely accepted during the 1930s and 1940s.[3] Biologists in a number of fields rejected descriptive methods and enthusiastically embraced experimental techniques.[4] In general, biologists became more specialized and professional.[5]

Less well-documented is the dissatisfaction some biologists felt with the fragmentation of biology. Though widespread, this dissatisfaction tended to be expressed in highly individualistic styles and was never articulated into a single, unified critique. Many of these critics were not opposed to the basic thrust of biology, but rather with what they saw as an unnecessary lack of unity among biological disiplines.

The British embryologist and philosopher J.H. Woodger (1894-), wrote perhaps the most extensive and coherent critique of the period. His *Biological Principles* published in 1929 purported to be an analysis of basic antitheses which existed in biology.[6] Woodger, an intellectual follower of Bertrand Russell (1982-1970), Alfred North Whitehead (1861-1947), and C.D. Broad (1887-1971), felt that a basic philosophical reorientation was inevitable in biology.[7] According to Woodger, biology had reached the point where a period of theoretical and conceptual revaluation was necessary. Like a crab which must periodically molt to accomodate a growing body, the restrictive theoretical exoskeleton of biology required replacement.[8] Not only was this replacement necessitated by an increasing body of data but the theoretical framework of the natural sciences in general had become suspect. However, according to Woodger only physicists had taken this problem seriously. Biologists were making brillant advances in methodology while ignoring the theoretical and metaphysical implications of their work. Woodger's succint diagnosis of this imbalance was that "Nothing is more striking in this science [biology] than the contrast between the brilliant skill, ingenuity and care bestowed upon observation and experiment, and the almost complete neglect of caution in regard to the definition and use of the concepts in terms of which its results are expressed"[9]

Woodger saw his work as an attempt to redress this imbalance. The *Biological Principles* was to be a twentieth century analog of the *Skeptical Chemist*.[10] Like Robert Boyle's seventeenth century classic, the *Biological Principles* would be a critical and impartial analysis of the poorly articulated and unacknowledged assumptions of modern biology. The criticism would be "friendly" in the sense that Woodger would refrain from taking sides in the controversies he analyzed.[11] By logically analyzing the disputes Woodger hoped to overcome the polemical and short-sighted arguments which he believed characterized twentieth century theoretical discussions in biology.

Very different in tone, if not in substance, was the assessment of theoretical biology made by the American entomologist W.M. Wheeler (1865-1937).[12] Wheeler had little patience with those who made unfavorable comparisons between the state of theoretical biology and that of the physical sciences. Nonetheless, according to Wheeler, "We must ruefully admit, I believe that biology does present an appearance of extreme confusion."[13] This disorderly state could be accounted for by a number of characteristics of biology. "This [confusion] is manifestly due in part to the inconceivable intricacy of the sector of reality which the biologists have undertaken to explore and partly to the situation of this sector midway between physics and chemistry on the one hand and philosophy on the other."[14] Not only were biologists buffeted by the winds of change come from the new discoveries in physics and modern philosophy but also from the "...oderiferous doctrinal gusts that are always rising from the more active portions of the biological field itself."[15] Wheeler concluded, "How can we blame the investigator if he complains of the draughts and hurries away to the seclusion of his own specialty?"[16]

Among the "oderiferous doctrinal gusts" on which Wheeler elaborated were the constant disputes among specialists over which biological field was most fundamental. Such bickering might partially be resolved by admitting that biology was not composed of a hierarchy of fields but rather consisted of a loosely organized array of more or less autonomous fields. However, doctrinal disputes would still exist in such new fields as genetics and ecology which were in fact composites of not entirely compatable, previously established biological discplines. Because of this fundamental fragmentation Wheeler noted, "It is not surprising, therefore, that the sciences [of biology] should be afflicted with an extraordinary number of logical oppositions, dilemmas, or contingencies between their theories."[17]

The position of twentieth century theoretical biology described by Wheeler is very similar to that of J.H. Woodger. Nonetheless, the way the two biologists evaluated this state of affairs was strikingly different. Woodger deplored the chaotic state of theoretical biology and saw it as a fundamental weakness in an immature science which had yet to find its Isaac Newton.[18] Conversely, Wheeler, though admitting that "a few super-Einsteins" might be required to unify biology, regarded the theoretical turmoil as a sign of vigor and vitality within a basically healthy science.[19]

The recognition of basic antitheses within biology was not limited to the decade of the 1920s. In 1938 the British taxonomist, W.B. Turrill (1890-1961), noted fundamental problems which existed not only within systematics but within biology in general. As Turrill pointed out,

> There is no doubt that discussions on the basis of classification soon touch some of the deeper issues of philosophy. Not only do epistemological theories come under consideration, but fundamental beliefs of the nature of existence must be accepted or rejected - at least in any given practice. Any one of a dozen oft-repeated sayings of biologists can, on analysis, be shown to involve the acceptance of some broad philosophical dogma, which if expressed in general terms and its logical consequences set out plainly would rather shock the biologist.[20]

In their daily activities biologists rarely had to worry about the philosophical implications of their work. Nonetheless, Turrill warned that the permanent advance of science required a sound philosophical basis, and that biology lacked such a logical foundation. According to Turrill, "We biologists would welcome a full logic of biology, or a 'biologic', or at least such help from trained logicians and philosophers as would give us new tools to replace such as we have worn out, or to use along with those still serviceable."[21] Turrill did not forsee such an improvement in biology as immanent although he saw hopeful signs that some biologists were at least considering the problems of theory. Like Woodger and Wheeler, Turrill realized that a major change in theoretical biology might require a figure of imposing intellectual stature, "An inspector-general of biological methodology is badly needed. Until he arrives we have to do the best we can with rather an undue amount of dissatisfaction and superficial quarreling among ourselves."[22]

Much more optimistic in his appraisal of modern biology was the British polymathic biologist, Julian Huxley (1887-1975). Huxley was not uncritical of the state of biology, although he saw a clear and attainable solution to the problems facing the science. Like the biologists referred to above, Huxley noted the extreme fragmentation of biology. This fragmentation was exacerbated, according to Huxley, by the antiquated biological curricula in British universities. Education during the 1920s had not adequately reflected fundamental changes in the science. Not only was there much new data that was inadequately presented but the basic orientation of biology teaching was misguided.

> Biological science has been of late years growing and expanding at a prodigious rate. As a result, teachers of zoology and also of botany - but I shall confine myself to Animal Biology - have

> had to face the gravest difficulties in regard to their curriculum. The first difficulty is a purely quantitative one: now that the subject has invaded so many new fields, how to stuff this tenfold bulk of knowledge into the brains of students in the same time as before. The second difficulty concerns the relative value of the different biological disciplines. Shall Comparative Morphology continue in the future to dominate the undergraduate's learning period, with Genetics, Cytology, *Entwicklungsmechanik*, Animal Behavior, Systematics, Distribution, Ecology, Histology, Comparative Physiology, and Evolution tacked or thrown on like valances or frills or antimacassars? or can it and should it renounce its pretensions and become one of a society of equals? 23

Huxley's critique is telling for a number of reasons. First of all he expressed the common feeling that biology was suffering from a basic disunity. Secondly, he, like a number of other biologists of the period, clearly felt that biology was still encumbered by an outmoded bias toward morphology.[24] Finally, he saw that the new fields of biology offered a possibility for unifying biology. Much of Huxley's work during the 1930s was aimed at bringing about the unification of biology. In the course of this work Huxley coined two terms which would become modern biological catchwords.

In 1936 Huxley delivered the presidential address to the Zoology Section of the British Association for the Advancement of Science.[25] This speech entitled, "Natural Selection and Evolutionary Progress" championed the neo-Darwinian evolutionary theory primarily as outlined by R.A. Fisher (1890-1962) and J.B.S. Haldane (1892-1964). This evolutionary theory, according to Huxley, was to be the cornerstone of a new biology.

> Biology at the present time is embarked upon a phase of synthesis after a period in which new disciplines were taken up in turn and worked out in comparative isolation. Nowhere is this movement towards unification more likely to be fruitful than in the many-sided topic of evolution; and already we are seeing its first

> fruits in the reanimation of Darwinism which is such a striking feature of post-war biology.[26]

This lecture became the outline for Huxley's well-known text, *Evolution: the Modern Synthesis.*[27] The "modern synthesis" which Huxley described in this book has quite rightly been viewed as a major event in twentieth century biology.

The second activity which Huxley undertook during the 1930s was to organize a group of systematists, geneticists, ecologists, and other interested biologists to discuss common ideas and problems. This group elected Huxley as its chairman and formally organized itself in 1937 under the title, the Association for the Study of Systematics in Relation to General Biology.[28] One of the early accomplishments of this group was the publication of a set of essays under the editorship of Huxley entitled the *New Systematics.*[29]

Huxley's book may have popularized the term "new systematics," but it did little to clarify the meaning of the term.[30]* The essays in the *New Systematics* presented an extremely heterogenous set of perspectives. Not all of the authors advocated any radical departures from taxonomic theory or practice. One contributor, John Ramsbottom (1895- ?), president of the Linnean Society, went so far as to claim that there was nothing new in "new systematics."[31] Later writers have also disagreed, at times violently, about the significance of the new systematics.[32] In short, to the extent that the "new systematics" implies a unified tendency in systematics it has not been a particularly happy term. Although the contributors to Huxley's book

---

*Attempts have been made to distinguish between the terms "taxonomy" and other systematists of the period viewed their discipline as a continually developing one, there was little agreement on the exact direction this development should take.

Certainly Huxley, in his eclecticism, saw the new systematics and the modern synthesis as largely compatible enterprises. According to Huxley a revitalized systematics would have a central place in the unified evolutionary biology which was developing. As a result of the changing orientation of biology

> ...the outlook for taxonomy has altogether changed. Even a quarter of a century ago it was possible to think of systematics as a specialized, rather narrow branch of biology, on the whole empirical and lacking in unifying principles, indispensable as a basis for all biological workers, but without much general interest or application to other branches of their science. To-day, on the other hand, systematics has become one of the focal points of biology. Here we can check our theories concerning selection and gene spread against concrete instances, find material for innumerable experiments, build-up new inductions: the world is our laboratory, evolution itself our guinea-pig.[33]

For Huxley, the major problem facing the new systematics was to be the detection of "evolution at work."[34]

Huxley's evaluation of the relationship between the new systema-

---

and "systematics." For example, see: W.B. Turrill, "Taxonomy and Phylogeny," *Botanical Review* 8 (1942): 247-270, 473-532, 655-707, p. 247-252; and George G. Simpson, *Principles of Animal Taxonomy* (New York: Columbia University Press, 1961), p. 1-11. A distinction, though not a particularly clear one, between these terms is also presented in the *Oxford English Dictionary* (Oxford: Clarendon Press, 1933), s.v. "taxonomy" and "systematics." Taxonomy is defined as "Classification, esp. in relation to its general laws or principles; that department of science, or of a particular science or subject, which consists in or relates to classification." Systematics is defined as "the subject or study of systems, esp. of classification." Despite these distinctions the terms, in practice, appear interchangeable. Following Ernst Mayr, I will use the two terms as synonyms. See: Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), p. 6.

tics and the modern synthesis was shared by a number of other contributors to his volume of essays, notably the geneticists Sewell Wright (1889-   ) and H.J. Muller (1890-1967).[35] Other biologists who were involved with both systematics and evolutionary theory during the period, such as Ernst Mayr (1904-   ) and Theodosius Dobzhansky (1900-1975), held similar views.[36] Mayr, in particular, has argued forcefully that major conceptual changes associated with the new systematics were also pivotal to the success of the modern synthesis. For example, to the question, "What then is the new systematics?" Mayr has replied, "Perhaps it is best described as a viewpoint, an attitude, a general philosophy. It started primarily as a rebellion against the nominalistic-typological and thoroughly non-biological approach of certain, alas all too many taxonomists of the preceding period."[37] In his influential text, *Animal Species and Evolution*, Mayr states that this conceptual shift was of overriding significance for the modern Darwinian synthesis as well. In fact, according to Mayr, "The replacement of typological thinking by population thinking is perhaps the greatest conceptual revolution that has taken place in biology."[38] This position is reiterated in a recent memoir in which Mayr recounts the contributions made by systematists to the modern synthesis. According to Mayr,

> The fifty to seventy-five years preceding the synthesis were characterized by much ferment in systematics. An increasing number of taxonomists rejected the static Linnean species concept, indeed essentialistic taxonomy as a whole. This rejection eventually led to the development of the new systematics, the most distinctive aspect of which was the study of populations (the reason it is also referred to as "population systematics").[39]

Mayr's analysis of the new systematics and its relationship to the modern synthesis gives an intriguing insight into the development of modern evolutionary thought from the perspective of a systematist who was instrumental in establishing the neo-Darwinian theory. Nonetheless, Mayr's historical evaluation of the new systematics is problematic on two counts. First, the dichotomy between typological and populational thinking is unsatisfactory. Second, however important the interrelationships between the new systematics and the modern synthesis were, viewing systematics only from this perspective cannot adequately account for the activities of a number of biologists who identified their work with the new systematics.

Historical dichotomies tend to be simplistic, and the dichotomy between typological and populational thinking is no exception. The terms "typological" or "type concept" are notoriously vague. Historically the terms have had a variety of meanings.[40] A type concept, in the sense of a "collection type concept," involved the designation of a particular specimen, usually the first one described for a species, as the "type." The "classification type concept" was used in reference to a particular group within a higher taxon which was typical of that taxon. For example, a particular species might be designated as the "type" for a given genus. Finally, the "morphological type concept" referred to the idea of an underlying structural plan which characterized a particular group. Each of these three uses of the term "type concept" have had numerous interpretations in the past two centuries. Certain forms of typological thinking have undoubtedly been misused.[41] Nonetheless, different type concepts are not necessarily related to one another. For example, the collection type concept entails a minimum of philosophical content and little or no commitment to the philosophical essentialism which Mayr identifies with typological thinking. As W.B. Turrill pointed out, the collector's practice of naming type specimens is in no way antagonistic to thinking in terms of populations.[42] Furthermore, as Turrill noted, the designation of a "typical" species or other taxon does not necessarily imply anything more than priority of publication.[43] According to some present day systematists a certain amount of thinking in terms of abstract types is a necessary part of any classification procedure.[44] Nonetheless, this use of abstract types does not necessarily commit one to essentialism, as Mayr claims, but can, in fact, be based on a thorough relativism.[45]

Historically, the terms "population" and "populational thinking" are nearly as nebulous as typological thinking. Certainly, biologists used the term "population" widely during the 1930s and 1940s. Nonetheless, these biologists rarely defined the term rigorously and indeed, made use of a number of rather distinct population concepts.[46]

The relationship between populations and such taxonomic units as species or subspecies was particularly unclear.[47] Some biologists considered the term "population" to be taxonomically neutral in the sense that it was not to be part of the orthodox taxonomic nomenclature.[48] Nonetheless, biologists did see some relationship between populations and taxonomic units. Ernst Mayr considered populations to be natural groups which formed parts of a species.[49] Other systematists argued that populations were natural groups from which taxonomic units were abstracted.[50] This ambiguous relationship between populations and taxonomic units has been the source of considerable controversy among systematists.[51]

Populations could simply be considered as groups or collections of organisms.[52] Despite this methodological or "sampling" conception of populations, most biologists considered populations to be groups with some inherent structure. Often this structure was expressed in genetic terms. However, as J.S.L. Gilmour (1906-   ), J.W. Gregor (1900- ?), and J. Heslop-Harrison (1920-   ) pointed out, populations were defined in ecological and geographical terms as well, and the distinctions among these forms of populations or "demes" ought to be explicitly made.[53]

Genetically, populations were generally used in the sense of being groups of interbreeding organisms. While biologists like Mayr and Dobzhansky considered populations to be natural groups discoverable in nature, they also considered populations in more abstract terms. For example, Mayr spoke of ideal populations of perfectly isolated groups of individuals.[54] Dobzhansky, Sewell Wright, and other theoretical geneticists described populations in even more abstract terms. In describing the "genetic structure" of populations Dobzhansky and Wright pictured populations of "gene combinations" scattered over the "adaptive peaks" and valleys of "landscapes" described in terms of relative fitness.[55] C.H. Waddington (1905-1975), a geneticist who worked throughout this period, has claimed that the conceptual shift from thinking in terms of individual genes to thinking in terms of "populations of genes" was the major change in evolutionary theory during the late 1930s.[56] Nonetheless, as Waddington noted, theoretical geneticists did not clearly formulate the relationship between genetic populations and organismal populations.

In all of the senses described above, populations were considered to be groups of conspecific organisms or else systems of genes based on common gene pools. However, populations could denote groups of organisms whether of the same species or not. For example, in a highly influential book, *The Struggle for Existence*, the Soviet biologist G.F. Gauze (1910-), described experiments using "mixed populations" made up of groups of *Paramecium* from two species.[57]

Aside from the vagueness of terms, the dichotomy between typological and populational thinking is difficult to apply in a historical analysis of twentieth century systematics. A number of systematists of the 1930s and 1940s cannot be adequately characterized by either of these categorical terms. As I will show, some systematists rejected "populational" interpretations for rational reasons having little or nothing to do with adherence to a type concept. Furthermore, it should be pointed out that attempts were made in theoretical systematics to combine type concepts and population concepts. For example, in an article written in the early 1940s but published posthumously after 1950, B.H. Danser (1891-1943) advocated the use of a type concept, in the sense of an abstract morphological groundplan, and a set of population concepts referring to various levels of interbreeding genetic systems.[58] J.S.L. Gilmour, whose "deme" terminology was an attempt to classify populations, advocated a form of typological systematics based on Wittgenstein's theory of family resemblances.[59] The usefulness in history of a dichotomy between typological thinking and populational thinking is further hindered by the fact that it is currently being used in a polemical controversy in theoretical systematics.[60] This brings into question the very possibility of using this dichotomy as a critical historical tool. Consequently, typological and populational thinking should probably be completely abandoned as historical categories.

Analyzing the new systematics solely from the perspective of the modern synthesis is also problematic. Such an analysis does shed a good deal of light on the heuristic power of Huxley's vision of systematics as a means of detecting "evolution at work." For example, the impact of neo-Darwinian thinking is readily apparent in the systematics of Ernst Mayr and Theodosius Dobzhansky.[61] Conversely, Julian Huxley pointed out that Mayr's *Systematics and the Origin of Species* was a "...distinctive and valuable contribution to modern evolutionary studies."[62] Nonetheless, not all aspects of the new systematics revolved around neo-Darwinism. A number of contributors to the new systematics appeared unconcerned with the theoretical aspects of their science, evolutionary or otherwise. The motivation for their work came from more practical concerns.[63] Others, although interested in evolution, looked elsewhere for theoretical justifications for their work.[64] Even those whose primary interest in systematics was evolutionary, could be motivated by very general ideas concerning evolution, without committing themselves to any particular theory of evolution.[65]

The relationship between evolutionary theory and systematics has been a stormy one. A number of commentators have noted that there is a fundamental tension between the idea of organic change and the activity of categorizing living things within a classification system.[66] Probably no other issue in systematics generated so much heat during the 1930s and 1940s as the attempted reconciliation of phylogeny and taxonomy. As one participant in the controversy noted in 1951, "...those who took part in the Systematic Association's discussions just before the War on this subject [phylogeny and systematics] will not easily forget the arguments put forth on both sides, nor the heat they engendered, and this year at Leeds the battle was joined again under the auspices of the same Association."[67] The "battle" over the use of phylogeny in systematics tended to polarize systematists during the 1930s and 1940s.[68] Extreme polemics were issued both by supporters and by critics of phylogenetic classification. For example, critics of phylogenetic classification were accused of aspiring to no more than "pigeon-holing" or "cataloging" dead specimens.[69] On the other hand, phylogenetic classifications were criticized for being "speculative" or even "fictitious" and in principle unverifiable.[70]

The arguments over the use of phylogeny in systematics illustrates a great deal about the differing motivations of systematists during the 1930s and 1940s. Nearly everyone agreed that there were major problems with implementing phylogenetic classification systems. Direct evidence in the form of fossil series was lacking in many groups of organisms. Particularly in the plant kingdom this appeared to be a problem without any promise of quick solution.[71] One could assume that similarity between organisms was a sound indication of phylogenetic relationship, but this was not invariably true. In fact a number of systematists agreed with F.A. Bather (1863-1934) that "The whole of our System, from the great Phyla to the very unit cells, is riddled through and through with polyphyly and convergence."[72] However, disagreements over the use of phylogeny in systematics ran a good deal deeper than problems involved with reconstructing particular phylogenies. As W.B. Turrill noted in an extended critique of phylogenetic systematics, two schools of thought existed regarding the philosophical foundations of taxonomy.

> The first states that phylogeny is the only basis for a truly scientific system of classification of plants and animals; the second accepts a broader basis for a general classification in attempting to utilize all available data and constructing the classes on the maximum correlation of characters, discontinuities and breaks in correlation determining the boundaries of the classes.[73]

As Turrill added, these broad schools of thought were not absolute and indeed a number of different views existed on the relationship between phylogeny and systematics. Some supporters of phylogenetic systematics suggested that phylogeny gave systematics a scientific foundation.[74] According to these biologists, depriving systematics of this foundation would deny the field any claim to being scientific. This feeling was so strong among some taxonomists that they could not even conceive of the possibility of a non-evolutionary classification system.[75] According to others, phylogeny gave systematics a radically new basis which distinguished it from pre-Darwinian systematics. For example in *Systematics and the Origin* *of Species*, Ernst Mayr stated,

> The theory of evolution solved the puzzle of the high degree of perfection of the natural system in a manner that was as simple as it was satisfactory: The organisms of a "natural" systematic category agree with one another in so many characteristics because they are descendants of one common ancestor! The natural system became a "phylogenetic" system. The natural system is based on similarity, the phylogenetic system on degree of relationship. It seems probable that a complete change of classification is necessitated by changing the criterium on which the system is based.[76]

Other supporters of phylogenetic systematics, while noting the inherent problems involved in developing phylogenetic schemes, stressed the heuristic value of phylogenetic thinking. For example, O.W. Richards (1901-) pointed out that evolutionary biologists ought to take evolution seriously and apply it in their work.[77] According to Richards, phylogenetic interpretations tended to creep into classification schemes in any case, and an explicit use of phylogeny would at least avoid unacknowledged assumptions. Finally, some biologists believed that although phylogenetic classifications were an ideal that might not be attainable, at least phylogeny gave to systematics a rationality which they believed was otherwise lacking.[78]

Critics of phylogenetic classification tended to stress the distinction between evolutionary explanation and taxonomic principles. For example, C.E.B. Bremekamp (n.d.) stated, "The explanation of the system may be left out of consideration: the question is not whether the system can be explained, but whether it is serviceable."[79] Those who agreed with Bremekamp were not necessarily "practical" systematists with no interest in theory. For example, J.S.L. Gilmour and W.B. Turrill agreed with Bremekamp that the best classification was that which was most generally useful.[80] Turrill, and particularly Gilmour, justified this view on the grounds that biological classification was only one form of classification. As such, taxonomy had to adhere to the logic of general classification. According to Gilmour,

> ...biologists have almost completely ignored, or dismissed as irrelevant, the fundamental principles of classification which apply to all objects, whether living or non-living, and which have been discussed and re-discussed from the time of the Greeks until the present day. This isolation of biological from general classification has, in my view, been fatal to a proper appreciation of the aims and methods of taxonomy and is largely responsible for the confusion that exists to-day.[81]

The form of the general principles of logic which Gilmour and Turrill relied on was that laid down by nineteenth and twentieth century logicians, particularly J.S. Mill (1806-1873), W.S. Jevons, (1835-1882), and A.D. Ritchie (1891-1967).[82] These principles, as interpreted by Gilmour, demanded that the primary criteri~~a~~on for judging any classification system, whether biological or not, was its usefulness. Classification was, for Gilmour, a fundamental prerequisite for all conceptual thought. Primarily, classification served to create classes from which useful inductive generalizations could be derived. The "usefulness" of these inductive generalizations was dependent upon the particular purposes for which the system was devised. Therefore, there could be no single "true" classification system, but only numerous more or less useful systems. Some systems, of course, were more generally useful than others and in this sense could be said to be more "natural" or "general" than others. However, the fact that taxonomists in general accepted an "orthodox" system of classification was less an indication that the system reflected "true affinities" than it had proved to be generally useful for biological research.

In putting forth this utilitarian view of biological classification Gilmour and Turrill argued that most "phylogenetic systems" were not even based on phylogenetic relationship, which was rarely known, but rather on similarities and differences.[83] Phylogenetic interpretations were generally made from the classification scheme, not vice versa. Two options were, therefore, open to those who wished to incorporate phylogeny into classification systems. A truly phylogenetic system could be devised based solely upon known phylogenetic relationships. This would be a specialized classification system which would be of use in particular situations. Alternatively, information about phylogenetic relationships could be incorporated into a general classification system. This general system would be based not only upon phylogenetic relationships but also upon cytological, ecological, genetic, morphological, and other relationships. The point that Gilmour stressed was that evolutionary relationships were only one form of biologically important relationship. A general classification system was the most useful because it took into account the greatest number of criteria and therefore allowed the derivation of the greatest number of inductive generalizations. Any number of more specialized systems based upon particular relationships could be and should be devised, but these ought to remain subsidiary to the general classification system.

Gilmour and Turrill were major figures in modern theoretical systematics and must be taken seriously by the historian. Both men wrote extensively on the philosophy of systematics. Their criticism of phylogenetic classification came neither from an ignorance of evolutionary theory nor from a rejection of it, since both Gilmour and Turrill were evolutionary biologists. Gilmour, realizing the importance of population biology for evolutionary theory, developed the "deme" terminology as an attempt to systematize different concepts related to evolutionarily important groups or populations. Turrill was named to the editorial board of the journal *Evolution* shortly after it was established in 1947. Gilmour and Turrill criticized phylogenetic taxonomy not because they were critical of evolutionary theory, but because they were opposed to using evolutionary theory as a foundation for taxonomy. Evolution served as an explanation for taxonomic relationship, yet this explanation, historically, had been developed largely on the basis of pre-Darwinian taxonomy. Therefore, according to Gilmour and Turrill, taxonomy was not based on evolutionary theory; rather evolutionary theory had its basis fundamentally in the field of taxonomy. Taxonomy had to be both the foundation for all biological research and the final repository for all biological knowledge. In the conclusion of his most extensive critique of phylogenetic taxonomy Turrill cited with approval the nineteenth century botanist Asa Gray (1810-1888): "Botanical classification, when complete and correct, will be an epitome of our knowledge of plants."[84]

The problematic relationship between phylogeny and systematics was not resolved between 1930 and 1950. Furthermore, discussions on evolutionary systematics were not the only focal points of the new systematics. If the Association for the Study of Systematics in

Relation to General Biology, the group which published the *New Systematics*, is viewed as a microcosm of systematics in the 1930s and 1940s, the aims and purposes of the new systematics appear diverse.* As W.B. Turrill, one of the founding members, noted, the purposes of the new Association were threefold.[85] First, the group would investigate the basic philosophical principles of classification. The Association would attempt to define and stabilize terms, and clarify the purposes of classification. Second, the group would initiate and encourage cooperative research especially on the "borderline" between systematics and other biological fields. Finally, the Association would coordinate research, publication, and discussion among biologists from different fields. These general purposes were extended by the chairman of the Association, Julian Huxley.[86] Huxley enumerated ten general aims of the group. Some of these aims were quite utilitarian. For example, the Association would lobby for more jobs in taxonomic research. Handbooks of British flora and fauna would be improved by the group. The Association would hold discussions on the teaching of systematics in the schools and universities. Research efforts by amateurs and local natural history societies would be coordinated by the Association. Other aims were more theoretical. For example the Association would promote research on speciation and evolution. The group would arrange discussions on the historical and

---

*In 1946 the Association for the Study of Systematics in Relation to General Biology changed its name to the current title, Systematics Association. See: Systematics Association: Annual Report VI, *Proceedings of the Linnean Society of London* 160 (1948): i-iv.

philosophical bases of systematics and how these related to the practical aims of the systematist. The correlation of systematic theory with more general biological principles would also be a focus of the group's discussions. Finally, a major aim of the Association would be to develop new lines of cooperative research combining the methods of systematics with those of other biological fields. In the light of new data from other fields the group would discuss the possibility of modifying systematics. These diverse aims of the Association are mirrored in the diversity of viewpoints expressed by the new systematists in Huxley's *New Systematics*.

The Association for the Study of Systematics in Relation to General Biology was not the only group to promote discussions on the problems of systematics. Numerous professional societies sponsored symposia on various topics related to systematics.[87] In the United States, the Committee on the Common Problems of Genetics, Paleontology, and Systematics was established in 1943. This group was expanded and reorganized after World War II as the Society for the Study of Evolution. In 1947 this group held a conference at Princeton University which resulted in the publication of an influential set of essays entitled *Genetics, Paleontology, and Evolution*.[88] This conference has been portrayed as a sort of watershed in evolutionary biology. According to Ernst Mayr, one of the organizers of the conference, this meeting epitomized the general acceptance of the modern neo-Darwinian synthesis.[89]

In some ways the Association for the Study of Systematics and the Committee on Common Problems of Genetics, Paleontology, and Systematics were quite similar. Both groups were attempts to bring together biological specialists to discuss common problems. Both groups included in their memberships a number of outstanding scientists from a variety of biological disciplines.[90] Both groups attempted, despite the limitations of wartime conditions, to promote discussions which would reach a wider audience than the groups themselves.[91] Finally, throughout the late 1930s and 1940s there was informal cooperation between the groups. From the beginning, the Association for the Study of Systematics in Relation to General Biology had discussed the possibility of starting a journal or bulletin.[92] This publication would serve as a bibliography of current research in zoology, botany, ecology, and cytogenetics, which might be relevant to systematics. On a trip to the United States in 1939 the chairman, J.S. Huxley discussed with American biologists the possibility of a cooperative publication effort.[93] These plans were stymied by World War II. However, after the war when the Society for the Study of Evolution decided to inaugurate the journal, *Evolution*, negotiations were undertaken to include members of the Association on the editorial board.[94] W.B. Turrill and J.S. Huxley were named to the board when the new journal began publication. Cooperation between the societies was further encouraged by the offer of subscription to *Evolution* at a substantial discount to Association members.[95]

The groups were, nonetheless, not identical. The Committee on Common Problems of Genetics, Paleontology, and Systematics seems, from its inception, to have had a much stronger commitment to evolutionary theory than the Association for the Study of Systematics in Relation to General Biology. This commitment, of course, became explicit in the purpose of the Committee's daughter group, the Society for the Study of Evolution. The essays dealing with systematics in *Genetics, Paleontology, and Evolution* if not all of the same cloth, certainly share a common evolutionary perspective. Furthermore, Ernst Mayr points out that there was near unanimity on the correctness of neo-Darwinian evolutionary theory at the Princeton conference.[96]

If Mayr's analysis of the Princeton conference accurately portrays the degree of agreement among the participants, then the American group was considerably less heterogenous than its British counterpart. Such unanimity of perspective on evolutionary theory would have been unlikely among the members of the Association for the Study of Systematics in Relation to General Biology. As I have pointed out the relationship between evolutionary theory and systematics was hotly debated within the Association throughout the 1930s and 1940s. Acrimonious remarks were aired on this topic during symposia held by the Association well into the 1950s.[97]

The diversity of opinions expressed by members of the Association for the Study of Systematics in Relation to General Biology makes this group a particularly useful microcosm of systematics in the twentieth century. The Association actively promoted discussion on the whole gamut of taxonomic problems. This group was by no means a unified school of thought, much less a unitary movement toward an evolutionary synthesis in systematics. What the members of the Association did share was a very general and rather ill-defined interest in broadening the scope of systematics. It is my contention that a satisfying history of the new systematics must focus upon what W.B. Turrill aptly referred to as the "expansion of taxonomy."[98]

The modern synthesis has been an impressive attempt to unify biology. As Ernst Mayr and others have demonstrated, this synthetic, evolutionary scheme has had a profound impact on systematics.[99] Much of the expansion of systematics during the 1930s and 1940s revolved around explicitly evolutionary foci that can be identified with the modern synthesis. During this period there were, however, other attempts to unify biology. For example, following the publication of his critical *Biological Principles*, J.H. Woodger devoted his career to an extended, constructive attempt to unify biology on the foundation of formal axiomatic logic.[100] While Woodger was not primarily interested in systematics, his works have been widely referred to by systematists.[101]

A satisfactory history of the new systematics cannot, however, be totally preoccupied with unifying tendencies in modern biology. As the publications and discussions of the Association for the Study of Systematics in Relation to General Biology demonstrate there was a considerable amount of dissension within systematics during the 1930s and 1940s. In some important respects systematics continues to exhibit sharp divisions. Even a casual reading of the works of such contemporary systematists as R.E. Blackwelder, David L. Hull, Ernst Mayr, P.H.A. Sneath, and R.R. Sokal, indicates the existence of fundamental differences among systematists of the present day.[102] Most of these disagreements existed in one form or another in the new systematics of the 1930s and 1940s. Biologists of the 1930s and 1940s such as J.H. Woodger, W.M. Wheeler, and W.B. Turrill noted the disunity of their science and suggested that it would perhaps take "philosophical inspectors general," "Newtons," or "Super-Einsteins," to bring about a unification of biology. At least one systematist writing in the 1960s suggested that this unifier had yet to arrive. According to J.S.L. Gilmour, "Biological taxonomy still awaits its Einstein. The more biologists there are giving thought to the problems that beset it, the more likely it is that an Einstein will appear."[103]

This dissertation can hardly attempt to do more than analyze one small aspect of the "expansion of taxonomy" that characterized the new systematics. One important aspect of this expansion was the utilization of methods and theories from cytology, ecology, and genetics by taxonomists of the 1930s and 1940s. Cytology, ecology, and genetics were not the only fields to impinge on taxonomy during this period. Nonetheless, several taxonomists cited these disciplines as being particularly relevant to their work.[104] A number of papers and symposia were devoted to the relationships between taxonomy and each of these fields.[105] Perhaps most significantly, taxonomists who saw in experimental methods a means of placing taxonomy on a more objective basis regularly used a combination of techniques and theories borrowed from cytology, ecology, and genetics.[106]

The terms "experimental taxonomy," "synthetic taxonomy," "genonomy," "genecology," and "biosystematy" have all been used to refer to aspects of the "expansion of taxonomy."[107] This expansion of taxonomic methods and theories links together a disparate group of biologists. These scientists could share little in common other than their interest in extending the boundaries of systematics. For example, both those, like Theodosius Dobzhansky, who advanced an explicitly phylogenetic systematics and those, like W.B. Turrill, who were highly critical of phylogenetic systematics, were equally interested in implementing cytological, ecological, and genetic methods in biological classification. These systematists were, however, doing more than simply expanding the use of experimental methods borrowed from other fields. Much more significantly, in practicing "experimental taxonomy" they were experimenting with the science of taxonomy itself.[108]

NOTES

CHAPTER ONE

1. Considerable attention has been devoted by historians to the rise of genetics. For example, see: Garland Allen, *Life Science in the Twentieth Century* (New York: John Wiley & Sons, Inc., 1975): Garland Allen, *Thomas Hunt Morgan: The Man and His Science* (Princeton: Princeton University Press, 1978); William Provine, *The Origins of Theoretical Population Genetics* (Chicago: University of Chicago Press, 1971). Several geneticists have published memoirs of the development of their discipline. For example, see: Elof A. Carlson, *The Gene: A Critical History* (Philadelphia: W.B. Saunders Co., 1966); L.C. Dunn, *A Short History of Genetics* (New York: McGraw-Hill Book Co., 1965); Richard Goldschmidt, "Fifty Years of Genetics," *American Naturalist* 84 (1950) 313-339; A.H. Sturtevant, *A History of Genetics* (New York: Harper & Row, Publishers, Inc. 1965). Very little has been written about the development of ecology. Some idea of the rapid development of this field can be gained from articles appearing in the 1929 edition of the *Encyclopedia Brittanica,* the first edition to include articles specifically devoted to animal and plant ecology. See: Charles S. Elton, "Animal Ecology," and E.J. Salisbury, "Plants: Distribution and Ecology," both in: *Encyclopedia Brittanica* (14th edition).

2. For a concise list of technical improvements in cytology during the early decades of the twentieth century, see: C.D. Darlington, *Recent Advances in Cytology* (Philadelphia: P. Blakiston's Son & Co., Inc., 1932), Appendix II, pp. 491-492. For the close ties between cytology, genetics, and evolutionary theory, see: Hampton Carson, "Cytogenetics and the Neo-Darwinian Synthesis," C.D. Darlington, "The Evolution of Genetic Systems: Contributions of Cytology to Evolutionary Theory," and Alexander Wettstein, "Cytology in the T.H. Morgan School," all of which appear in: Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge: Harvard University Press, 1980); C.D. Darlington, *The Evolution of Genetic Systems* (Cambridge: Cambridge University Press, 1939): L.T. Hogben, "Cytology," and J.B.S Haldane, "Heredity," both in: *Encyclopedia Brittanica* (14th edition); C.H. Waddington, *An Introduction to Modern Genetics* (New York: Macmillan Co., 1939).

3. The exact date of the "modern synthesis" is difficult to pinpoint. Much of the theoretical foundation of neo-Darwinism was laid during the 1920s, see: Provine, *Origins*, chap. 5. The general acceptance of neo-Darwinism, according to Ernst Mayr, came considerably later, around 1947. See: Ernst Mayr, "Prologue: Some Thoughts on the History of the Evolutionary Synthesis," in: Mayr and Provine, *Evolutionary Synthesis*.

4. See: G. Allen, *Life Science* , chaps. II and III. This interpreta- of the relationship between descriptive and experimental biology has recently been challenged; see: Keith R. Benson, "Problems of Individual Development: Descriptive Embryological Morphology in America at the Turn of the Century," *Journal of the History of Biology* 14 (1981): 133-146.

5. Relatively little historical research has been explicitly devoted to the professionalization of biologists during the twentieth century. For suggestive studies of the professionalization of genetics, see: G. Allen, *Thomas Hunt Morgan*. A more detailed account can be found in: Hamilton Cravens, *The Triumph of Evolution* (Philadelphia: University of Pennsylvania Press, 1978), chap. 1.

6. J.H. Woodger, *Biological Principles*, (New York: Harcourt, Brace and Co., 1929).

7. For an account of Woodger's intellectual development and philosophy, see: Marshall W. Allen, "J.H. Woodger and the Emergence of Supra-Empirical Orders of Discussion in Early Twentieth Century Biology," (M.S. Thesis, Oregon State University, 1975). See also: W.F. Floyd and F.T.C. Harris, "Joseph Henry Woodger, Curriculum Vitae," in: J.R. Gregg and F.T.C. Harris, eds., *Form and Strategy in Science* (Dordrecht-Holland: D. Reidel Publishing Co., 1964).

8. Woodger, *Biological Principles*, p. 1.

9. Ibid., p. 3.

10. Ibid., pp. 1-3.

11. Ibid., p. 7.

12. W. M. Wheeler, "Present Tendencies in Biological Theory," in: W.M. Wheeler, *Essays in Philosophical Biology* (Cambridge: Harvard University Press, 1939).

13. Ibid., p. 187.

14. Ibid.

15. Ibid.

16. Ibid.

17. Ibid., p. 193.

18. Woodger, *Biological Principles*, p. 483.

19. Wheeler, "Present Tendencies," p. 208.

20. W. B. Turrill, "The Expansion of Taxonomy with Special Reference to the Spermatophyta," *Biological Review* 13 (1938): 342-373, p. 345. For a short sketch of Turrill's life and a complete bibliography of his work, see: C.E. Hubbard, "William Bertram Turrill," *Royal Society of London: Biographical Memoirs* 17 (1971): 689-712.

21. Turrill, "Expansion," p. 346.

22. Ibid.

23. J.S. Huxley, "Editor's Introduction," in: Charles Elton, *Animal Ecology* (New York: Macmillan Company, 1927; reprint edition, 1935), p. ix.

24. The turn away from morphology by younger biologists of the early twentieth century has been described by Garland Allen as the "Revolt from Morphology." See: G. Allen, *Life Science*, chaps. II and III.

25. J.S. Huxley, "Natural Selection and Evolutionary Progress," *Report of the British Association for the Advancement of Science* (1936): 81-100.

26. Ibid., p. 81.

27. J.S. Huxley, *Evolution: The Modern Synthesis* (New York: Harper & Brothers, Publishers, 1943), p. 7.

28. "Association for the Study of Systematics in Relation to General Biology," *Nature* 140 (1937): 163-164; "Systematics in Relation to General Biology," *Nature* 140 (1937): 211-212; W.B. Turrill, "The Association for the Study of Systematics in Relation to General Biology," *Chronica Botanica* 4 (1938): 5-7.

29. J.S. Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940).

30. A number of commentators noted that the title of Huxley's book was not the first time that the term "new systematics" had been used. Nonetheless, these commentators noted the significance of Huxley's book for publicizing the concept of a new systematics. See: Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), p. 6; George G. Simpson, *Principles of Animal Taxonomy* (New York: Columbia University Press, 1961), pp. 63-66; G. Ledyard Stebbins, *Variation and Evolution in Plants* (New York: Columbia University Press, 1950), p. 7.

31. J. Ramsbottom, "Taxonomic Problems in Fungi," in: Huxley, *New Systematics*, p. 411.

32. For example, compare Mayr, *Systematics*, pp. 6-8; with R.E. Blackwelder, *Taxonomy* (New York: John Wiley & Sons, Inc., 1967), pp. 341-346. See also: Simpson, *Principles*, pp. 63-66; Arthur Cronquist, "The Old Systematics," and Ernst Mayr, "The New Systematics," both in: Charles A. Leone, ed., *Taxonomic Biochemistry and Serology* (New York: The Ronald Press, Co., 1964).

33. J.S. Huxley, "Introductory: Towards the New Systematics," in: Huxley, *New Systematics*, pp. 1-2.

34. Ibid.

35. H.J. Muller, "Bearings of the 'Drosophila' Work on Systematics," and Sewell Wright, "Statistical Consequences of Mendelian Heredity in Relation to Speciation," both in: Huxley, *New Systematics*.

36. Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), chap. X; Mayr, *Systematics*, chap. V.

37. Ernst Mayr, *Principles of Systematic Zoology* (New York: McGraw-Hill Book Co., 1969), p. 51.

38. Ernst Mayr, *Animal Species and Evolution* (Cambridge: Harvard University Press, Belknap Press, 1963), pp. 5-6.

39. Mayr, "Prologue," Mayr and Provine, *Evolutionary Synthesis*, p. 127.

40. Paul Lawrence Farber, "The Type-Concept in Zoology During the First Half of the Nineteenth Century," *Journal of the History of Biology* 9 (1976): 93-119; Paul Lawrence Farber, "A Historical Perspective on the Impact of the Type Concept on Insect Systematics," *Annual Review of Entomology* 23 (1978): 91-99.

41. C.B. Williams, "On 'Type' Specimens," *Annals of the Entomological Society of America* 33 (1940): 621-624.

42. W.B. Turrill, "Plant Taxonomy, Phytogeography and Plant Ecology," in: W.B. Turrill, ed., *Vistas in Botany; Vol. 4 : Recent Researches in Plant Taxonomy* (London: Pergamon Press, 1964), pp. 210-212.

43. Ibid.

44. For example, see: Blackwelder, *Taxonomy*, pp. 344-346; Arthur Cronquist, *The Evolution and Classification of Flowering Plants* (Boston: Houghton Mifflin Co., 1968), p. 7; J.S.L. Gilmour and S.M. Walters, "Philosophy and Classification," in: Turrill, *Vistas*, pp.6-7.

45. Gilmour and Walters, "Philosophy and Classification," pp. 6-7.

46. For example, G. Ledyard Stebbins suggested that the term "population had "no precise meaning" and an "elastic definition." See: Stebbins, *Variation*, pp. 38-39. See also: Mayr, *Systematics*, p. 24.

47. Compare: Stebbins, *Variation*, pp. 38-39; Mayr, *Systematics*, p. 7; G.C. Robson and O.W. Richards, *The Variation of Animals in Nature* (New York: Longmans, Green and Co., 1936), pp. 10-11.

48. Stebbins, *Variation*, pp. 38-39; J.S.L. Gilmour and J. Heslop-Harrison, "The Deme Terminology and the Units of Micro-Evolutionary Change," *Genetica* 27 (1954): 147-161. Robson and Richards also indicated a distinction between populational terms and taxonomic terms; they did not elaborate on the exact nature of this distinction. See: Robson and Richards, *Variation of Animals*, pp. 10-11, 58-61.

49. For example, Mayr referred to the "populations of a species." See: Mayr, *Systematics*, pp. 24-25, 33-36.

50. Robson and Richards, *Variation of Animals*, p. 10. W.B. Turrill suggested a similar relationship between populations and species. See: Turrill, "Taxonomy and Phylogeny," p. 479; W.B. Turrill, "Principles of Plant Geography," *Kew Bulletin* (1939): 208-237, pp. 217-220.

51. Turrill, "Taxonomy and Phylogeny," p. 479; Gilmour and Heslop-Harrison, "Deme Terminology," p. 448. The logician and taxonomist J.R.Gregg has claimed that the whole "species problem" was based on linguistic ambiguities and logical errors. According to Gregg a major problem in taxonomy has been the confusion between "parts-wholes" and "members-class" relationships among systematic categories. See: J.R. Gregg, "Taxonomy, Language and Reality," *American Naturalist* 84 (1950): 419-435.

52. Robson and Richards, *Variation in Animals*, p. 60.

53. Gilmour and Heslop-Harrison, "Deme Terminology," p. 448. See also: J.S.L. Gilmour and J.W. Gregor, "Demes: a Suggested New Terminology," *Nature* 144 (1939): 333.

54. Mayr, *Systematics*, p. 24.

55. Dobzhansky, *Genetics and the Origin*, (1937), pp. 185-191.

56. C.H. Waddington, *The Evolution of an Evolutionist* (Ithaca: Cornell University Press, 1975), p. v.

57. G.F. Gause, *The Struggle for Existence* (New York: Dover Publications, inc., 1934; reprint edition, 1971).

58. B.H. Danser, "A Theory of Systematics," *Bibliotheca Biotheoretica* 4 (1950): 117-180.

59. Gilmour and Gregor, "Demes;" Gilmour and Heslop-Harrison, "Deme Terminology;" Gilmour and Walters, "Philosophy and Classification."

60. For example, R.E. Blackwelder has complained that the term "typological" has been used in a derogatory and propagandistic manner. See: Blackwelder, *Taxonomy*, p. 345.

61. For example, see: Dobzhansky, *Genetics and the Origin*, (1937), chap. X; Mayr, *Systematics*, chap. VII.

62. J.S. Huxley, "Evolution in Action," *Nature* 151 (1943): 347-348.

63. For example, see: W.J. Arkell and J.A. Moy-Thomas, "Paleontology and the Taxonomic Problem," and J. Ramsbottom, "Taxonomic Problems in Fungi," both in: Huxley, *New Systematics*.

64. For example, see: J.S.L. Gilmour, "A Taxonomic Problem," *Nature* 139 (1937): 1040-1042; J.S.L. Gilmour, "Taxonomy and Philosophy," in: Huxley, *New Systematics*; J.S.L. Gilmour and W.B. Turrill, "The Aim and Scope of Taxonomy," *Chronica Botanica* 6 (1941): 217-219.

65. For example, see G.C. Robson and O.W. Richard's critical evaluation of competing evolutionary theories in: Robson and Richards, *Variation of Animals*. Robson and Richards were both interested in taxonomy primarily as it applied to evolutionary questions.

66. For example, Ernst Mayr and David Hull have argued that despite the acceptance of evolution, many taxonomists continue to think of species in static, essentialistic terms. See: Mayr, *Systematics*, p. 103; David L. Hull, "The Effect of Essentialism on Taxonomy — Two Thousand Years of Stasis," *The British Journal for the Philosophy of Science* 15 (1965): 314-326, 16 (1965): 1-18: Quite a different argument has been put forward by J.S.L. Gilmour, who suggests that phylogenetic thinking has confused taxonomic problems rather than solved them. According to Gilmour, many evolutionist continue to follow special creationists in chasing the chimera of "essential" species. See: J.S.L. Gilmour, "The Development of Taxonomy Since 1851," *Nature* 168 (1951): 400-402 [note: erratum on p. 500].

67. Gilmour, "Development of Taxonomy," p. 400. The "lively discussions" over phylogenetic taxonomy and "the great lack of unanimity" among biologists on this topic were also referred to in the annual report of the Systematics Association for 1946-47. See: "Systematics Association: Annual Report VI," *Proceedings of the Linnean Society of London* 152 (1948): i-iv, p. iii. For summaries of the discussions to which Gilmour referred, see: "A Discussion on Phylogeny and Taxonomy," *Proceedings of the Linnean Society of London* 152 (1940): 234-255; "Phylogeny in Relation to Classification," *Nature* 167 (1951): 503-505.

68. Turrill, "Taxonomy and Phylogeny," p. 687.

69. For example, see: Dobzhansky, *Genetics and the Origin*, (1937), p. 316; comments of E.I. White, in: "A Discussion of Phylogeny," p. 250.

70. For example, see: C.E.B. Bremekamp, "The Principles of Taxonomy and the Theory of Evolution," *South African Biological Society, Pamphlet* 5 (1932): 1-8; C.E.B. Bremekamp, "Phylogenetic Interpretations and Genetic Concepts in Taxonomy," *Chronica Botanica* 5 (1939): 398-403. See also: Turrill, "Taxonomy and Phylogeny," pp. 508-516, 686-690.

71. Turrill, "Taxonomy and Phylogeny," pp. 508-516.

72. F.A. Bather, "Biological Classification, Past and Future," *Quarterly Journal of the Geological Society* 83 (1927): lxii-civ, p. ci. For references to Bather's statement, see: Robson and Richards, *Variation of Animals*, p. 61; Gilmour, "Taxonomy and Philosophy," p. 471; Turrill, "Taxonomy and Phylogeny," p. 511.

73. Turrill, "Taxonomy and Phylogeny," p. 687.

74. For example, see: comments of E.I. White in: "A Discussion of Phylogeny," pp. 248-250.

75. For example, see: comments of K.M. Wiegand in: a symposium on the "Significance of Taxonomic Units and Their Natural Basis," *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1571-1589, p. 1575.

76. Mayr, *Systematics*, p. 276.

77. Comments of O.W. Richards, in: "A Discussion on Phylogeny," pp. 240-243.

78. Comments of T.A. Sprague, in: "A Discussion on Phylogeny," pp. 243-248.

79. Bremekamp, "Phylogenetic Interpretations," p. 399.

80. Gilmour and Turrill, "Aim and Scope."

81. Gilmour, "Development of Taxonomy," p. 401.

82. Gilmour, "A Taxonomic Problem," p. 1040; Gilmour, "Development of Taxonomy," p. 401; Turrill, "Expansion," p. 345-350.

83. Gilmour, "A Taxonomic Problem."

84. Turrill, "Taxonomy and Phylogeny," p.686.

85. Turrill, "Association."

86. "Association for the Study."

87. Papers delivered at symposia sponsored by the American Association for the Advancement of Science can be found in: "Supra-Specific Variation in Nature and Classification," *American Naturalist* 71 (1937): 206-276; "Speciation," *American Naturalist* 74 (1940): 232-321; "The Species Concept," *American Naturalist* 75 (1941): 193-263. Papers presented at symposia sponsored by the Linnean Society of London can be found in: "The Concept of Species from the Time of Linnaeus to the Present Day," *Proceedings of the Linnean Society of London* 150 (1938): 224-252; "Geographic Isolation as a Factor in Species Formation," *Proceedings of the Linnean Society of London* 150 (1938): 253-293.

88. Glenn L. Jepsen, George G. Simpson, and Ernst Mayr, eds., *Genetics, Paleontology, and Evolution* (Princeton: Princeton University Press, 1949).

89. Mayr, "Prologue," pp. 42-43.

90. For a list of the founding members of the Association for the Study of Systematics in Relation to General Biology, see: "Association for the Study." For a list of the members of the Committee for the Common Problems of Genetics, Paleontology, and Systematics, see: Jepsen, Simpson, and Mayr, eds., *Genetics, Paleontology, and Evolution*, p. xi.

91. Jepsen, Simpson, and Mayr, eds., *Genetics, Paleontology, and Evolution*, p. vi-vii. Almost from its beginnings the Association for the Study of Systematics in Relation to General Biology was hampered by wartime conditions. Conditions deteriorated to the point that the Association suspended formal activities on June 2, 1942. See: "Association for the Study of Systematics in Relation to General Biology: Annual Reports II, III, IV," *Proceedings of the Linnean Society of London* 152 (1941): 349-403; 153 (1941): 309; 156 (1944): 246-247.

92. "Annual Report II."

93. Ibid.

94. "Association for the Study of Systematics in Relation to General Biology: Annual Report V," *Proceedings of the Linnean Society of London* 157 (1946): 223-224.

95. "Annual Report VI."

96. Mayr, "Prologue," pp. 42-43.

97. For example, see: W.J. Arkell, "Species and Species," in: P.C. Sylvester-Bradley, ed., *The Species Concept in Paleontology* (London: The Systematics Association, 1956), pp. 97-99.

98. Turrill, "Expansion."

99. Ernst Mayr, "The Role of Systematics in the Evolutionary Synthesis," in: Mayr and Provine, eds., *The Evolutionary Synthesis*; Jean R. Beaudry, "The Species Concept: Its Evolution and Present Status," *Revue Canadienne De Biologie (Montreal)* 19 (1960): 219-240; David L. Hull, "The Metaphysics of Evolution," *British Journal for the History of Science* 3 (1967): 309-337.

100. M. Allen, "J.H. Woodger."

101. For example, see: Gilmour, "Taxonomy and Philosophy;" Gregg, "Taxonomy, Language and Reality;" J.R. Gregg, *The Language of Taxonomy: An Application of Symbolic Logic to the Study of Classificatory Systems* (New York: Columbia University Press, 1954); Blackwelder, *Taxonomy*, pp. 346-348.

102. Blackwelder, *Taxonomy*, chaps. 17-18; Hull, "Metaphysics;" Hull, "A Matter of Individuality," *Philosophy of Science* 45 (1978): 335-360; Mayr, *Principles of Systematic Zoology*; P.H.A. Sneath and R.R. Sokal, *Numerical Taxonomy* (San Francisco: W.H. Freeman and Co., 1973).

103. J.S.L. Gilmour, "Taxonomy," in: A.M. Mcleod and L.S. Cobley, eds., *Contemporary Botanical Thought* (Chicago: Quadrangle Books, 1961), p. 44.

104. For example, see: Gote Turesson, "Genecological Units and their Classificatory Value," *Svensk Botanisk Tidskrift* 24 (1930): 511-518; J.W. Gregor, V. McM. Davey, and J.M.S. Lang, "Experimental Taxonomy I. Experimental Garden Technique in Relation to the Recognition of Small Taxonomic Units," *New Phytologist* 35 (1936): 323-350; J. Clausen, D.D. Keck, and W.H. Hiesey, "The Concept of Species Based on Experiment," *American Journal of Botany* 26 (1939): 103-106; Gilmour and Heslop-Harrison, "The Deme Terminology;" J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: William Heinemann Ltd., 1953), p. 12.

105. For example, see: "Discussion on Genetics and Taxonomy," *Report of the British Association for the Advancement of Science* (1937): 426-428; W.B. Turrill, "Taxonomy and Genetics," *Journal of Botany* 76 (1938): 33-39; Turrill, "Expansion;" Edgar Anderson, "Cytology in its Relation to Taxonomy," *Botanical Review* 3(1937): 335-350; William Wright Smith, "Some Aspects of the Bearing of

Cytology on Taxonomy," *Proceedings of the Linnean Society of London* 145 (1933): 151-181; "A Symposium on the Reciprocal Relationship of Ecology and Taxonomy," *Journal of Ecology* 27 (1939): 401-435.

106. For example, see: J.W. Gregor, "Experimental Delimitation of Species," *New Phytologist* 30 (1931): 204-217; J. Clausen, D.D. Keck, and W.H. Hiesey, *Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants* Carnegie Institution of Washington Publication No. 520 (1940).

107. Gote Turesson, "The Scope and Import of Genecology," *Hereditas* 4 (1923): 171-176; W.B. Turrill, "Expansion;" W.B. Turrill, "Experimental and Synthetic Plant Taxonomy," in: Huxley, ed., *The New Systematics*, W.H. Camp and C.L. Gilly, "The Structure and Origin of Species," *Brittonia* 4 (1943): 323-385; Carl Epling, "Taxonomy and Genonomy," *Science* 98 (1943): 515-516.

108. W.B. Turrill suggested that experimenting with the science of classification was a necessary part of the process of development toward an ideal or "omega" taxonomy. See: Turrill, "Taxonomy and Genetics," p. 38. J. Heslop-Harrison suggested that experimental taxonomy was itself still in the "experimental" stage in the 1950s. See: Heslop-Harrison, *New Concepts*, chaps. VII and VIII.

Chapter Two: The Developing Relationships Between Taxonomy and Cytology, Ecology, and Genetics

None of the biological fields from which experimental taxonomists borrowed techniques and theories could be considered fully developed sciences in 1930. Fields such as cytology, ecology, and genetics were themselves undergoing major changes during the 1930s. The writings of biologists from this period and their later memoirs bear this out. For example, in 1932 when C.D. Darlington (1903-   ) published his *Recent Advances in Cytology* he caused a major stir among cytologists. According to the geneticist, J.B.S. Haldane, who wrote the Forward to the book, Darlington was ushering in a new era in the study of chromosomes. "In karyology it [*Recent Advances in Cytology*] marks the beginning of a new epoch, the transition from an essentially descriptive to a largely deductive science."[1] Parts of Darlington's book were admittedly speculative, an aspect of the work which the author defended.[2] These hypothetical "wills-o'-the wisp," Darlington claimed, were a necessary stimulus to further research. Haldane agreed. While admitting that some of Darlington's conclusions might turn out to be erroneous, Haldane noted, "Nevertheless, I am convinced that the last chapter is a prolegomenon to every future theory of evolution. I do not pretend that I have fully digested it. Until I do so my opinions on evolution will be of somewhat restricted value."[3] Not all of Darlington's audience was as receptive to *Recent Advances in Cytology* as Haldane was. The book was immensely controversial and became a focal point for a good deal of critical discussion during the early 1930s.[4]

A detailed discussion of the critical reception of Darlington's book is well beyond the scope of this dissertation. The controversy surrounding *Recent Advances in Cytology*, however, indicates that experimental taxonomists in the 1930s who wished to use cytological techniques and theories were not turning to a fully unified discipline but rather to one that was itself going through fundamental changes. Much the same situation existed in genetics. In his highly influential book *Genetics and the Origin of Species*, Theodosius Dobzhansky delineated three major areas of genetics: the transmission of hereditary characters, the physiological action of genes, and the genetic constitution of populations. By 1937, according to Dobzhansky, "Although a large amount of work remains to be done in this field, it is indeed fair to say that the genetics of transmission of hereditary characters is, by and large, understood now."[5] The same could not be said for the other two areas of genetics. In the area of physiological genetics not only were there many unanswered questions but, according to Dobzhansky, adequate tools had not even been developed with which to investigate these questions. The genetics of populations was also a relatively undeveloped area, although as reviewers noted, Dobzhansky's book was a major contribution to the development of the field.[6]

Ecology was also in a rather undeveloped state during the 1930s. Ecologists, themselves, noted that the boundaries of their discipline were only beginning to be defined in 1930. J. Arthur Thomson (1861-1933) had suggested that ecology might adequately be described as "the new natural history."[7] Charles Elton (1900-), a pioneer in the field of animal ecology, approved of Thomson's very general definition and argued that there could be no more rigorous definition of ecology at that time. The reasons for the rather nebulous scope of ecology were, according to Elton, diverse.

> Animal ecology is a rather difficult subject to define, because it lies on the borderlines of so many other subjects, and also because comparatively little work has so far been done on it, so that its exact scope and limits still remain to be established. In a general way animal ecology seeks to give some definite form to the vast number of observations which have been accumulated during the last few hundred years by field naturalists and various other people interested in wild animals.[8]

E.J. Salisbury (1886- ?) presented a rather similar picture of the status of plant ecology around 1930.[9] Salisbury made a distinction between "floristic plant geography," which was concerned with purely descriptive studies of the geographical distribution of plants, and "ecological plant geography" or "plant ecology" proper. In addition to the purely geographical study of plant distribution, plant ecology considered the causes of distribution. In short, "It is this relationship of plants to their environment in its widest sense, and the mutual effect of environment and organism, which is the province of...plant ecology."[10] Given the broad scope of the discipline which ecologists were constructing — including distribution, succession, environmental gradients, population numbers and fluctuations, and the structure of communities — it is not surprising that ecology appeared to be in its infancy in 1930*[11]

---

*The development of ecology, the scope and nature of the field, and the relationships between plant and animal ecology during this

Nonetheless, enough work had been done in "ecology" by this time that experimental taxonomists had reasonable grounds for taking the developing discipline seriously. Like genetics and cytology, ecological studies became a focus of active taxonomic research.

Biogeography, which both Elton and Salisbury indicated was part of ecology, was by no means a new field in 1930. In fact during the 1930s it was possible for two commentators to suggest that the field was so well-worked that the subject had been "worn threadbare."[12] Hans Gadow (1855-1928) in his 1913 book *The Wanderings of Animals* traced a lineage of zoogeographical studies back to the eighteenth century writings of Georges-Louis Leclerc, Comte de Buffon (1707-1788).[13] Phytogeography had also been pioneered prior to the twentieth century. For example, much of the work of Joseph Dalton Hooker (1817-1911) was during the period immediately preceding and following the publication of Darwin's *Origin of Species*.[14] Certainly there can be little doubt that the advent of Darwinism had a major impact on both plant and animal geography. The studies of John T. Gulick (1832-1923), Moritz Wagner (1813-1887), David Starr Jordan (1851-1931), and Karl

---

period are virtually uncharted waters in the history of biology. It is not even clear whether during this period plant and animal ecology ought to be considered parts of a common discipline. Certainly, all three terms: "ecology," "plant ecology," and "animal ecology," were widely used during the 1930s and 1940s. Throughout this work I will use "ecology" in a general, non-technical way to refer both to studies of local adaptation and to studies of biogeographic distribution. For an initial attempt to delineate the early development of ecological studies in botany, see: Eugene Cittadino, "Ecology and the Professionalization of Botany in America 1890-1905," *Studies in History of Biology* 4 (1980): 171-198.

Jordan (1861-1954) can be seen as responses to Darwinian theory and were consciously evolutionary in their perspective.[15] During the early decades of the twentieth century the British botanist J.C. Willis (1868-1958) tabulated voluminous data on the distribution of tropical plants to support his anti-Darwinian theory of evolution.[16] According to Willis the age of a species could best be determined by the relative size of the area over which it was distributed. The "Age and Area Hypothesis" immediately provoked controversy and discussion that persisted for a number of decades.[17] Although most biologists criticized the generalizations forwarded by Willis, a decade after the publication of *Age and Area* so eminent a biologist as J.B.S. Haldane could write,

> As an example of criticism [of Darwinism] of an extremely competent student of wild life I should like to cite Willis' "Age and Area" (1922), a book packed with facts which any theory of evolution will ultimately have to incorporate. The fact that it offers no theory as to the causes of the evolutionary process may explain the (to my mind) entirely unmerited neglect of the data presented in it.[18]

It seems unlikely that Willis was quite as neglected as Haldane indicated. Competent biologists continued to discuss the implications of Willis's data throughout the 1930s.[19] Furthermore, Willis's writings were sufficiently provocative that twenty years after the original controversy over the "hypothesis" a neo-Darwinian of the stature of Sewell Wright felt compelled to publish an extended refutation of "age and area."[20]

Biologists took Willis seriously for a number of reasons. First, if "age and area" were confirmed it would necessitate major revisions in evolutionary, taxonomic, and biogeographical thought.

> The importance of this interesting hypothesis, in support of which Dr. Willis has brought forward an abundance of evidence, would obviously be very great if it should be proved correct. It would upset the traditional belief in Natural Selection as the most important factor in determining distribution. It would make it possible to tell at a glance the relative antiquity of the various elements in any flora and thus reconstruct with ease the phytogeographical history of a region. It would enable us to identify the most widespread species in a given genus or the most widespread genus in a given family as the most ancient type in that particular genus or family, and thus to clear up at once many vexatious problems, and its verification is consequently a matter well worthy of our attention.[21]

Second, a number of biologists were impressed with the large body of statistical evidence which Willis had amassed in support of his hypothesis. Finally, even the harshest critics suggested that at the very least Willis had stimulated a great deal of interest in the dynamics of plant distribution. For example, in a review of *Age and Area* William Bateson (1861-1926) wrote,

> Whatever doubts arise regarding the new deductions, Dr. Willis once more makes geographical distribution a live study, showing quite unexpected lines along which it may be pursued. The delimitation of floral areas - or, for that matter, zoological areas too - was, as he says, a dull and almost futile exercise of scholasticism. The introduction of statistical methods, here altogether appropriate, offers great possibilities.[22]

Other commentators applauded the new attention to phytogeography that had been stimulated not only by Willis, but also by his critics.

> It can also be said with little exaggeration that, to most botanists phytogeography meant nothing more than the determination by observation of the natural boundaries of species, while now, thanks to Willis and his critics equally, phytogeography is a dynamic subject, capable of yielding valuable ideas to the phylogenist and the taxonomist.[23]

Willis was only one example of a growing group of biogeographers who used statistical methods in their studies. Although a commentator in 1918 could suggest that such use of statistics was "distasteful to the biological mind," it seems doubtful that such a statement would have been made in the 1930s.[24] During the 1920s and 1930s a significant number of rigorously quantitative field studies on geographical distribution were undertaken. Leading field biologists advocated statistical analysis as a standard tool for all collecting studies.[25] Furthermore, in contrast to the global generalizations of Willis, there seems to have been an increasing emphasis on detailed monographic studies of the distribution of specific taxonomic groups, or of limited geographical regions.[26]

Typical of such studies was the investigation carried out by H.E. Crampton (1875-1956) on the variation and distribution of land snails in the genus *Partula* inhabiting the Polynesian islands. Crampton's field work began in 1906 and culminated in the publication of three massive volumes of data in 1916, 1925, and 1932.[27] Land snails were well-suited to zoogeographical study. Not only were groups of species isolated on individual islands, but each island was itself subdivided by high volcanic ridges into more or less completely isolated valleys. Thus Crampton's studies concerned not only the geographic distribution of species in the genus *Partula*, but also local geographic variation within isolated species.

Crampton's studies were considered valuable not only because they were so extensive, but also because they were rigorously quantitative.[28] For example, in Crampton's analysis of ten endemic species on the island of Moorea over 116,000 snails were collected.[29] These included samples not only of adults, but also of juvenile and embryonic life stages. Furthermore, Crampton presented extensive biometrical data including standard deviations for a number of quantitative characters such as dimensions of the shell.[30] Statistical analyses were also presented on characteristics bearing on fecundity such as percentage gravid individuals, numbers of eggs per individual, and numbers of embryonic snails carried by adults. Crampton even dealt with such qualitative characteristics as shell color in a statistical manner.

Just as impressive as Crampton's collecting studies was the slightly later work of Alfred Kinsey (1894-1956). During the 1920s and 1930s Kinsey studied the geographical distribution of gall wasps in the genus *Cynips*.[31] These studies were important for a number of reasons. First of all, Kinsey realized the significance of geographical studies both for taxonomy and evolutionary theory. Kinsey was highly critical of taxonomic and evolutionary generalizations based on earlier geographical studies, many of which he considered too limited.

> Although there is a slowly increasing list of truly monographic revisions of plant and animal groups, too many of the European studies are still restricted to Central Europe or to a politically narrower area; and most of those from American workers are limited to "North America North of Mexico" or, more often, to the single state which supports the agricultural experiment station, the conservation commission, the natural history survey, or the university from which the study proceeds. This provincialism handicaps our grasp of biologic problems which are in actuality continental in their scope.[32]

Second, Kinsey's work dramatically demonstrated the large amount of taxonomic information that could be generated when poorly known groups were intensively studied.[33] Finally, Kinsey's work demonstrated the limitations placed on even the most extensive field collecting expeditions.

Kinsey's collections of cynipid wasps extended from the north central United States to southern Mexico. During the course of this study Kinsey and his colleagues collected 35,000 adult specimens and 124,000 galls.[34] Despite the size of this collection Kinsey considered his labors inadequate for a rigorous analysis of some species within the genus *Cynips*. Since his study involved 164 species each collected from an average of thirteen localities, Kinsey's taxonomic descriptions were based on an average of only sixteen adult wasps and 60 galls per locality.[35] According to Kinsey, an adequate description of species of cynipid wasps would require from 100 to more than 1000 specimens per locality depending on the homogeneity of the group. By Kinsey's calculations such a collecting effort would require the staggering sum of up to 1.5 million adult wasps and perhaps 4 million galls.[36]

Kinsey presented a formidable compilation of data in his monographic studies of *Cynips*, data that could not be taken lightly. At a symposium devoted to supra-specific variation, George Gaylord Simpson (1902-) noted,

> Kinsey's review of this subject [variation above the species level] is the most recent and in many respects the most complete, and it is based on a remarkably thorough and profound study of an exceptionally large mass of data.[37]

Furthermore,

> Kinsey disarms differences of opinion by suggesting that it be based on studies as extensive and complete as his work on *Cynips*. This work is, indeed, so extensive and so complete... that it is a truly monumental and in many ways incomparably fine work.[38]

Simpson, a vertebrate paleontologist, could not hope to collect such comprehensive data on fossil groups of mammals. Nonetheless, in disagreeing with many of Kinsey's evolutionary and zoogeographical generalizations, Simpson presented a detailed critical analysis of Kinsey's work. A number of zoogeographers were also critical of Kinsey. For example, biologists as different in their evolutionary beliefs as Richard Goldschmidt (1878-1958) and Ernst Mayr were equally opposed to Kinsey's identification of taxonomic species with the smallest local groups of gall wasps found in the field.[39] Goldschmidt, in particular, was not "disarmed" by Kinsey's extensive data and the two biologists exchanged rather acrimonious criticisms of one another's zoogeographical, evolutionary, and taxonomic work.[40] Furthermore, while perhaps in sheer numbers their zoogeographical collections could not match those of Kinsey, both Goldschmidt and Mayr had extensive zoogeographical experience. Mayr's studies of tropical birds and Goldschmidt's work on moths in the genus *Lymantria* were only two of a number of highly sophisticated studies on geographic distribution and variation undertaken between 1920 and 1940. Other notable examples were William Sumner's (1874-1945) work on deer mice in the genus *Peromyscus*, and both Theodosius Dobzhansky's early studies on lady bird beetles in the family *Cochinellidae* and his later work on fruitflies in the genus *Drosophila*.[41]

Large scale distributional studies in botany were also being carried out during the 1920s and early 1930s. For example, Edgar Anderson (1897- ?) spent several years studying the distribution and variation within species of related *Iris*.[42] Not only did Anderson study large scale distributional patterns of the species whose combined ranges extended from the southeastern United States, through Canada, to the west coast of Alaska, but also the local distribution of colonies of each species. Such local studies were particularly important in *Iris*. Just as Kinsey had found "insular species" of gall wasps Anderson found that *Iris* were distributed in small semi-isolated colonies. Such colonies, relatively separated from other members of their species, might have relatively independent evolutionary histories.[43]

Anderson's geographical studies on *Iris* would quite clearly fall under the heading of "plant ecology" as defined by E.J. Salisbury. Aside from describing the local and continental distributions of the three species of *Iris*, Anderson was primarily interested in the causes of these distribution patterns. To determine these causes Anderson used a combination of genetic, cytological, and morphological analyses. This combination of techniques from various biological disciplines places Anderson's work in the category of "experimental taxonomy" and his studies will be considered in greater detail from this perspective in the following chapter.

Quite different from Anderson's "ecological" work, were the studies undertaken by the Swedish botanist, Göte Turesson (n.d.). According to Turesson, plant species had not received the same attention from ecologists that they had from geneticists.[44] Turesson sought to present an ecological parallel to the genetic conception of species as "genotype compounds."[45] Turesson's ecological work was much less concerned with geographical distribution than with the adaptive responses of plants to local habitats. Variation in plants was, according to Turesson, due to two distinct causes.[46] Plants could be directly modified by local environmental conditions. On the other hand, much variation within species clearly had a hereditary basis. To distinguish between plastic modifications and true hereditary variations Turesson transplanted closely related specimens from very different habitats into controlled experimental gardens. Much of the variation found under natural conditions continued to be expressed by the offspring of the transplants even though they had been reared under nearly identical conditions. According to Turesson, this indicated that taxonomic species were broken up into a number of hereditarily stable, locally adapted groups. Each small group of plants had been selected for existence under a particular set of environmental conditions.

Quite different from the transplant technique used by Turesson, but no less important, was the "variable habitat" transplant method perfected by H.M. Hall (1874-1932) in California.[47] This technique, in a more primitive form, had been used as early as the final decades of the nineteenth century by the botanist, Gaston Bonnier (1853-1922).[48] The variable habitat transplant method involved transplanting genetically similar plants into a series of different habitats. In its most sophisticated form this technique involved taking a series of cuttings from a single individual and transplanting these clones into different habitats.[49] The variable habitat transplant method was used in conjunction with Turesson's controlled garden transplant method both by Hall and by his followers, the highly successful experimental taxonomists, Jens Clausen (1891-1969), David Keck (1903-), and William Hiesey (1903-).[50] While Turesson's method allowed the investigator to analyze hereditary and non-hereditary characteristics of a group of plants, Hall's method allowed the investigator to study the limits of the group's adaptability.

Transplant studies of the type used by Turesson and Hall were not applicable to most zoological studies. Nonetheless, zoologists too, were interested in the correlation between the environment and subspecific variation. Like their botanical counterparts, zoologists found that variation in animal species was correlated with environmental variables. For example, Theodosius Dobzhansky found numerous series of color pattern variations on the elytra, or wing covers, of Cochinellid ladybird beetles.[51] By comparing the color pattern distribution within a single species Dobzhansky was able to divide the species into geographic races or subspecies. In some cases these geographic races were very well-defined. One particular color pattern might predominate while others were rather scarce or completely absent. In other cases, however, several color patterns were found within a single geographic area. In such cases, geographic races could only be distinguished statistically.[52]

In a number of cases Dobzhansky found a dramatic parallel in coloration between geographically widely separated groups. For example, the species *Coccinella transversogutta*, found both in Asia and North America, had similar color-pattern races on both continents.[53] Populations of beetles in Central Asia and the southwestern United

States were more similar to one another than either was to populations inhabiting the northern regions of their own continents.

Such striking correlations between morphological characteristics and environmental gradients were by no means limited to the insects studied by Dobzhansky. Julian Huxley suggested that these intergradations or "clines" were a general feature both within individual groups and among closely related groups.[54] So pervasive were these clines that Huxley suggested that a subsidiary system of classification be developed specifically based on this phenomenon.[55] The German zoogeographer Bernard Rensch (1900-   ) was so impressed with the correlation between morphological characters and environmental gradients that he codified these into a series of "ecological rules."[56] These rules seemed to hold for groups throughout the animal kingdom. For example, Gloger's Rule, that animals in warm, humid areas tend to be darker than related animals in cold, dry habitats, applied both to birds and to ladybird beetles.[57]

Like ecology, genetics was opening up new perspectives on the status and composition of taxonomic units. If during its early development, genetics had been viewed as a strictly laboratory science with little to offer those involved with studies of wild species, the same could not be said about genetics in the 1930s and 1940s. The geneticist, L.C. Dunn (1893-1974), expressed the relatively new interest of geneticists in field studies of wild species in the editor's preface of Theodosius Dobzhansky's *Genetics and the Origin of Species*. According to Dunn,

> Variation and heredity had first to be studied for their own sakes and genetics grew up in answer to the interest in these

> problems and to the need for rigorous methods for testing by experiment all ideas we might hold about them. The requirements of this search drove genetics into the laboratory, along an apparently narrow alley hedged in by culture jars of Drosophila and other insects, the breeding cages of captive rodents, and by maize and snapdragons and other plants. Biologists not native to this alley thought sometimes that those who trod along it could not or would not look over the hedge; they admitted that the alley was paved with honest intentions but at its end they thought they could see a red light and a sign "The Gene:Dead End."[58]

Dunn's evaluation of the insularity of early genetics may have been overdrawn, a possibility that he himself admitted.[59] Nonetheless, a somewhat similar evaluation of the relationship between genetics and taxonomy has been presented by Ernst Mayr. In reference to the period 1910 to 1935, Mayr states,

> In my interpretation I place considerable stress on the tenuousness of the line of communication between genetics and taxonomy. The representatives of both areas were little interested in what the others were doing and did not read the literature of the other field. We cannot ask why the systematists did not keep up better with the advances in genetics; we will never understand the nature of the argument between the Mendelians and the naturalists if we do not accept the situation as it was.[60]

Certainly some taxonomists and geneticists were interested in the potentials of genetics for solving taxonomic problems prior to 1935. For example, as early as 1923 the taxonomist G.C. Robson (1888-1945) suggested that genetics could be a very useful tool for studying species.[61] According to Robson there was an urgent need to study the parallels between the taxonomist's conception of a species as a "character complex" and the geneticist's conception of a species as "gene complex." This suggestion for the fruitful possibilities of using genetics in taxonomy was presented in more extended form in Robson's 1928 book *The Species Problem*, and in collaboration with the taxonomist O.W. Richards in a paper published in 1926, and a book, *Variation of Animals in Nature*, completed in 1933.[62] A similar interest in the use of genetics in taxonomy was expressed in a paper presented by the geneticist G.H. Shull (1874-1954) at the 1926 International Congress of Plant Sciences.[63] Like Robson, Shull was concerned with the correlation between the heritable core of variability studied by geneticists and the total expressed variability generally studied by taxonomists. Although hereditary variation arising from the gene complex constituted "the fundamental basis of all valid taxonomic distinctions," taxonomists also had to consider the "fluctuations" and "inductions" caused by the environment. According to Shull, the total variability found in a group could be symbolized by a series of concentric circles.[64] Non-heritable variation was superimposed upon the core of genetic variation (Fig. 1). Part of this variation was open to experimental analysis. For example, by artificial selection for pure lines the variation symbolized by circle (3) could be greatly reduced or eliminated. Likewise, by growing plants under controlled garden conditions circle (4) could be minimized. While a residue of unanalyzable variation remained within all species, Shull argued that the implementation of experimental methods, "experimental taxonomy," was necessary for more natural systems of classification. According to Shull,

> As the geneticist sees the situation, *innumerable natural lines of cleavage traverse the fields of living organisms*, and these lines are generally capable of discovery by the application of appropriate experimental methods, but many of these natural lines of cleavage are unavailable for taxonomic use among organisms which must be grouped solely on the basis of the phenotypic

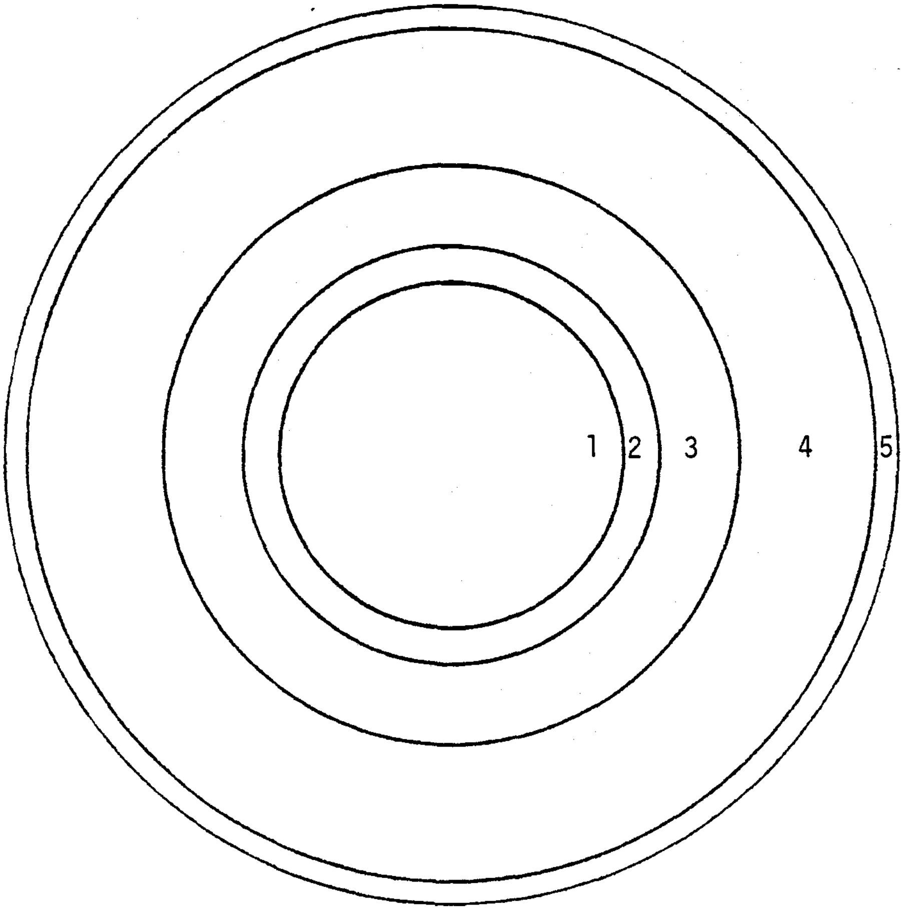


Figure 1. Diagram symbolizing the total variability found within a freely interbreeding group of organisms. (From Shull).

1) That part of the genotype held in common by all members of the group, and therefore not open to genetic analysis.
2) That part of the genotype made up of genes held by some individuals and not others.
3) Variation due to recombinations of different genes.
4) "Inductions" produced by environmental conditions in various habitats in the area occupied by the group.
5) "Fluctuations" found within each particular habitat.

> morphological characteristics which they exhibit. If it is desirable to make taxonomic distinctions more natural, it will be necessary to resort more and more to experimental methods... Why should there not be *gardens for experimental taxonomy* established at every institution in which research in taxonomy is in progress? The utilization of genetical methods in the study of taxonomy have already made notable contributions toward an understanding of relationships in certain great and difficult groups of plants...a more extensive adoption of experimental methods would deepen and strengthen the work of the taxonomist by leading him to the discovery of natural relationships which mere superficial inspection, however carefully it may be done, could never discover.[65]

The relationships between taxonomy and genetics outlined by Robson and by Shull were very suggestive, yet there were major problems involved with implementing genetic data into biological classification. Genetics was itself a rapidly developing science during the 1920s and 1930s. Even in the 1940s major theoretical disagreements existed in precisely the areas in which Shull and Robson had suggested that genetics could aid taxonomy.[66] In the 1930s the number of genetically well-studied groups was very small. Even in genetically well-understood groups such as *Drosophila*, the extent of genetic similarities among related species was only hinted at rather than rigorously determined. For example, Theodosius Dobzhansky admitted in 1938,

> We may conclude that the total number of genes responsible for the differences between a pair of species has in no published instance been accurately determined. This is simply another way of saying that the genetic analysis of the difference between species has been in no case complete. The work on interspecific hybrids has produced so far only very general evidence showing that differences between species are due to coöperation of numerous genes, and that these genes produce characteristically complex segregations wherever the conditions of the chromosome pairing provide a physical basis for any segregation at all.[67]

Few taxonomic groups appeared to be as readily analyzable genetically as *Drosophila*. As the geneticist, J.T. Patterson (1878- ?), pointed out, genetics was a powerful tool, but like all tools it required proper materials.[68] The remarkable characteristics of fruitflies made them perfect genetic test organisms. Fruitflies were easily cultured in the laboratory, they had short and uncomplicated lifecycles, they had readily analyzable chromosomes, and they had many morphological characteristics that were analyzable in Mendelian terms.[69] Other groups of organisms were not nearly so amenable to genetic analysis. For example, Alfred Kinsey noted the particular difficulties involved with studying the genetics of gall wasps. Kinsey's wasps had complicated lifecycles, involving both asexual and sexual generations of insects. Furthermore, gall wasps required specific host plants, namely oak trees, for egg laying. These characteristics virtually precluded the laboratory study of genetics for gall wasps.[70]

The ideal method for studying evolutionary relationships among organisms was, according to Kinsey, a combination of experimental genetic analysis and extensive field studies using traditional taxonomic analysis of variation.[71] Kinsey was even willing to concede that genetics was the more fundamental method of study. Yet the genetic method, however fundamental it was, could not replace taxonomic analysis.

> ...the unfortunate fact remains that the methods of experimental genetics are not applicable to most wild species. They are not applicable to elephants or whales or even ideally adapted to an animal which is as slow a breeder as man. They are not adapted to any of the vast number of organisms that cannot be brought into the laboratory, greenhouse, or garden...
>
> We cannot hope, short of the millenium to have the experimental analysis of anything more than a very small proportion of the

> species of the world, and we must depend upon the coordination of the work of the geneticists and taxonomists if we are to have any sort of interpretation of the peculiarly interesting data that may be offered by such non-laboratory forms as the Cynipidae.[72]

While Kinsey advocated cooperation between taxonomists and geneticists, he was highly critical of the theoretical interpretations of some geneticists, notably those of Richard Goldschmidt. Furthermore, Kinsey was somewhat skeptical about the generality of conclusions reached by experimentalists from studies of specific organisms such as *Drosophila*.[73] This skepticism was shared by a number of other taxonomists. For example, A.J. Wilmott (1888-1950) noted that most genetic analyses of plants had been done on cultivated varieties and that it was unclear whether the conclusions from these studies would apply to wild species.[74] W.B. Turrill, an advocate of genetics, also noted that cultivated plants had received the greatest share of the geneticists' attention.[75] Although Turrill believed that the same genetic principles applied in both groups, he suggested that the genetics of wild plants tended to be much more complex than that of cultivated varieties.

Despite the problems which genetics faced, the study of hereditary variation had a major impact on taxonomy. Undoubtedly, part of this impact was due to the fact that a number of geneticists began to study wild populations of organisms. This trend is perhaps best illustrated by Theodosius Dobzhansky's book *Genetics and the Origin of Species*. As Dobzhansky's editor, L.C. Dunn noted,

> ...Professor Dobzhansky's book signalizes very clearly something which can only be called the Back-to-Nature movement. The

> methods learned in the laboratory are good enough now to be put to the test in the open and applied to that ultimate laboratory of biology, free nature itself.[76]

Dobzhansky's book was widely acclaimed and a number of reviewers echoed Dunn's belief that *Genetics and the Origin of Species* was an important indicator of a new direction in genetics.[77] The impact of genetics on taxonomy was also due to the fact that a number of geneticists, including Dobzhansky, J.T. Patterson, A.H. Sturtevant, Jens Clausen, and J.W. Gregor were interested in systematics as well as genetics. Finally, although the methods of genetics might be difficult to apply to most wild groups of organisms, the conception of taxonomic groups, particularly species, as "gene complexes" was a powerful explanatory tool. For example, although Alfred Kinsey did not do an experimental analysis of the genetics of gall wasps, he did express his taxonomic conclusions in genetic terms.[78] In fact Kinsey went so far as to estimate the number of genes which separated related species in the genus *Cynips*. Similarly, although Dobzhansky could produce no direct evidence for the exact genetic basis of color pattern variations in *Cochinellid* beetles, he explained the racial differences within species of this group in genetic terms.[79]

Much of the force of the genetic conception of species derived from the close association of genetics and cytology. Indeed, these fields were so closely allied that W.B. Turrill remarked, "Genetics is now so intimately related to cytology (cytogenetics) that much research could equally well be classified under either heading."[80] Several writers pointed out that cytology, and more specifically karyology, the study of the chromosomes, was integral to the idea of species as genetic systems.[81] Since the chromosomes were theoretically the carriers of the genes, their behavior during cell division and their relative stability of structure explained the stability of the characteristics of a species. Just as importantly, gross changes in chromosome structure, at times visible under the microscope, were theoretically similar to invisible gene mutations as a source of hereditary variability within a species. Furthermore, chromosomal changes could act as barriers to cross fertilization among related species. The theoretical implications of cytology, so forcefully presented by C.D. Darlington and others, were not lost on taxonomists. As Turrill noted,

> A considerable amount of cytological research is essentially morphological. From one standpoint the intimate details of cell structure, and even such karyological features as the number, sizes, and shapes of the chromosomes, might be considered taxonomic characters to be treated equally with other morphological characters. The early realization that the chromosomes carry the entire or at least main hereditary equipment of the organism gave cytology (more strictly karyology) a unique position in biology...we are forced to acknowledge that cytology is much more than high-powered morphology.[82]

Theoretical considerations were not the only factor that made cytology so influential in taxonomic research. As C.D. Darlington pointed out in his influential text *Recent Advances in Cytology*, a number of methodological developments had dramatically improved the resolving power of cytology.[83] Such improvements in technique made cytology a potent tool for determining taxonomic relationships. According to Turrill,

> In the early days of cytological research a laborious and often unsatisfactory technique prevented more than a few organisms

> being investigated cytologically by any one individual within a reasonable time. Nowadays one investigator can relatively quickly and precisely examine the chromosomes of many species of a taxonomic group, or of many individuals of a species.[84]

This potential for cytological research was quickly realized. Turrill noted,

> A glance through any of the periodicals devoted to genetics and cytology (*Journal of Genetics*, *Genetics*, *Genetica*, *Hereditas*, etc.) shows how rapidly cytological data of a kind useful to the systematist is accumulating. It might be held that till cytologists have fully investigated many more genera it is undesirable to modify existing categories and nomenclature. The time, however, appears to be rapidly approaching when such an argument will be invalid within a wide range of genera. Already it is desirable that some tentative practical conclusions should be reached by joint discussion and co-operative research between taxonomists and cytologists.[85]

Biologists like Turrill and Edgar Anderson, while noting unresolved problems in cytology, saw this discipline as a powerful aid for determining taxonomic relationships. Both fields, according to Anderson, studied the same phenomena, but from different perspectives. Always ready with an analogy, Anderson aptly summarized the beneficial relationship between cytological and taxonomic analysis.

> The two viewpoints are like the insight into a family of strangers gained by (1) meeting the members of the family on the street or (2) looking in their cellar windows. The analogy is quite precise; the first is essentially the method of taxonomy, the second that of cytology. There is a big element of chance in the additional information gained by means of the new approach. In the language of the analogy one sometimes learns nothing new about a family from looking in the cellar windows; on the other hand one sometimes finds evidence which puts the family in an entirely new light and clears up points which had previously been mysterious.
>
> Continuing the analogy, it is sometimes difficult to see through the windows because they are small or dirty, as is the case of the Hamamelidaceae where cytological examination is difficult...In other cases, the windows are large and clear, as in the genus *Tradescantia* where the chromosomes are enormous and

> the reduction divisions are easy to find. In every case the two views supplement each other; the taxonomic observations or the cytological data may be incomplete or partially in error, or one may be puzzled as to how the two sorts of information are to be reconciled, but there is no possible chance of real disagreement.[86]

Cytological data was useful to taxonomists in a number of ways. Even disregarding the theoretical importance of chromosomes, their morphology and number could be used as relatively constant and specific characteristics of a taxonomic group.[87] Cytology could give a clear indication of the hybrid origin of some species.[88] This was particularly important for botanical studies. Also of great importance for botanists was the evidence which cytology provided for the polyploid relationships among certain species of plants.[89] Numerous closely related series of plant species were found to have chromosomal complements differing in whole number ratios. The likelihood that these species had arisen from the duplication of the parental genome (autopolyploidy) or through hybridization followed by duplication of the hybrid genome (allopolyploidy) was strongly indicated by such chromosome series. C.D. Darlington suggested that perhaps half of the species of flowering plants might have had a polyploid origin.[90]

Though extremely restricted in application, the study of salivary gland chromosomes in *Drosophila* became a major cytological tool for determining taxonomic relationships among groups of fruit-flies. The chromosomes in the salivary glands of larval *Drosophila* and certain other dipteran flies were up to one hundred times longer than ordinary chromosomes. Furthermore, these chromosomes were apparently duplicated numerous times with the duplicate strands tightly bound together. The resulting structures, which, according to C.D. Darlington, resembled "contorted earthworms," were clearly and continuously visible in cell preparations taken from the salivary glands of certain larval stages of flies.[91] The salivary gland chromosomes had been noted in the late nineteenth century by cytologists, but their significance was not fully recognized until the 1930s.[92] In fact although the second edition of Darlington's *Recent Advances in Cytology* published in 1937, gave a detailed account of the salivary chromosomes, the first edition of the text published in 1932 had not even mentioned the structures.

The analysis of salivary gland chromosomes opened up a number of research possibilities in *Drosophila* systematics. The differential staining of various segments of the chromosomes produced characteristic patterns of striations. Although these striations could not be identified with particular genes, they could be used as fairly precise markers which allowed easy detection of chromosomal aberrations.[93] Aberrations, particularly inverted segments of chromosome, could be used to characterize species and even races of *Drosophila.*[94] Furthermore, since multiple inversions were found to be a common phenomenon in *Drosophila*, the patterns of interlocking inversions could be used to indicate evolutionary relationships among races or species of fruitflies. A.H. Sturtevant and Theodosius Dobzhansky, among others, used this technique to develop phylogenetic trees of "chromosomal races" of *Drosophila pseudoobscura.*[95] The elegance of Dobzhansky's theoretical deductions from salivary gland chromosome analysis and the significance of these deductions for systematics, population genetics, and evolutionary theory, gave the technique of salivary chromosome analysis an importance far out of proportion to its applicability as a general cytological tool.

Dobzhansky was well-aware of the unique advantages of using the giant salivary chromosomes for cytological analysis. An investigator could, with much less expenditure of time and effort, study structural variations in giant salivary chromosomes than in any other cytological material. These unique chromosomes, combined with the other favorable characteristics of fruitflies, made *Drosophila* an "unrivaled" subject for cytogenetic studies.[96] Furthermore, according to Dobzhansky, the biologist was totally justified in exploiting the unusual properties of fruitflies because,

> The mechanisms which control heredity are fundamentally the same in all organisms, no matter to what subdivision of the animal or plant kingdom they belong; the principles of genetics are perhaps the most universal of all biological principles. The investigator in genetics is, consequently, free to choose and should choose the organism which offers the most advantage for his study, whether it be in the laboratory or in the field.[97]

As a leading young geneticist Dobzhansky was understandably enthusiastic about the generality of his cytogenetic conclusions. During the 1930s Dobzhansky instituted what was to become a long-lived, highly successful research program.[98] This research program involved an extensive study of the cytology, genetics, local ecology, zoogeography, evolutionary relationships, and taxonomy of a number of species of *Drosophila*. In his taxonomic writings Dobzhansky was able to draw on this large body of varied data which came both from laboratory and field studies.

While few organisms proved so amenable to combined cytological, ecological, and genetic study as *Drosophila*, a number of taxonomists instituted extensive research programs similar in scope to Dobzhansky's. These synthetic studies had a number of important consequences for taxonomy. Taxonomists were exposed to and actively pursued new techniques originally developed in other biological fields. Such taxonomists as Edgar Anderson, Ernst Mayr, and W.B. Turrill worked to integrate taxonomy with other biological disciplines. Conversely a number of specialists from other biological disciplines became actively involved with taxonomic research. Because the synthetic approach to taxonomy required a combination of highly sophisticated techniques, synthetic studies often involved the cooperative efforts of groups of taxonomists and biological specialists. Such cooperative research stimulated discussion among practitioners of various biological disciplines. The Association for the Study of Systematics in Relation to General Biology and similar forums for discussion of common problems were an important outcome of these bridges between biological disciplines. Finally, although the synthetic approach was not applicable to many groups of organisms, several taxonomists believed that where it could be applied, synthetic or "experimental" taxonomy provided the possibility for a broader, more objective system of classification.

NOTES

CHAPTER TWO

1. J.B.S. Haldane, "Forward," in: C.D. Darlington, *Recent Advances in Cytology* (Philadelphia: P. Blakiston's Son & Co., Inc., 1932), p. v.

2. Darlington, *Recent Advances in Cytology* (1932), pp. ix-x.

3. Haldane, "Forward," p. vi.

4. For example, see: John Belling, "Critical Notes on C.D. Darlington's 'Recent Advances in Cytology,'" *University of California Publications in Botany* 17 (1933): 75-110. See also: J.B.S. Haldane, "Forward," in: C.D. Darlington, *Recent Advances in Cytology*, 2nd edition (Philadelphia: P. Blakiston's Son & Co., Inc., 1937); Hampton Carson, "Cytogenetics and the Neo-Darwinian Synthesis," in: Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis* (Cambridge: Harvard University Press, 1980), pp. 89-91.

5. Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), p. 10.

6. For example, see: A.E. Emerson, "The Origin of Species," *Ecology* 19 (1938): 152-154; F.W.S., "Genetics and the Origin of Species," *Nature* 141 (1938): 310; "Genetics and the Origin of Species," *Quarterly Review of Biology* 13 (1938): 211-212.

7. J. Arthur Thomson, quoted in: Charles S. Elton, "Animal Ecology," *Encyclopedia Brittanica* (14th edition).

8. Ibid.

9. E.J. Salisbury, "Plants: Distribution and Ecology," *Encyclopedia Brittanica* (14th edition).

10. Ibid.

11. For a brief reminiscence of this "pioneering" period in ecology, see: Charles Elton, "Preface to the Paperback Edition," *Animal Ecology* (London: Methuen & Co., Ltd., and Science Paperbacks, 1927; reprint edition, 1966). pp. vii-xiii.

12. G.C. Robson and O.W. Richards, *The Variation of Animals in Nature* (New York: Longmans, Green and Co., 1936), p. 2.

13. Hans Gadow, *The Wanderings of Animals* (New York: G.P. Putnam's Sons, 1913), pp. 3-18.

14. W.B. Turrill, *Pioneer Plant Geography* (The Hague: Martinus Nijhoff, 1953).

15. For example, the early twentieth century commentator on evolutionary theory, Vernon Kellogg, presented the work of these biologists as "alternatives" or "auxiliary" to Darwinism. See: Vernon L. Kellogg, *Darwinism To-day* (New York: Henry Holt and Co., 1907), chap. 1X.

16. J.C. Willis, *Age and Area* (London: Cambridge University Press, 1922). For a short sketch of Willis's life and scientific work see: W.B. Turrill, "John Christopher Willis," *Royal Society of London: Biographical Memoirs* 4 (1958): 353-357.

17. For example, see: a Symposium on "The Age and Area Hypothesis," *American Journal of Botany* 11 (1924): 541-578; A.G. Thacker, "The Dynamics of Distribution," *Science Progress* 17 (1923): 474-477; J.C. Willis, *The Course of Evolution* (London: Cambridge University Press, 1940); G. Ledyard Stebbins, *Variation and Evolution of Plants* (New York: Columbia University Press, 1950), pp. 531-532; W.B. Turrill, "Plant Taxonomy, Phytogeography and Plant Ecology," in: W.B. Turrill, ed., *Vistas in Botany, Vol. 4: Recent Researches in Plant Taxonomy* (London: Pergamon Press, 1964), p. 205.

18. Haldane, *Causes of Evolution*, pp. 29-33.

19. For example, see: Robson and Richards, *Variation of Animals* pp. 82-86; W.B. Turrill, "Principles of Plant Geography," *Kew Bulletin* (1939): 208-237.

20. Sewell Wright, "The 'Age and Area' Concept Extended," *Ecology* 22 (1941): 345-347.

21. Edmund W. Sinnott, "The 'Age and Area' Hypothesis and the Problem of Endemism," *Annals of Botany* 31 (1917): 209-216, p. 209.

22. William Bateson, "Area of Distribution as a Measure of Evolutionary Age," *Nature* 111 (1923): 39-43, p. 43.

23. H.A. Gleason, "Age and Area from the Viewpoint of Phytogeography," *American Journal of Botany* 11 (1924): 541-546, p. 543.

24. James Small, "The Age and Area Law: A Fundamental Law of Geographic Distribution," *Science Progress* 12 (1918): 439-449, p. 441.

25. For example, see: Edgar Anderson, "The Technique and Use of Mass Collections in Plant Taxonomy," *Annals of the Missouri Botanical Garden* 28 (1941): 287-292; Edgar Anderson and W.B. Turrill, "Biometrical Studies on Herbarium Material," *Nature* 136 (1935): 986.

26. Turrill, "Principles of Plant Geography," p. 209.

27. H.E. Crampton, *Studies on the Variation, Distribution, and Evolution of the genus* Partula. *The Species Inhabiting Tahiti.* Carnegie Institution of Washington, Publication No. 228 (1916); H.E. Crampton, *Studies on the Variation, Distribution, and Evolution of the genus* Partula. *The Species of the Mariana Islands, Guam and Saipan.* Carnegie Institution of Washington, Publication No. 228A (1925); H.E. Crampton, *Studies on the Variation, Distribution, and Evolution of the genus* Partula. *The Species Inhabiting Moorea.* Carnegie Institution of Washington, Publication No. 410 (1932).

28. For critical evaluations which note the significance of the quantitative aspects of Crampton's studies see: Robson and Richards, *Variation of Animals*, p. 76; Dobzhansky, *Genetics and the Origin*, (1937), pp. 48-49; Richards, "The Formation of Species," in: G.R. De Beer, ed., *Evolution* (Oxford: Clarendon Press, 1938), p. 97; Mayr, *Systematics*, p. 8.

29. Crampton, *The Species Inhabiting Moorea*, p. 4.

30. Ibid., passim.

31. Alfred C. Kinsey, *The Origin of Higher Categories in Cynips*. Indiana University Publication, Science Series No. 4 (1936).

32. Ibid., p. 17.

33. Ibid., p. 67.

34. Ibid., p. 21.

35. Ibid.

36. Ibid.

37. George Gaylord Simpson, "Supraspecific Variation in Nature and in Classification from the View-point of Paleontology. *American Naturalist* 71 (1937): 236-267, p. 236.

38. Simpson, "Supraspecific Variation," p. 250-251. See also: Kinsey, *Origin of Higher Categories*, p. 61.

39. Richard Goldschmidt, "Cynips and Lymantria," *American Naturalist* 71 (1937): 508-514; Ernst Mayr, "Speciation Phenomena in Birds," *American Naturalist* 74 (1940): 249-278, p. 252; Mayr, *Systematics*, pp. 117-118.

40. Compare: Kinsey, *Origin of Higher Categories*, pp. 61-66; and Goldschmidt, "Cynips and Lymantria."

41. Theodosius Dobzhansky, "Geographical Variation in Lady-Beetles," *American Naturalist* 67 (1933): 97-126; Dobzhansky, *Genetics and the Origin*, (1937), pp. 51-53, 55-56. For an account of F.B. Sumner's work, particularly it's impact on neo-Darwinian theory, see: William B. Provine, "Francis B. Sumner and the Evolutionary Synthesis," *Studies in the History of Biology* 3 (1979): 211-240.

42. Edgar Anderson, "The Species Problem in *Iris*," *Annals of the Missouri Botanical Garden* 23 (1936): 457-509.

43. Ibid., pp. 485-498.

44. Göte Turreson, "The Genotypical Response of the Plant Species to the Habitat," *Hereditas* 3 (1922): 211-347, p. 344.

45. Ibid., pp. 344-347.

46. Ibid., pp. 340-341.

47. H.M. Hall, "Heredity and Environment - As Illustrated by Transplant Studies," *Scientific Monthly* 35 (1932): 289-302. See, also: F.E. Clements, H.M. Hall, W.T. Penfold, and H.L. Mason, "Transplant Experiments," *Carnegie Institution of Washington Yearbook* 24 (1925): 314-315; H.M. Hall and Associates, "Experimental Taxonomy," *Carnegie Institution of Washington Yearbook* 25 (1926): 345-346.

48. Jens Clausen, David D. Keck, and William M. Hiesey, *Experimental Studies on the Nature of Species* I. *Effect of Varied Environments on Western North American Plants*, Carnegie Institution of Washington Publication No. 520 (1940), pp. 3-4.

49. Ibid., pp. 15-18.

50. Ibid.

51. Dobzhansky, "Geographic Distribution."

52. Ibid., pp. 100-103.

53. Ibid., pp. 108-115.

54. Julian Huxley, "Clines: an Auxiliary Taxonomic Principle," *Nature* 142 (1938) 219-221.

55. Ibid.

56. Bernard Rensch, *Das Prinzip Geographischer Rassenkreise und das Problem der Artbildung* (Berlin: Begrüder Barntraeger, 1929), pp. 131-161.

57. Mayr, *Systematics*, p. 90. Note: Dobzhansky discusses this phenomenon under the heading of "Allen's Rule." See: Dobzhansky, "Geographic Distribution," pp. 114-115.

58. L.C. Dunn, "Editor's Preface," in: Dobzhansky, *Genetics and the Origin*, (1937), p. viii.

59. Ibid.

60. Ernst Mayr, "The Role of Systematics in the Evolutionary Synthesis," in: Mayr and Provine, *Evolutionary Synthesis*, p. 124.

61. G.C. Robson, "A Note on the Species as a Gene Complex," *Annals and Magazine of Natural History* 11 (1923): 111-115.

62. G.C. Robson, *The Species Problem* (London: Oliver and Boyd, 1928), chap. VII; G.C. Robson and O.W. Richards, "The Species Problem and Evolution," *Nature* 117 (1926) 345-347, 382-384, p. 382; Robson and Richards, *Variation in Animals*, chap. II, pp. 71-73. Note: Robson and Richard's book was completed in 1933. While the work was still in galley proofs Robson suffered a breakdown, apparently the effects of shell-shock from World War I battle experiences. Robson never fully recovered and the publication of *Variation in Animals* was delayed for three years. See: E. Hindle, "Dr. G.C. Robson," *Nature* 156 (1945): 75; *Variation in Animals*, p. vi; O.W. Richards, private communication, December 9, 1980.

63. George H. Shull, "Significance of Taxonomic Units: Point of View of Genetics," *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1578-1586.

64. Ibid., p. 1583.

65. Ibid., p. 1585-1586.

66. W.B. Turrill, "Taxonomy and Phylogeny," *Botanical Review* 8 (1942): 247-270, 473-532, 655-707, pp. 476-478. See also: W.B. Turrill, "Taxonomy and Genetics," *The Journal of Botany* 76 (1938): 33-39; W.B. Turrill, "The Expansion of Taxonomy With Special Reference to the Spermatophyte," *Biological Review* 13 (1938): 342-373, pp. 355-358.

67. Dobzhansky, *Genetics and the Origin*, (1937), pp. 67-68.

68. J.T. Patterson, "Drosophila and Speciation," *Science* 95 (1942): 153-159.

69. Patterson, "Drosophila and Speciation." See also: Theodosius Dobzhansky and Carl Epling, *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and its Relatives*, Carnegie Institution of Washington Publication No. 554 (1944) p. 3.

70. Kinsey, *Origin of Higher Categories*, p. 65.

71. Ibid., p. 64.

72. Ibid., pp. 65-66.

73. Ibid., pp. 61-66.

74. A.J. Wilmott, "Experimental Delimitation of Species," *Journal of Botany* 70 (1932): 49-50.

75. Turrill, "Experimental Taxonomy," p. 357.

76. Dunn, "Editor's Preface," p. viii.

77. Emerson, "Origin of Species;" F.W.S., "Genetics and the Origin of Species;" "Genetics and the Origin of Species;" [see footnote 6 for full reference].

78. Kinsey, *Origin of Higher Categories*, p. 62.

79. Dobzhansky, "Geographic Distribution," pp. 115-125, especially p. 121.

80. Turrill, "Expansion," p. 355.

81. For example, see: E.B. Babcock, "Cyto-Genetics and the Species Concept," *American Naturalist* 65 (1931): 5-18; J.B.S. Haldane, "Forward," and C.D. Darlington, "Preface," both in: C.D. Darlington, *Recent Advances in Cytology* (Philadelphia: P. Blakiston's Son & Co., Inc., (1932); Dobzhansky, *Genetics and the Origin*, (1937), pp. 73-77; Turrill, "Expansion," pp. 350-358; C.D. Darlington, "Taxonomic Species and Genetic Systems," in: Julian Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940).

82. Turrill, "Expansion," pp. 350-351.

83. Darlington, *Recent Advances*, (1932), Appendix II, pp. 491-492; Darlington, *Recent Advances*, (1937), Appendix II, pp. 569-571.

84. Turrill, "Expansion," p. 351.

85. Ibid., pp. 354-355.

86. Edgar Anderson, "Cytology in its Relation to Taxonomy," *Botanical Review* 3 (1937): 335-350.

87. William Wright Smith, "Some aspects of the Bearing of Cytology on Taxonomy," *Proceedings of the Linnean Society of London* 145 (1933): 151-181; Babcock, "Cyto-Genetics;" Anderson, "Cytology," p. 347; Turrill, "Expansion," p. 352.

88. Anderson, "Cytology;" Turrill, "Expansion," pp. 352-354.

89. Ibid.

90. C.D. Darlington, *The Evolution of Genetic Systems* (Cambridge: Cambridge University Press, 1939), p. 21. See also: J. Heslop-Harrison, *New Concepts in Flowering Plant Taxonomy* (London: William Heinemann Ltd., 1953), p. 93.

91. Darlington, *Recent Advances*, (1937), p. 175.

92. Ibid., pp. 175-182.

93. Dobzhansky, *Genetics and the Origin*, (1937), p. 89.

94. Ibid., pp. 92-95, 108-114.

95. Dobzhansky, *Genetics and the Origin*, (1937), pp. 92-95. See also: H.J. Muller, "Bearing of the 'Drosophila' Work on Systematics," in: Julian Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940), pp. 232-234.

96. Dobzhansky and Epling, *Contributions*, p. 3.

97. Ibid.

98. For a short sketch of Dobzhansky's scientific career, curriculum vitae, and bibliography, see: Howard Levene, Lee Ehrman, and Rollin Richmond, "Theodosius Dobzhansky Up to Now," in: Max K. Hecht and William C. Steere, eds., *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky* (New York: Appleton-Century-Crofts, Meredith Corporation, 1970).

Chapter Three: Experimental Studies in Taxonomy

Enthusiasm for expanding the use of cytological, ecological, and genetic methods in taxonomy was widespread during the 1930s and 1940s. In particular, a number of plant taxonomists strongly advocated this expansion of taxonomic methods. Many of these workers identified their research with the term "experimental taxonomy."[1] This term requires some qualification since taken literally it does not accurately describe the total approach of most experimental taxonomists. As W.B. Turrill pointed out, many of the techniques used by these taxonomists were not experimental at all.[2] Turrill suggested that the term "synthetic taxonomy" was a more appropriate designator for the combination of experimental techniques borrowed from other biological disciplines and the descriptive, non-experimental methods that characterized not only much taxonomic work, but also much cytological and ecological research as well. Though more accurate, the term "synthetic taxonomy" seems to have gained little currency during this period. Furthermore, the emphasis on experimentalism explicit in the title "experimental taxonomy" indicates the clear distinction that a number of taxonomists saw between their work and that of earlier taxonomists. For example, according to Jens Clausen, David Keck, and William Hiesey, among the most enthusiastic advocates of experimental methods in taxonomy,

> A unique opportunity to improve the established technique of interpreting the natural units of plants has existed ever since new tools for taxonomic study have become available in recent

> years. The new methods include experiments with living plants, integrated with cytogenetic analysis. As contrasted with purely observational and descriptive approaches of the past, experimental methods are laborious and time-consuming; therefore improvement in classification is slow. Nevertheless, it is now clear that the relationships between plants can be determined much more accurately by applying experimental methods, and from the facts already brought to light new concepts of the organization of the plant kingdom are coming into view.[3]

While enthusiasm for the expansion of experimental methods in taxonomy was widespread, this did not indicate a clear break with taxonomic tradition. Even the most avid exponents of experimental taxonomy admitted the important role that morphological description continued to play in their studies.[4] Furthermore, such taxonomists as W.B. Turrill and Edgar Anderson explicitly defended traditional taxonomic methods which they believed were completely harmonious with experimental methods. Both Turrill and Anderson promoted innovations in taxonomic methods that would bring experimental and traditional taxonomy together. For example, both pushed for expanding museum collections to include quantitative data and larger, more comprehensive samples from natural populations of plants.[5] Turrill advocated the construction of special herbaria to house the preserved remains of plants used in genetic experiments.[6] Such specimens would be readily available if questions arose over the results of genetic crosses. In the conclusion of a critical review of experimental taxonomy Turrill noted,

> It is only by a combination of all methods, herbarium or museum, library, laboratory, field, and breeding that there is any hope of obtaining satisfactory evidence on the nature and genesis of taxonomic units. No method is sufficient by itself, yet each is essential. As an important part of the synthetic method experimental taxonomy will take its place in the scheme of 'The New Systematics.'[7]

Beginning in the 1920s and especially in the 1930s and 1940s a number of extensive and sophisticated taxonomic research programs began that attempted to combine at least some of the methods cited by Turrill. A number of these, such as Ernest Babcock's (1877-1954) research on the genus *Crepis*, and E.M. Marsden-Jones (n.d.) and Turrill's studies of the genus *Silene* required several decades of research before final publication.[8] Other projects such as that instituted by H.M. Hall during the late 1920s with the financial backing of the Carnegie Institution of Washington are still in existence. Even more modest projects undertaken by a single investigator such as Edgar Anderson's study of three species in the genus *Iris*, could require over a decade of data collection and follow tortuous paths to their conclusions.

Although experimental taxonomic studies shared a number of characteristics it would be difficult to select a "typical" research program that epitomized experimental taxonomy. As I will argue experimental taxonomy was neither a single well-defined method nor a unified school of thought. Even among those taxonomists who used a combination of cytological, ecological, and genetic techniques there were differences in emphasis placed on particular techniques. To some extent these differences can be attributed to the inclinations and background of different researchers. However, to a large degree, the characteristics of the group of organisms under study dictated the types of techniques that could best be used for taxonomic analysis. Because of this diversity within experimental taxonomy I will not attempt a critical analysis of a single case study. Rather, in this chapter I will present a description of a number of research projects which, although different, bear a strong family resemblance to one another. This primarily descriptive chapter will be followed by an analysis of the critical reception of experimental taxonomic research.

Beginning in the early 1920s Edgar Anderson began a study of variation in the Northern Blue Flags, (*Iris versicolor* and related species). Anderson chose irises for a number of reasons.[9] He wanted a group of plants suitable to study what he believed to be the most important aspects of the "species problem": the nature of species, and their mode of origin. A resolution of the problem of species would, according to Anderson, require both an intensive and extensive analysis of the variation present in a species.

> So far as is known, no such complete survey of variation within a species or group of species has ever before been made with plant material. It is an ambitious attempt for a single individual unless the problem be made as simple as possible. If we are to learn anything about the ultimate nature of species we must first of all reduce the problem to the simplest possible terms and study a few easily recognized well-differentiated species. The group to be studied should therefore possess few subgroups and intergrading forms. Unfortunately those species which have been selected for intensive study in the past have been chosen by reason of their very complexity.[10]

Aside from the apparent simplicity of the group, Anderson chose the Northern Blue Flags because they were "common, conspicuous, colonial, and perennial."[11] All of these characteristics combined to insure not only ease of collection but reliability in analyzing the variation found within the species.

While Anderson initiated his study in the 1920s he relied primarily upon comparative morphology. In reference to the still embryonic *Iris* study Anderson noted,

> It has as yet been almost purely morphological in scope. Though the morphological differences between individuals and groups of individuals undoubtedly rest upon basic physico-chemical ones, our knowledge of these physiological differences is as yet too incomplete, among the flowering plants, to possess much phylogenetic significance.[12]

However, by the 1930s the scope of Anderson's research had broadened dramatically. In the major presentation of his research, published in 1936, Anderson reiterated his interest in the species problem but noted, "When, however, one takes up the problem, *as a problem*, and studies it from the diverse viewpoints of genetics, taxonomy, cytology, and biometry, he realizes that he not only needs most of the existing techniques but that he must devise new ones as well."[13] Undoubtedly, Anderson had been compelled to turn to new techniques by the unforseen complexity of the project he had undertaken.[14] Furthermore, during the intervening years Anderson used a National Research Council fellowship to study cytological and statistical techniques at the John Innes Horticultural Institution and the Rothamsted Experimental Station.[15] J.B.S. Haldane and R.A. Fisher, two stellar figures in biometry and evolutionary theory who were associated with these British research institutions, provided Anderson with statistical advice in the later years of the study. During this period Anderson also spent two months with another eminent mathematician and evolutionary theorist, Sewell Wright.[16] The final result of Anderson's research was a synthesis of data from morphology, cytology, genetics, biogeography, and studies of local habitat preferences.

Iris virginica and *Iris setosa* were fairly widely separated taxonomically, being placed in different subsections of the genus.[17] They were also widely separated geographically. While *Iris virginica* ranged widely throughout the eastern United States, *Iris setosa* was restricted to Alaska and the Pacific coast of Canada.[18] Nonetheless, though difficult to bring into bloom at the same time, the two species were partially interfertile.[19] Furthermore, a third species, *Iris versicolor*, was intermediate both morphologically and geographically to *Iris virginica* and *Iris setosa.*[20]

During the current geological period the distributions of *Iris virginica* and *Iris versicolor* overlapped. Both species were highly variable, being made up of large numbers of more or less isolated colonies which Anderson believed were fairly independent evolutionary entities.[21] Nonetheless, the two species were clearly distinct.

> ...five years of hard work showed that *Iris versicolor* might vary greatly and that *Iris virginica* might vary greatly but that each remained itself. They were of different fabrics. One might compare them to two old English villages, one in a sandstone region and the other in limestone. In each village there would be no two houses alike but all the houses in one village would be made of limestone, all those in the other made of sandstone. The conclusion was reached that closely related though these irises might be, variation within either species was of quite another order of magnitude from the hiatus between them... The variation *within* could never be compounded into the variation *between*. The two species were made of two different materials.[22]

If the two species had not diverged as the result of accumulations of small variations, the alternative, according to Anderson, was that *Iris versicolor* was the allopolyploid product of hybridization between *Iris virginica* and *Iris setosa.*[23] The hybridization which had occurred during an interglacial period was obscured by the restriction in the range of *Iris setosa* caused by a later glaciation.

This hypothetical relationship between *Iris versicolor* and its putative parents was strengthened by a number of different data.[24] An analysis of the chromosomal complements of the three species indicated that *Iris versicolor* with a diploid (2n) chromosomal number of 108 could be the product of hybridization between *Iris setosa* (2n=38) and *Iris virginica* (2n=70-72). If *Iris versicolor* were of this hybrid origin it would have almost twice as many chromosomes from *Iris virginica* as from the other parent. It might be expected, therefore, that *Iris versicolor* would be morphologically closer to *Iris virginica* that to *Iris setosa*. This appeared to be the case. Albinism, a fairly common trait in the genus, was generally absent in *Iris versicolor*. This lack of albinism also indicated an allopolyploid origin. If *Iris versicolor* had multiple genomes which were essentially similar, the recessive gene for albinism would have to be represented twice in each genome in order to be expressed. Not only was the geographic distribution of *Iris versicolor* intermediate to the ranges of its supposed parents but it was also part of an apparently younger flora, indicating that it too was a relatively young species. Finally, in terms of local habitat preferences, *Iris versicolor* was intermediate between *Iris virginica* and *Iris setosa*.

The evolutionary patterns and taxonomic relationships within *Iris*, as envisioned by Anderson were highly complex. At least three processes had been involved in the differentiation of the group;

hybridization, polyploidy, and local colonial differentiation.[25] These processes precluded the classification of the genus into clear and natural sections. According to Anderson,

> The presence of even occasional amphidiploidy within a genus will so complicate the phylogenetic relationships that it will be impossible to divide and subdivide it naturally into sections and subsections. We would therefore predict for the genus *Iris* that while there might be evidence of groups of related species, it would be impossible to arrange all these groups in a clear-cut natural system. Such is actually the case.[26]

Rather than forming a phylogenetic tree, the genus could better be likened to a series of parallel cables.[27] Each species, or cable, was made of up numerous colonies, which like the cords making up a cable maintained their separate identities. The cords themselves were made up of short threads, each of which existed for only a short time, but which intertwined to maintain the integrity of the cord. These threads were "individual" plants which might continue themselves indefinitely through vegetative reproduction or form new threads through cross-fertilization. Occasionally threads or cords from one species-cable might intertwine with those of another cable giving rise to an entirely new species.

The complex interrelationships among species of *Iris* would have been impossible to delineate without the use of cytological, ecological, and genetic data. On the other hand, although Anderson completed some experimental crosses between species of *Iris*, most of his work was non-experimental. Furthermore, purely morphological description, though not decisive in delineating relationships between species of *Iris*, was an integral part of the synthetic study of the group.

More extensive than Anderson's synthetic study of *Iris* was the taxonomic study of California plants initiated by Jens Clausen, David Keck, and William Hiesey during the 1930s.[28] The roots of this research program were diverse. Principally, Clausen and his colleagues continued and elaborated on work begun by H.M. Hall.[29] During the 1920s Hall instituted a number of experimental gardens running along an east-west transect from the Pacific coast of California, through the San Joaquin Valley, and over the Sierra Nevada mountains. Primarily, Hall's studies analyzed the effects of transplanting various plant species into new habitats. Although Hall used a number of transplant methods, the most successful was the use of clones taken from a single individual and transplanted simultaneously at different field stations.[30] Hall continued the transplant experiments until his death in 1932, after which the research was taken up by Clausen, Keck, and Hiesey.[31]

In addition to the influence of Hall, the Clausen team was greatly inspired by the Swedish ecologist, Göte Turesson. Turesson's influence was twofold. Methodologically, Turesson added a second technique to the arsenal of experimental taxonomy.[32] H.M. Hall, following the pioneering work of Gaston Bonnier, had perfected the technique of varied habitat transplants. Genetically similar or identical plants were grown under different conditions. In contrast, Turesson used the technique of standard environmental transplants.[33] Plants from diverse habitats were grown together under standardized, essentially identical conditions. The technique of standard environment transplantation complemented the varied environment transplant technique. The standard environment experiments could give an indication of the hereditary diversity within a group of genetically similar plants. Under standardized conditions stable hereditary characteristics could be distinguished from "modifications" induced by particular environmental conditions. The varied environment transplant experiments could indicate the adaptability of a single genotype or closely related set of genotypes to diverse conditions. Both techniques were utilized by Clausen and his associates.[34]

Along with his innovations in experimental garden technique, Turesson's theoretical writings were enormously influential. Turesson's conception of species in terms of "genecological" units was complex and a detailed discussion of the development of these ideas will have to be postponed until Chapter Five. Briefly, Turesson argued that species as they existed in nature could be experimentally analyzed into a hierarchy of ecologically or "genecologically" defined units.[35] Turesson's concepts were widely discussed during the decades following their inception.[36] Furthermore, enough experimental taxonomists implemented Turesson's terms that they could be considered "units of experimental taxonomy."[37]

Turesson, himself, modified the definitions of his terms throughout his career. Later experimental taxonomists also interpreted these terms in different ways. As envisioned by Clausen and his colleagues, a closely related group of organisms could be analyzed into three natural categories. The "coenospecies" was the most inclusive genetic unit found in nature and consisted of "...a group of plants 'of common evolutionary origin, so far as morphological, cytological, and experimental facts indicate.'"[38] Members of a coenospecies could exchange genes either directly through crossing or indirectly through a series of intermediate crosses.* In other words, a coenospecies was the largest group within which any amount of gene exchange was possible. Coenospecies were, therefore, quite extensive groups. According to the Clausen team, "More than one taxonomic species and more than one ecospecies are usually involved in a cenospecies, which sometimes corresponds to a taxonomic section or genus."[39] An "ecospecies" denoted "...a group of plants within the cenospecies whose members are able to interchange their genes without detriment to the offspring."[40] In other words, offspring of crosses within an ecospecies were more or less fully viable and fertile. The ecospecies, often, though not necessarily, corresponded to a taxonomic species. An "ecotype" was a group within an ecospecies which resulted from the "...genotypical response of an ecospecies to a particular habitat."[41] These were stable genetic entities developed through natural selection for life under a given set of environmental conditions.

While his terminology implied a genetic basis for related

---

*The term "coenospecies" was spelled "cenospecies" throughout the works of Clausen, Keck, and Hiesey. Aside from direct quotes taken from these works I will use Turesson's original spelling, "coenospecies."

groups of plants, Turesson's own research was largely restricted to ecological experiments. Clausen and his colleagues followed out the genetic implications of Turesson's theoretical writings by adding cytological and genetic analyses to the experimental transplant studies. This synthetic method required a team effort. Clausen, whose background was in genetics and cytology, carried out most of the cytogenetic analysis. Hiesey supervised the transplant studies. Keck concentrated on the systematic and nomenclatorial aspects of the research.[42]

When H.M. Hall began experimental studies on the taxonomy of California plants he utilized gardens at eleven stations along the east-west transect.[43] As more intensive studies were undertaken by Clausen, Keck, and Hiesey these stations were gradually reduced to three major experimental stations.[44] These gardens were chosen to represent three very different habitat types. The major station was the central laboratory of the Division of Plant Biology of the Carnegie Institution of Washington, located on the campus of Stanford University. This station at an elevation of 30 meters above sea level, had a mild climate suitable for year-round growth of many species of plants. The second station, at Mather, on the western slope of the Sierra Nevada mountains, was at an elevation of 1,400 meters. The Mather station was characterized by a growing season extending from early June until October. The third station, Timberline, was located at an elevation of 3,000 meters in an alpine meadow of the Sierra Nevada mountains. The growing season at

Timberline was greatly reduced, with only three to six weeks of frost-free weather.

During the early years of the research project, species in 31 families of plants were investigated.[45] Relatively few groups within these families proved amenable to intensive experimental analysis. The major groups intensively studied by Clausen, Keck, and Hiesey included *Potentilla* (Cinquefoils), *Achillea* (Yarrows), *Zauschneria* (California Fuchsias) and *Artemesia* (Sagebrush).

Transplant experiments revealed a number of striking patterns of variation. When individuals of a single ecotype were grown under similar conditions in the same garden easily visible variations persisted.[46] These variations appeared to be hereditary. Furthermore, non-hereditary variations also appeared. For example, plants that were dwarfs under wild conditions often grew taller under cultivation.[47] Both hereditary and non-hereditary variation were found consistently in tested individuals. As Clausen and his colleagues noted, "Modifications induced by environment are superimposed on hereditary differences, so that a plant's appearance at any time is the resultant of these two distinct kinds of variation."[48] Extensive variation was also found when clones of a single individual were grown in different habitats. For example, when clones of the coastal ecotype of *Potentilla glandulosa* were transplanted at Stanford, Mather, and Timberline, modifications appeared in a number of characteristics including height, number of flowers per stem, and time required to flower.[49] Ecotypes of *Potentilla glandulosa* were able to respond adaptively to some new environments. For example, clones transplanted at Mather thrived and were only slightly modified. Nonetheless, there were limits to ecotypic adaptability. Clones from the coastal ecotype transplanted at Timberline failed to flower or survive through the winter, even though the alpine ecotype of this species was able to thrive in this severe environment.[50]

Variation within groups of related plants could be characterized in a number of ways.[51] First, individuals had varied genetic constitutions and this variation was expressed even when these individuals were grown under similar conditions. Second, genetically similar or identical individuals could be modified in various ways by different environmental conditions. Third, groups of related individuals, or ecotypes, shared a set of common, constant characteristics which set them apart from other related groups. Fourth, within a range of tolerance members of an ecotype could adjust adaptively without losing their ecotypic identity.

These forms of variation could be accounted for by Turesson's genecological conception of plant groups. Within a species, ecotypes existed in each region of the species' range. These ecotypes were more or less stable groups and were the products of natural selection for particular sets of environmental requirements. Ecotypes themselves were complex groupings of slightly different individuals. Therefore, even within an ecotype there could be considerable individual variation. Although in many cases ecotypes were readily distinguishable, many complicating factors insured that this would not always be the case. The ecological conditions that determined the ecotypes were often not clearly delimited, but extended irregularly resulting in ecotypes made up of indefinite "race complexes."[52] For example, the foothill ecotype of *Potentilla glandulosa* extended to fairly high elevations on some sunny slopes. At the higher elevation this ecotype had the short stature of the alpine ecotype but retained other foothill characteristics such as early flowering.[53] The mixing of attributes of two different ecotypes was more pronounced where ecotypes met. Since ecotypes of the same ecospecies were fully interfertile, hybridization could confuse the delimitation of these units. Finally, ecotypes were dynamic evolutionary units which were themselves continually developing. Therefore, cases of partially differentiated ecotypes were to be expected. Because of these complicating factors some ecotypes could only be distinguished statistically. This was an inevitable limitation placed on the ecotype concept by the reality of evolution. As Clausen and his associates noted,

> ...the individual ecotype itself presents a complex picture. It may, however, be statistically distinguishable from other ecotypes in characters of importance for survival in a given habitat. Such complexity is to be expected in a dynamic world.[54]

Transplant studies indicated that ecotypic differences were not simply due to environmental modification, but had a hereditary core. From cytological analysis and breeding experiments Clausen and his colleagues concluded that ecotypic and ecospecific differentiation had both a genic and a chromosomal basis. Some groups such as the cosmopolitan *Potentilla glandulosa* appeared to consist of single ecospecies made up of numerous ecotypes.[55] The ecotypes of *Potentilla glandulosa* in most cases appeared to be well-marked both morphologically and physiologically. Nonetheless, all of the ecotypes were fully interfertile and all shared the same number of chromosomes. Heritable variation in this group appeared to be completely genic. In contrast, groups such as *Zauschneria*, a taxonomic genus with four species, appeared to form a single coenospecies.[56] The ecospecies of *Zauschneria* differed in numbers of chromosomes, indicating that polyploidy had been involved in the differentiation of the group. At least partly due to the differences in chromosomal complements, the ecospecies varied greatly in their abilities to hybridize with one another. Therefore, although there was the possibility of at least indirect gene flow within the entire *Zauschneria* group, certain ecospecies were relatively isolated. Most of the ecospecies of *Zauschneria* were further broken up into ecotypes (Fig. 2). According to the Clausen team it was in the analysis of complex groups such as *Zauschneria* that experimental taxonomy was most successful. As Clausen and his colleagues noted,

> The power of experimental methods in elucidating plant relationships has been most clearly demonstrated in *Zauschneria*. The innumerable intergradations of form within this genus have long puzzled botanists who depended on morphological criteria alone. Now, however, the relationships have become so clarified that one can evaluate with assurance the systematic rank of the various forms.[57]

Using Turesson's conception of plant groups, Clausen and his associates could interpret plant groups as ecological, genetic, and evolutionary systems. The Clausen team was particularly impressed

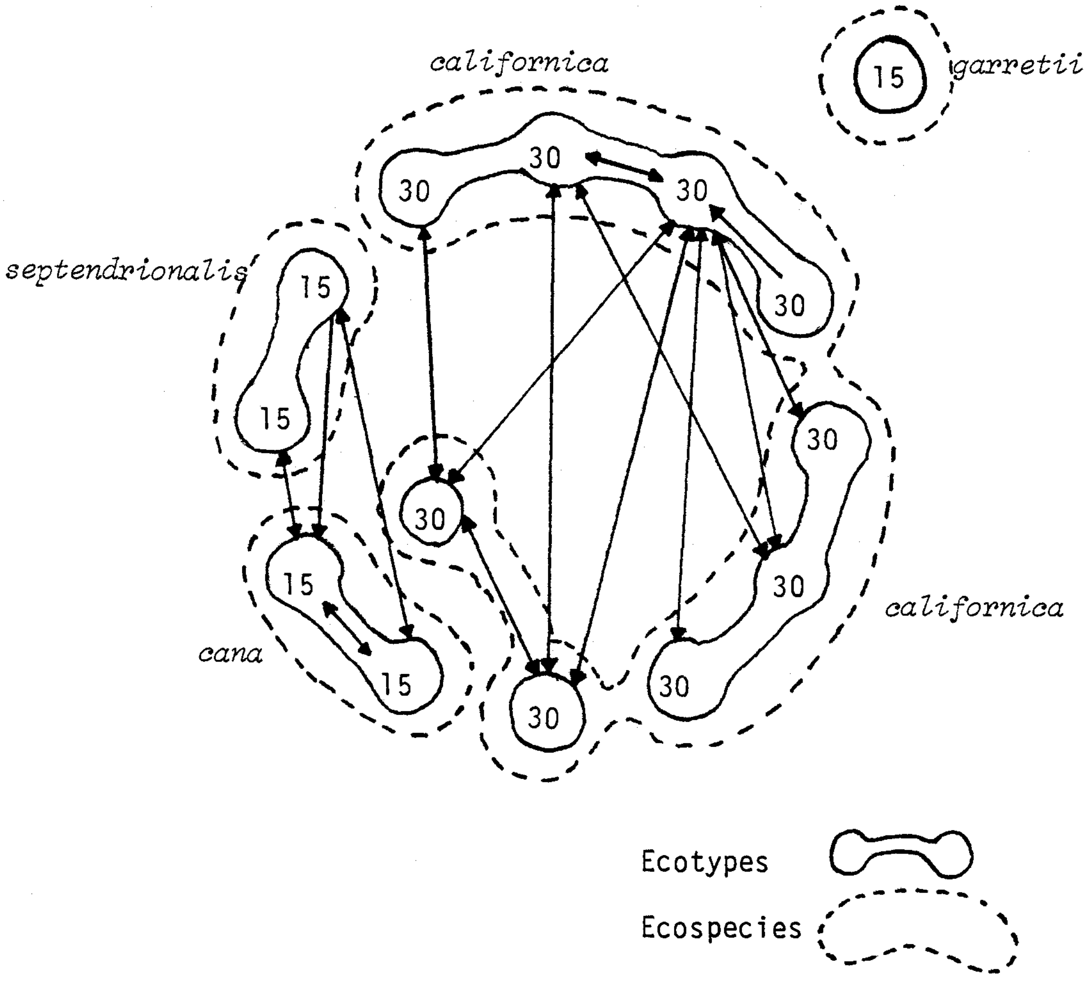


Figure 2. The Coenospecies comprised of species in the genus *Zauschneria*. Numbers represent chromosomal numbers. Arrows represent crosses resulting in at least partially fertile offspring. Direction of arrows indicates direction of pollen in the cross. (Considerably simplified from Clausen, Keck, and Hiesey).

environment, they were also stages in evolutionary divergence.^{60}

by the role of the environment in shaping plant groups. According to the Clausen research group,

> Natural selection doubtless determines the character of the plants that occupy a given environment. Since physiological processes, which change in rate with differences in temperature, moisture supply, and other external variables, are profoundly influenced by environment, successful plants must be fairly accurately adjusted to their surroundings. When they are removed from this environment and brought to a climatically different region, their physiological processes will act at a pace determined by the physical conditions of the new environment, and by heredity. If the plant's heredity is such as to enable it to accomodate itself to the new environs and to compete, the plant may prove to be a success in the new climate.[58]

The requirements for a successful plant group were not entirely external, however. According to Clausen and his colleagues,

> Not only must a plant be in equilibrium with its environment in order to succeed, but its entire gene activity must be in balance. Even a single pair of genes of the sublethal type may throw the physiologic process entirely off balance, but individuals with such genes face elimination by selection. Hundreds, possibly thousands of genes interreact in each individual, all influencing the plant slightly in one direction or another. Of necessity, all processes regulated by them must be synchronized in the proper order and adjusted to the environmental conditions if the plant is to succeed.[59]

Both the requirement for internal harmony within the genetic system and the requirement for external adaptation to the environment were molding forces of plant groups. The ability to exchange genes gave ecotypes and ecospecies a certain amount of flexibility. Once groups had diverged sufficiently that hybridization resulted in disharmonious genetic systems, natural selection acted to isolate these groups into distinct intersterile coenospecies. Therefore, not only were ecotypes, ecospecies, and coenospecies correlated with various demands of the environment, they were also stages in evolutionary divergence.[60]

Clausen and his colleagues were not the only group to be influenced by Turesson's genecological concepts. An earlier, though less extensive experimental study had been completed in Scotland by J.W. Gregor and F.W. Sansome (1902-?) on grasses in the genus *Phleum*.[61] Within this genus were two complex groups designated *Phleum alpinum* and *Phleum pratense*. These groups had been treated taxonomically both as distinct species and as subspecies of the same species.[62] Ecologically, *Phleum alpinum* and *Phleum pratense* appeared to be well-defined units.[63] Although *Phleum alpinum* could be cultivated at sea level, it was a poor competitor and its natural habitat was restricted to elevations above 2,000 feet. *Phleum pratense* was restricted to lowland habitats. There appeared to be no overlap in the habitats of the two species.

Within each species a number of subgroups were distinguishable.[64] Each species was represented by two groups differing in numbers of chromosomes. *Phleum alpinum* was composed of a diploid group (2n=14) and a tetraploid group (4n=28). *Phleum pratense* was made up of a diploid type (2n=14) and a hexaploid type (6n=42). Diploid and polyploid forms within each species were intersterile. Aside from chromosomal varieties, a number of ecotypes were distinguishable, particularly in *Phleum pratense*. Both the diploid and the hexaploid forms of *Phleum pratense* were represented by hereditarily stable groups which manifested themselves most noticeably in their growth forms. For example, some plants had erect stems while others were prostrate, or flattened against the ground.

By initiating an extensive series of experimental crosses Gregor and Sansome were able to artificially bridge several of the sterility barriers which naturally existed both within and between *Phleum alpinum* and *pratense*.[65] On the basis of these crosses Gregor concluded that the two species formed a single natural group, *Phleum pratense-alpinum* (Fig. 3).[66] Using Turesson's terminology this group was a coenospecies; although there were barriers to gene flow among the groups, these barriers were at least potentially bridgeable. Within the coenospecies were four partially intersterile ecospecies: the diploid and hexaploid forms of *Phleum pratense*, and the diploid and tetraploid forms of *Phleum alpinum*. Within each ecospecies, and particularly within the two *Phleum pratense* groups, there existed a number of distinct ecotypes which were, however, completely interfertile.

Although the terms experimental taxonomy and synthetic taxonomy were usually used in reference to botanical studies, zoologists also expanded taxonomic techniques to include methods taken from cytology, ecology, and genetics. Perhaps the most notable example of this synthetic method in zoological taxonomy was the work of Theodosius Dobzhansky and his associates on the group of fruit flies related to the species *Drosophila pseudoobscura*. Dobzhansky's major interest was not in the taxonomy of fruit flies, but rather in the population dynamics and evolutionary genetics of this group of organisms. Nonetheless, Dobzhansky was more than an amateur taxonomist and was very much concerned with the taxonomic implications of his work.[67]

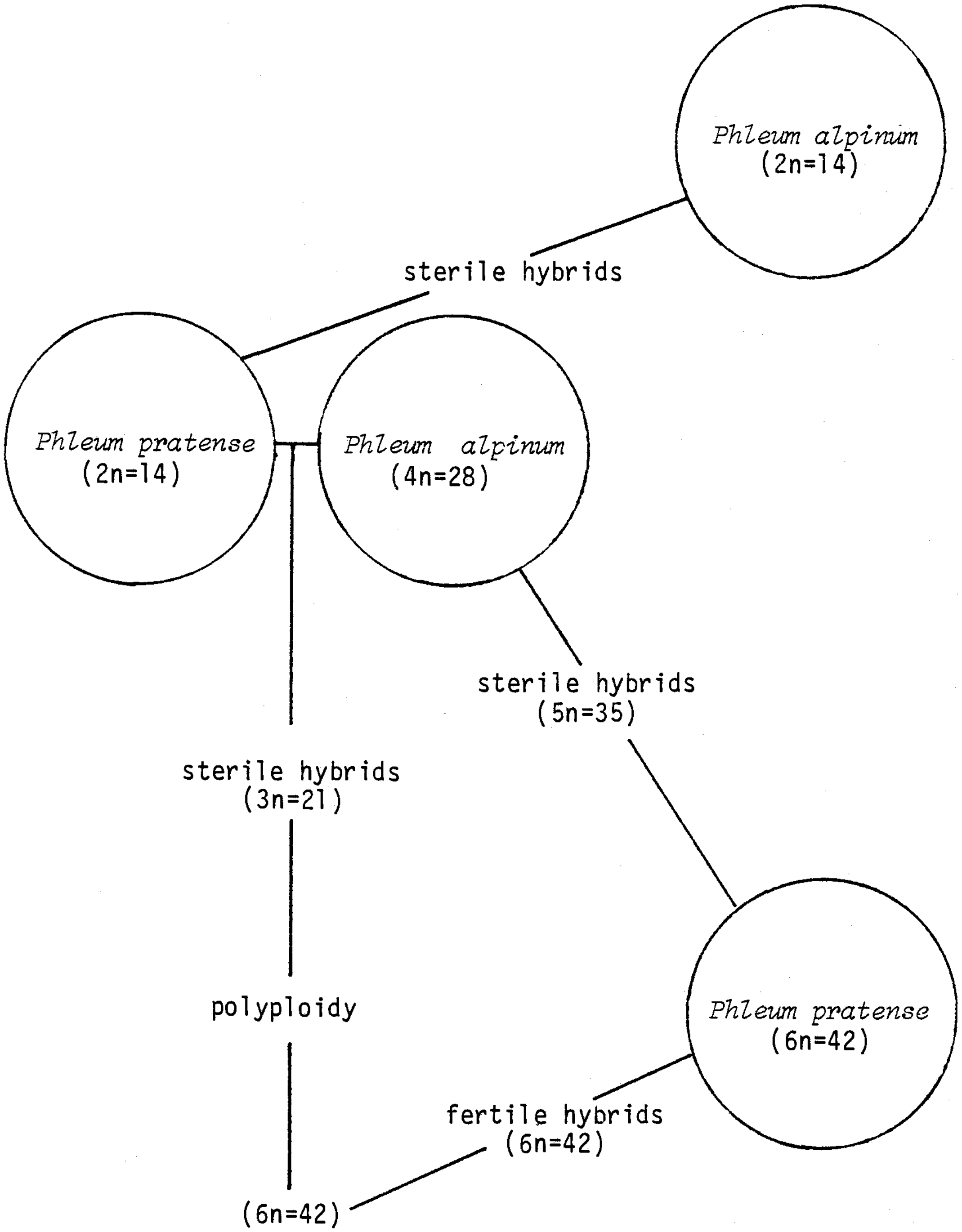


Figure 3. The Coenospecies *Phleum pratense-alpinum*. Circled groups are those found in nature. (From Gregor).

In many ways *Drosophila* was an outstanding subject for "experimental" taxonomy. As I have pointed out above, *Drosophila* workers, themselves, were well aware of the advantages which this genus held for genetic and cytological study.[68] The major obstacle to a synthetic study of the taxonomy of the genus *Drosophila* was the poorly studied ecology of the group.[69] The species used most extensively for genetic experiments, *Drosophila melanogaster*, was a particularly poor choice for ecological studies due to its cosmopolitan distribution and close association with humans. Ecological studies of *Drosophila melanogaster* were difficult according to Dobzhansky because, "Its populations are constantly churned up because of unintentional transport by man."[10] *Drosophila pseudoobscura*, which was not so intimately associated with humans, proved to be a much better choice for studies of population dynamics. During the 1930s and 1940s Dobzhansky and his co-workers carried out an extensive research program on the nature and causes of variation, the distribution of variation, migratory patterns, and habitat and mating preferences of *Drosophila pseudoobscura* and its allies.[71]

One of Dobzhansky's major preoccupations during this period was the study of geographical races and their relationship to species. This interest was expressed not only in experimental studies on *Drosophila pseudoobscura*, but also in a number of theoretical writings.[72] *Drosophila pseudoobscura* proved to be a particularly fortunate choice for racial studies. The species was subdivided into a number of divisions of varying sizes. These ranged from extensive geographical races down to very small, semi-isolated local populations.[73] Cytological analysis became a major tool for investigating these groups, since the major characteristics differentiating groups were often structural rearrangements in the chromosomes.[74]

Particularly important taxonomically were two major races of *Drosophila pseudoobscura*. These races or "physiological species" had been distinguished soon after *Drosophila pseudoobscura* was discovered on the west coast of the United States. Race A and Race B, as they were designated, were apparently indistinguishable in terms of gross morphological characteristics.[75] However, interracial crosses produced completely sterile male hybrids.[76]

During the 1930s, Dobzhansky and his colleagues undertook a major investigation of the relationship between Race A and Race B of *Drosophila pseudoobscura*. The sterility of male hybrids was found to be a complex phenomenon involving both the degeneration of the testes and failure of meiosis during the development of sperm.[77] Sterility appeared to involve not only genes located on the sex chromosomes but also genes scattered throughout the autosomes.[78] Female hybrids, although fertile, produced offspring of lowered viability when backcrossed to males of the parental races.[79] When the giant chromosomes from the larval salivary glands of members of the two races were compared, readily identifiable structural differences were found in at least two of the five pairs of chromosomes.[80] A number of statistical differences in such physiological functions as developmental time, egg laying capacity, longevity, and oxygen consumption, were found, leading Dobzhansky to conclude that, "The two 'races' present different physiological reaction systems."[81] Although the two races were indistinguishable in terms of gross morphological characteristics, a number of statistical differences were found in such anatomical features as number of teeth in the sex combs, and size and shape of the wings.[82] Geographically, the races differed somewhat in distribution, although their ranges overlapped extensively.[83] Race A was by far the more widespread, extending from British Columbia south into Mexico, and from California east into Nebraska and Texas. The range of Race B was much more restricted, extending along the Pacific coast from southern California to British Columbia. Although the range of Race A appeared to completely include that of Race B, there was some indication that Race B might extend further north in British Columbia than Race A.

On the basis of these differences Dobzhansky and Carl Epling (1894-?) designated the two races of *Drosophila pseudoobscura* separate species. According to Dobzhansky and Epling,

> Because these supposed races are in fact species, although but little differentiated in external morphology, we propose the name *Drosophila persimilis* to replace the inconvenient and biologically meaningless designation "race B." The name *Drosophila pseudoobscura* Frolova is accordingly applicable only to the entity previously designated "race A."[84]

In defense of this change Dobzhansky and Epling stated,

> It is certain that if any kind of structural difference had been known between *D. pseudoobscura* and *D. persimilis*, they would have been classified as species from the start. Calling them races, and designating them by the letters A and B instead of by Latin names, was an attempt to appease conservative taxonomists who continue to adhere to the purely morphological concepts of species and race. Such a course is neither scientifically consistent nor practically sound. The species

> is the stage in the process of evolutionary divergence at which an array of populations actually interbreeding or capable of interbreeding has become split into two or more reproductively isolated arrays. Species exist in nature regardless of whether we can or cannot distinguish them by their structural characters.[85]

Cytological and genetical criteria were extremely important, if not the overriding considerations in Dobzhansky and Epling's designation of the new species *Drosophila persimilis*. As the authors noted,

> It happens that the characteristics of the chromosomes and the breeding behavior furnish the safest method for distinguishing *D. pseudoobscura* and *D. persimilis*. We are far from offering the preposterous advice that henceforth all entomologists should examine the chromosomes of their species before describing them. The methods of systematics in any given group are determined by the level which the knowledge of this group has attained and by the uses to which this knowledge is being put.[86]

This statement cannot be taken too literally. Dobzhansky and Epling portrayed genetic and chromosomal traits as more than simply constant and convenient taxonomic characters. Rather, genetic and chromosomal variations were the epitome of distinguishing characteristics for races and species.[87] Furthermore, the limitations placed on the use of genetic and cytological analysis by other entomologists had less to do with the state of knowledge about groups or the purposes to which classification systems were to be used, than with the technical difficulties of applying these analytical methods to other groups of insects.

Cytological analysis, in particular, was not exploited by animal taxonomists to nearly the same extent as by their botanical colleagues. In his influential *Animal Cytology and Evolution* the cytologist, M.J.D. White (1910-), noted,

> From time to time the hope has been expressed that chromosome cytology may become an important aid in taxonomic work. As far as plants are concerned, this situation already exists: chromosome studies are frequently employed in the discrimination of species and particularly in establishing their relationships to one another...
>
> In animals cytology has not been employed by taxonomists to anything like the same extent.[88]

White estimated that only about one-tenth of one per cent of all animal species had even been cytologically analyzed to the extent of determining numbers of chromosomes.[89] This situation could be rectified. Nonetheless, there appeared to be real limitations to the extension of cytological methods in zoology. According to White,

> Cytology is a tool that deserves more attention by taxonomists than it has received in the past, but as far as animals are concerned it is certainly not a magic key that will unlock all taxonomic problems (except in those Diptera which possess workable salivaries, where cytology can probably answer all problems of discrimination of 'difficult' species).[90]

White ironically noted that "Drosophily," the study of the genetics and cytology of *Drosophila*, had almost become a separate branch of biology.[91] Due to the "accidents" of nature, most taxonomists were precluded from emulating Dobzhansky's detailed analysis of chromosomes simply because of the small size of normal chromosomes. This situation was considerably worse for taxonomists interested in some particular groups of animals. For example, vertebrate systematists were barred from fully utilizing even the rudimentary cytological characteristic of chromosome numbers. According to White,

> It is now absolutely clear that the vertebrates (with the exception of a few groups such as Urodeles) are extremely unfavorable material for detailed cytological work. The difficulties arise partly from the fact that the chromosome numbers are usually high and the individual chromosomes

> extremely small; an even greater source of error and confusion, however, is the tendency of the chromosomes to clump together in aggregates if the fixation has not been quite perfect.[92]

Improvements in cytological technique gave some hope for remedying this situation. However, for birds in particular, White foresaw no immediate solution to cytological problems.

> In birds, however, these obstacles are still very serious. Thus the student of avian speciation must, for the present, resign himself to the fact that he cannot use the method of comparative cytology which has proved so valuable in other groups, simply because the technical obstacles do not permit us to arrive at an absolutely accurate morphological description of the chromosome set of any species of bird (the position as regards the mammals and reptiles is substantially better, but not entirely satisfactory even yet).[93]

Genetic analysis was also problematic in birds. Although the *theory* of genetics could be applied to this group, the detailed analysis of particular genetic differences between bird species was not a generally fruitful avenue of research in avian systematics. In reviewing the progress of systematic and evolutionary studies in birds from 1938 to 1950, Ernst Mayr noted,

> As far as the genetic factors are concerned, it is now realized that species differ by very many genes, certainly hundreds, perhaps even thousands. This has been established for animals other than birds since birds are particularly unsuitable for genetic research.[94]

As I pointed out in an earlier chapter, other zoological taxonomists such as Alfred Kinsey also outlined the extreme obstacles to applying rigorous genetic analysis in the taxonomic delimitation of more than a handful of animal groups.[95]

There were also obstacles to the general employment of experimental taxonomy in plants. For example, not all plant species were equally amenable to cytological analysis. Long-lived woody plants were not particularly suitable for transplant studies of the types used by Turesson, Hall and their followers. As most taxonomists who utilized the synthetic "experimental" approach pointed out, the plant groups chosen for study were often those which had particularly favorable characteristics for cytological, ecological, and genetic analysis.[96] Nonetheless, there were good reasons why the experimental taxonomy of plants was seen as a fruitful line of research. Polyploidy appeared to be a widespread phenomenon in plant evolution and a particularly vexing problem for plant classification. Cytological analysis provided the best tool for unraveling the complex relationships within polyploid groups.[97] Hybridization also appeared to be a more common phenomenon among plants than among animals. Even fairly wide crosses, for example between related genera, were sometimes possible. The occurence of both natural and artificial hybridization provided botanists with an impetus for using genetic methods for analyzing taxonomic relationships.[98] Finally, plants, which were firmly rooted to their substrates, were generally more conspicuously influenced by local environmental conditions than animals were. Plant taxonomists who were interested in the relationship between observed variation and habitat, found in transplant experiments a means for analyzing this relationship.[99] These experimental techniques had no close parallels in zoology.

Most experimental taxonomists realized that their approach to classification was not likely to find universal application either in the plant or animal kingdoms. Many of these taxonomists believed however, that where applicable, experimental taxonomy provided a new, more objective approach to classification. Despite this enthusiasm, the application of the "experimental" methods turned out to be problematic even in the classification of some groups that appeared to be amenable to experimental taxonomy.

NOTES

CHAPTER THREE

1. For example see: H.M. Hall and Associates, "Experimental Taxonomy," *Carnegie Institution of Washington Yearbook* 25 (1926): 345-346; Jens Clausen, David D. Keck, William M. Hiesey, "Experimental Taxonomy," *Carnegie Institution of Washington Yearbook* 31 (1932): 201-205; 32 (1933): 192-196; 34 (1935): 201-206; 35 (1936): 208-214; 36 (1937): 204-214; [Hiesey's name was spelled "Heusi" in the 1932 and 1933 reports]; J.W. Gregor, V. McM. Davey, and J.M.S. Lang, "Experimental Taxonomy I. Experimental Garden Technique in Relation to the Recognition of the Small Taxonomic Units," *New Phytologist* 35 (1936): 323-350; W.B. Turrill, "Experimental and Synthetic Plant Taxonomy," in: J.S. Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940).

2. Turrill, "Synthetic Plant Taxonomy."

3. Jens Clausen, David D. Keck, and William M. Hiesey, *Experimental Studies on the Nature of Plants. I. Effect of Varied Environments on Western North American Plants.* Carnegie Institution of Washington Publication No. 520 (1940), p. iii.

4. Clausen, Keck, and Hiesey, "Experimental Taxonomy," (1932; 1936; 1937); J.W. Gregor, "Experimental Delimitation of Species," *New Phytologist* 30 (1931): 204-217, pp. 206-207.

5. Edgar Anderson, "The Technique and Use of Mass Collections in Plant Taxonomy," *Annals of the Missouri Botanical Garden* 28 (1941): 287-292; Edgar Anderson, "Mass Collections," *Chronica Botanica* 7 (1943): 378-380; Edgar Anderson and W.B. Turrill, "Biometrical Studies on Herbarium Material," *Nature* 136 (1935): 986.

6. E.M. Marsden-Jones, V.S. Summerhayes, and W.B. Turrill, "Special Herbaria as Adjuncts to Modern Botanical Research," *Journal of Ecology* 18 (1930):379-383.

7. Turrill, "Synthetic Plant Taxonomy," p. 69.

8. Ernest Brown Babcock, *The Genus Crepis: Part One: The Taxonomy, Phylogeny, Distribution, and Evolution of Crepis; Part Two: Systematic Treatment*, [*University of California Publications in Botany* Vol. 21 and 22 (1947)]; E.M. Marsden-Jones and W.B. Turrill, *The Bladder Campions* (London: Adlard & Son, Ltd., 1957).

9. Edgar Anderson, "The Problem of Species in the Northern Blue Flags, *Iris versicolor* L. and *Iris virginica* L." *Annals of the Missouri Botanical Garden* 15 (1928): 241-333, pp. 243-244.

10. Ibid.

11. Ibid.

12. Ibid.

13. Edgar Anderson, "The Species Problem in Iris," *Annals of the Missouri Botanical Garden* 23 (1936): 457-509, p. 477.

14. Ibid., p. 471.

15. Ibid., p. 458.

16. Ibid.

17. Ibid., p. 474.

18. Ibid.

19. Ibid.

20. Ibid.

21. Ibid., p. 485.

22. Ibid., p. 471.

23. Ibid., p. 474.

24. Ibid., pp. 474-483.

25. Ibid., p. 499.

26. Ibid., pp. 503-504.

27. Ibid., pp. 500-501.

28. Clausen, Keck, and Hiesey, "Experimental Taxonomy," (1932).

29. Clausen, Keck, and Hiesey, "Experimental Taxonomy," (1932); Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. iii.

30. H.M. Hall, "Heredity and Environment - As Illustrated by Transplant Studies," *Scientific Monthly* 35 (1932):289-302; W.M. Hiesey, "Environmental Influence and Transplant Experiments," *Botanical Review* 6 (1940): 181-203; Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. 16, 396-401.

31. Clausen, Keck, and Hiesey, "Experimental Taxonomy," (1932); Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. iii.

32. Hiesey, "Environmental Influence," pp. 195-197; Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. 4.

33. Göte Turesson, "The Genotypical Response of the Plant Species to the Habitat," *Hereditas*, 3 (1922): 211-347, pp. 213-215.

34. Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. 4.

35. Turesson, "Genotypical Response," pp. 341-347; Göte Turesson, "The Scope and Import of Genecology," *Hereditas* 4 (1923): 171-176.

36. For example, Theodosius Dobzhansky presented rather different appraisals of the genecological units in the three editions of *Genetics and the Origin of Species*, see: Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), pp. 47, 167-169; 2nd edition (1941), pp. 196-202; 3rd edition (1951; Columbia Paperback Edition, 1964), pp. 145-148, 272-273. See also: Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), pp. 193-200; J.W. Gregor, "The Ecotype," *Biological Review* 19 (1944): 20-30; W.B. Turrill, "The Ecotype Concept: A Consideration with Appreciation and Criticism, Especially of Recent Trends," *New Phytologist* 45 (1946): 34-43; G. Ledyard Stebbins Jr., *Variation and Evolution in Plants* (New York: Columbia University Press, 1950), chap. 2; J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: William Heinemann Ltd., 1953), chap. VII.

37. J.W. Gregor, "The Units of Experimental Taxonomy," *Chronica Botanica* 7 (1942): 193-196; Heslop-Harrison, *New Concepts*, chap. VII.

38. Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. vii.

39. Ibid.

40. Ibid.

41. Ibid.

42. Ibid., p. iv.

43. Ibid., pp. 4-15.

44. Ibid.

45. Ibid., pp. 18-22.

46. For example, see photographs of *Potentilla glandulosa*: Ibid., pp. 49, 51.

47. For example, see photographs of *Potentilla glandulosa*: Ibid., p. 54.

48. Ibid., p. 53.

49. Ibid., for example, see table on p. 58. See also: pp. 55-62.

50. Ibid.

51. Ibid., pp. 408-411.

52. Ibid., p. 415.

53. Ibid.

54. Ibid.

55. Ibid., pp. 417-425.

56. Ibid.

57. Ibid., p. 213.

58. Ibid., p. 425.

59. Ibid., p. 426.

60. Ibid., pp. 427-428.

61. J.W. Gregor and J.W. Sansome, "Experiments on the Genetics of Wild Populations. Part I. Grasses," *Journal of Genetics* 17 (1927): 349-364; "Part II. *Phleum pratense* L. and the hybrid *P. pratense* L. x *P. alpinum* L.," *Journal of Genetics* 22 (1930): 373-387; J.W. Gregor, "Experimental Delimitation."

62. Gregor, "Experimental Delimitation," p. 211.

63. Ibid., pp. 208-210.

64. Ibid., pp. 207-208.

65. Ibid., p. 208.

66. Ibid., p. 212.

67. Dobzhansky published a number of taxonomic studies of *Drosophila*. For example, see: A.H. Sturtevant and Th. Dobzhansky, "Observations on the Species Related to New Forms of *Drosophila affinis*, with Descriptions of Seven," *American Naturalist* 70 (1936): 574-584; K. Mather and Th. Dobzhansky, "Morphological Differences Between the 'Races' of *Drosophila pseudoobscura*," *American Naturalist* 73 (1939): 5-25. Th. Dobzhansky and Carl Epling, *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and its Relatives*, Carnegie Institution of Washington Publication No. 554 (1944).

68. See my discussion of genetics and taxonomy, pp. 60-61.

69. Dobzhansky and Epling, *Contributions*, p. 3.

70. Ibid.

71. For example see: Th. Dobzhansky, "Genetic Structure of Natural Populations," *Carnegie Institution of Washington Yearbook* 37 (1938): 323-325; 38 (1939):287-289; 39 (1940): 244-247; 40 (1941): 271-276; 41 (1942): 228-234; 43 (1944): 120-127. See also: Dobzhansky, *Genetics and the Origin* (1937; 1941; 1951), passim.

72. For Dobzhansky's own evaluation of ongoing experimental research on the races of *Drosophila pseudoobscura* see: Dobzhansky, "Genetic Structure," (1940; 1941; 1942; 1944). For theoretical discussions of races and species see: Th. Dobzhansky, "A Critique of the Species Concept in Biology," *Philosophy of Science* 2 (1935): 344-355; Th. Dobzhansky, "Genetic Nature of Species Differences," *American Naturalist* 71 (1937): 404-420; Th. Dobzhansky, "What is a Species?," *Scientia* 61 (1937): 280-286; Th. Dobzhansky, "Speciation as a Stage in Evolutionary Divergence," *American Naturalist* 74 (1940): 312-321; Th. Dobzhansky, "The Race Concept in Biology," *Scientific Monthly* 52 (1941): 161-165. See also: Dobzhansky, *Genetics and the Origin*, (1937), chap. X; (1941), chap. XI; (1951), chap IX.

73. Dobzhansky, "Genetic Structure," (1940; 1941; 1942; 1944).

74. Ibid.

75. Mather and Dobzhansky, "Morphological Differences," p. 5.

76. Dobzhansky, *Genetics and the Origin*, (1937), pp. 278-287.

77. Ibid.

78. Ibid.

79. Ibid.

80. Dobzhansky and Epling, *Contributions*, pp. 5-6.

81. Ibid.

82. Mather and Dobzhansky, "Morphological Differences;" Dobzhansky and Epling, *Contributions*, p. 6.

83. Dobzhansky and Epling, *Contributions*, pp. 11-18.

84. Ibid., p. 6.

85. Ibid., p. 7.

86. Ibid., p. 10.

87. Dobzhansky, *Genetics and the Origin*, (1937), pp. 73-74; Carl Epling, "Taxonomy and Genonomy," *Science* 98 (1943): 515-516.

88. M.J.D. White, *Animal Cytology and Evolution* (Cambridge: Cambridge University Press, 1945), p. 311.

89. Ibid., p. 153.

90. Ibid., p. 313.

91. Ibid., p. vii.

92. M.J.D. White, "Chromosomes of the Vertebrates," *Evolution* 3 (1949): 379-381, p. 379.

93. Ibid.

94. Ernst Mayr, "Speciation in Birds," *Proceedings of the Tenth International Ornithological Congress* (1950): 91-131, p. 106.

95. See my discussion of genetics and taxonomy, pp. 61-62.

96. For example, see: Anderson, "Northern Blue Flags," pp. 243-244; Gregor, Davey, and Lang, "Experimental Taxonomy I," p. 327; Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. 18.

97. Edgar Anderson, "Cytology in its Relation to Taxonomy," *Botanical Review* 3 (1937): 335-350.

98. W.B. Turrill, "The Expansion of Taxonomy with Special Reference to the Spermatophyta," *Biological Review* 13 (1938): 342-373, pp. 355-358.

99. Hall, "Heredity and Environment," pp. 291-294; Hiesey, Environmental Influence," pp. 181, 199.

Chapter Four: The Critical Reception of Experimental Studies in Taxonomy

During the 1930s and 1940s there was widespread agreement that techniques and concepts from other biological disciplines were useful and even necessary for classification. There was, nonetheless, considerable disagreement over exactly how these new elements ought to be incorporated. The mixed reception of experimental taxonomy illustrated a number of fundamental differences among taxonomists. There were differences in the interpretation of particular data. Disagreements occurred over the relative importance of various types of data. On a more fundamental level the relationship between classification based on "experiment" and established classification schemes was unclear. This problem was further compounded by very real disagreements over the proper foundations and purposes of classification in general.

The ambiguous relationship between experimental taxonomy and traditional taxonomy is illustrated by the views of experimental taxonomists themselves. A number of these taxonomists believed that the new methods of experimental taxonomy were fundamentally different from, and superior to morphological description. Nonetheless, nearly all of these taxonomists admitted that descriptive taxonomy would continue to play a part in classification. For example, as early as 1905, a pioneer experimentalist, F.E. Clements, wrote,

> While interpretation will always play a part in taxonomy, the general use of experiment will leave much less opportunity for the personal equation than is at present the case. Taxonomy,

> like descriptive botany, is based on the species, but, while there may exist a passable kind of descriptive botany, there can be no real taxonomy as long as the sole criterion of a species is the difference which any observer thinks he sees between one plant and another.[1]

Clement's sentiments were echoed in the 1930s by his onetime co-worker H.M. Hall. According to Hall,

> The conclusions of taxonomy result largely from observation, description, and comparison; in other words, they are reached subjectively. There is now an ever-increasing movement to introduce objective methods, especially for the testing of criteria used as a basis for classification.[2]

The objective methods which Hall referred to included genetic, cytological, statistical, and biochemical techniques as well as the transplant experiments which Hall was perfecting.[3] Both Hall's transplant experiments and his enthusiasm for new "objective" methods were carried on after his death by Jens Clausen, David Keck, and William Hiesey. While Clausen and his co-workers noted the importance of morphology for classification they believed that experimentation placed taxonomy on an objective basis.[4] According to Clausen's team, "The work [in experimental taxonomy] has shown that it is possible to give a fairly objective delimitation and classification of species based upon experiment rather than upon speculation..."[5] Even biologists who took a less sanguine view of the potentials of experimental methods, noted the important contributions that only experimental methods could add to classification. For example, W.B. Turrill stated,

> It is obvious that such [experimental] methods are as yet little developed and that they have limitations which will always prevent them replacing other methods. Nevertheless, sufficient is already known of their potentialities to make it certain that

> they can provide valuable data, unobtainable by any other method. Moreover the data can be more precise and, since published results can be tested by repetition of experiments, more 'objective' than interpretations of dead herbarium and museum specimens.[6]

Despite the enthusiasm for experimental methods in taxonomy, the relationship between morphology and experimentation was more complex than simply an alternative between "subjective" or "speculative" descriptive methods on one hand and "objective" experimental methods on the other. Those, like Turrill, who defended morphology noted that taxonomy rested on a morphological foundation for a number of reasons.[7] To some extent the reliance on morphological characteristics had a historical basis. Taxonomy had developed during a period when morphology was the dominant field of biological study.[8] Perhaps more importantly, morphological characteristics could be preserved in museum or herbarium collections and were often much more readily determinable than physiological characteristics.[9] Nonetheless, as Turrill noted, there was no *a priori* reason why a classification system could not be developed completely on the basis of physiological characteristics.[10] However, although biology could be artificially divided into the study of form, including taxonomy, and the study of function, including much of experimental biology, the two were closely entwined.[11] Even when the taxonomist was specifically considering morphological characteristics, important physiological implications could never be completely ignored. Such important taxonomic characteristics as viviparity, lactation, warm bloodedness, seed habit, and angiospermy involved an intimate correlation between morphological and physiological characteristics.[12] Furthermore, the dichotomous distinction between descriptive morphological techniques and experimental techniques was at best imprecise.[13] There was widespread use of what might be considered "expanded morphology" even in such fundamentally experimental fields as genetics. According to Turrill,

> Exactly what is to be included under "morphology" and what excluded? Morphology (plant or animal) nowadays includes a good deal more than mere "study of shape." Anatomy is certainly morphology by dissection often with the aid of a compound microscope; much, but not all, cytology is morphology with a twelfth-inch oil-immersion lens; ontogeny, embryology, paleontology, etc. are very largely morphology; genetics is in theory physiological, but in practice largely uses morphological characters, and so on. Even within morphology in a very strict sense the taxonomist is forced to consider matters which involve physiology. The degree of correlation of characters are so closely related to internal and external factors that the taxonomist must, to a certain extent, consider the physiological working of these last.[14]

Even the traditional morphological techniques associated with herbarium and museum collecting were being reformed. As was pointed out earlier in this dissertation, taxonomists such as W.B. Turrill and Edgar Anderson advocated innovations in botanical collecting methods.[15] Both biologists argued that herbarium collections should better represent the variation found in natural populations and include more sophisticated quantitative data concerning the plant specimens.[16] Anderson noted that this "mass collecting" technique had been used to good effect by such ornithologists as Ernst Mayr and entomologists such as Alfred Kinsey.[17] The emphasis in these mass collections was not so much on large samples, although this was important, but rather, according to Anderson, on statistically valid representation of the sampled population. Mass collections would be immediately useful to taxonomists particularly in the study of complex groups of plants. Furthermore, according to Anderson,

> Eventually the greatest contribution made by mass collections should be the recognition that our great herbaria can be used for purposes besides pure taxonomy. There are innumerable biological problems of pressing importance which might be studied by the herbarium method, if only there were enough mass collections in herbaria which could be put to such use. Studies of this sort might be carried on either by taxonomists, or by experimentalists working in conjunction with them.[18]

Along with advocating more comprehensive traditional herbaria, Turrill and his colleagues suggested developing special herbaria as adjuncts to experimental laboratories.[19] Special herbaria would serve as permanent repositories for specimens used in genetic experiments or collected during the course of ecological field studies. These preserved specimens would be available for study if questions ever arose about experimental results.

Turrill's discussion of the sophistication of "morphological" techniques and the complex interrelations between these techniques and "experimental" methods is important. Experimental taxonomists too often drew an easy distinction between what they considered subjective or speculative morphological methods and objective experimental methods. Such a distinction obscures a good deal of the controversy over the results of some studies in experimental taxonomy.

The complexity of the reception of experimental studies is illustrated by the reception of J.W. Gregor's reclassification of the genus *Phleum*. In presenting the results of the *Phleum* study Gregor noted, "A system of classification based entirely on morphological distinctions and resemblances cannot do much more than supply to its smaller units an appellation of little or no evolutionary significance."[20] Furthermore,

> The [genecological] concept of Turesson appears to the present writer to be a constructive attempt to place the grouping of organisms on a more natural basis. His system is not dependent on one particular line of enquiry, but embraces the results of morphological, cytological, and experimental investigations.[21]

Gregor's criticism of traditional taxonomy and his optimistic view of the potential for experimental taxonomy and particularly genecology elicited a caustic rejoinder from the taxonomist A.J. Wilmott. According to Wilmott,

> ...although it is a pity that some taxonomists have an insufficient knowledge of modern genetics and cytology, it is at least equally to be regretted that some geneticists have no knowledge of taxonomy. The author's statement that "a system of classification based entirely on morphological distinctions and resemblances cannot do much more than supply to its smaller units an appellation of little or no evolutionary significance" will seem absurd to the really capable taxonomist, who from his knowledge of genetics could often predict many genetical factors within a group from a study of wild populations alone.[22]

Wilmott's rebuke of Gregor was followed by an exchange of rather acid letters in the correspondence column of the *Journal of Botany*.[23] The intensity of this disagreement is somewhat surprising. Wilmott was not a reactionary taxonomist. Like Gregor, he was a member of the Association for the Study of Systematics in Relation to General Biology and was an active participant in a number of the Association's symposia on taxonomic problems. Furthermore, Wilmott's own taxonomic work was cited as an example of ecologically significant taxonomy.[24] On the other hand, Gregor was not insensitive to the importance of traditional taxonomy. In his presentation of the *Phleum* study Gregor noted that his reclassification of the genus was not necessarily intended to be generally accepted, but rather was an attempt to demonstrate the possibilities of using experimental data in taxonomy.[25] Especially in later writings, Gregor suggested that classification based on experimental studies be kept separate from traditional classification systems.[26]

The disagreement between Gregor and Wilmott does demonstrate that different taxonomists emphasized different types of data. Gregor was not opposed to the use of morphological data which he acknowledged as an important taxonomic criterion and one which he clearly used in the description of ecotypes of *Phleum* species.[27] "Nevertheless," according to Gregor,

> I believe that, whenever practicable, the experimental study of a group from as many aspects as possible is the most reliable means of obtaining precise information regarding its component parts: this is proved by the fact that the observational method alone had failed to make the important distinction between the two groups [ecospecies] of *P. pratense*.[28]

Although he proposed "experimental study" from "as many aspects as possible" the primary aspects that Gregor considered were genetic and cytological. Morphological, edaphic, and geographical characteristics were considered by Gregor, however they were not decisive in defining genecological units other than ecotypes. The critical criteria for designating the groups included in the coenospecies, *Phleum pratense-alpinum*, were chromosomal numbers and experimentally determined sterility barriers. The four ecospecies which Gregor named corresponded to groups differing in chromosomal numbers. Furthermore, the trinomials which Gregor used to designate the ecospecies indicated the importance of chromosomal numbers for defining ecospecies. For example, Gregor differentiated *Phleum pratense* into the ecospecies *Phleum pratense diploidium* and *Phleum pratense hexaploidium*.[29] Gregor's emphasis on sterility barriers as inferred from cytological analysis and hybridization experiments was shared by a number of other experimental taxonomists.[30] Since reproductive isolation was imperative for evolutionary divergence, those whose interests in systematics were primarily evolutionary, often saw sterility as one criterion that could give taxonomic units undeniable evolutionary significance.[31]

Not all taxonomists, however, shared this explicitly genetic perspective on systematics. In criticizing Gregor, Wilmott noted,

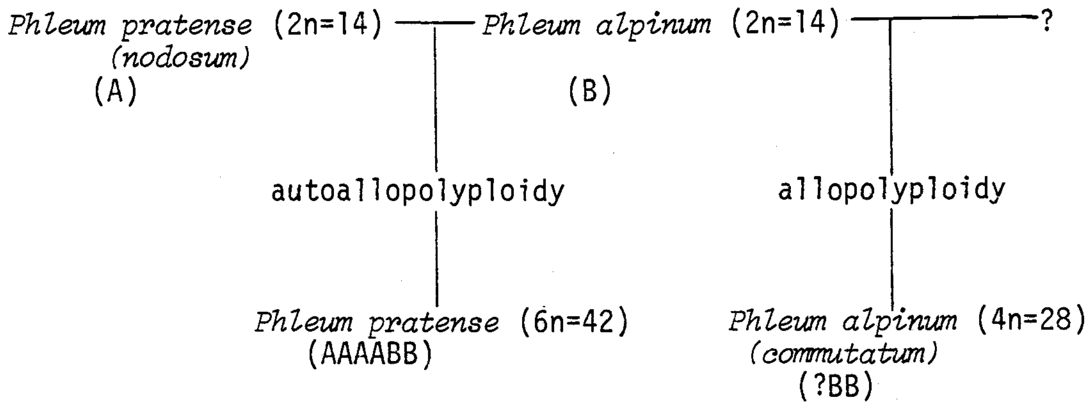
> After reading it [Gregor's paper] P. alpinum remains an entity morphologically, distributionally, and historically distinct from [diploid] P. pratense and from the hexaploid species which the author also identifies (?rightly) as P. pratense. Even if our tetraploid P. alpinum proves to be distinct from the Continental species, and all sorts of hybrids can be manufactured, these natural groups still exist, and I fail to see the clarification in evolutionary significance produced by the invention of a "coenospecies" P. pratense-alpinum.[32]

Wilmott was critical of Gregor's use of cytogenetics on two counts. First, Wilmott considered "natural" groups to be based on more than genetic criteria. The groups composing the genus *Phleum* were defined on the basis of "morphological, distributional, and historical" criteria as well as on genetic relationship. Furthermore, as Wilmott noted, "...relationship does not destroy individuality, e.g. I remain an entity in spite of my intimate genetical relationship with close relatives."[33] Second, and more importantly, Wilmott was skeptical of the significance of Gregor's hybridization experiments. As Wilmott noted, cytogenetical data was itself open to various interpretations, "...a comparison of the chromosome numbers given by various workers affords at least as great diversity of opinion as any found in taxonomy."[34]

Indeed, the cytogenetical evidence presented by Gregor for his classification of the species-complex in *Phleum* was not unequivocal. After an extensive investigation of the group, the botanist, Hedda Nordenskiöld proposed an alternative interpretation of Gregor's results.[35] According to Nordenskiöld, the hexaploid *Phleum pratense* was not the allopolyploid product of diploid *Phleum pratense* and tetraploid *Phleum alpinum*.[36] Rather, the hexaploid was an autopolyploid which had originated from chromosome doubling within a single ancestral species (Fig. 4)* On the basis of morphological similarities,

---

*G. Ledyard Stebbins, using data from studies by Nordenskiöld and other botanists, interpreted the phylogenetic relationships within this group differently than either Gregor or Nordenskiöld. Using "A" to represent the haploid genome of *Phleum pratense (nodosum)* and "B" to represent the haploid genome of *Phleum alpinum*, Stebbins gives the following representation of the group:



See: G. Ledyard Stebbins Jr., *Variation and Evolution in Plants* (New York: Columbia University Press, 1950), p. 333.

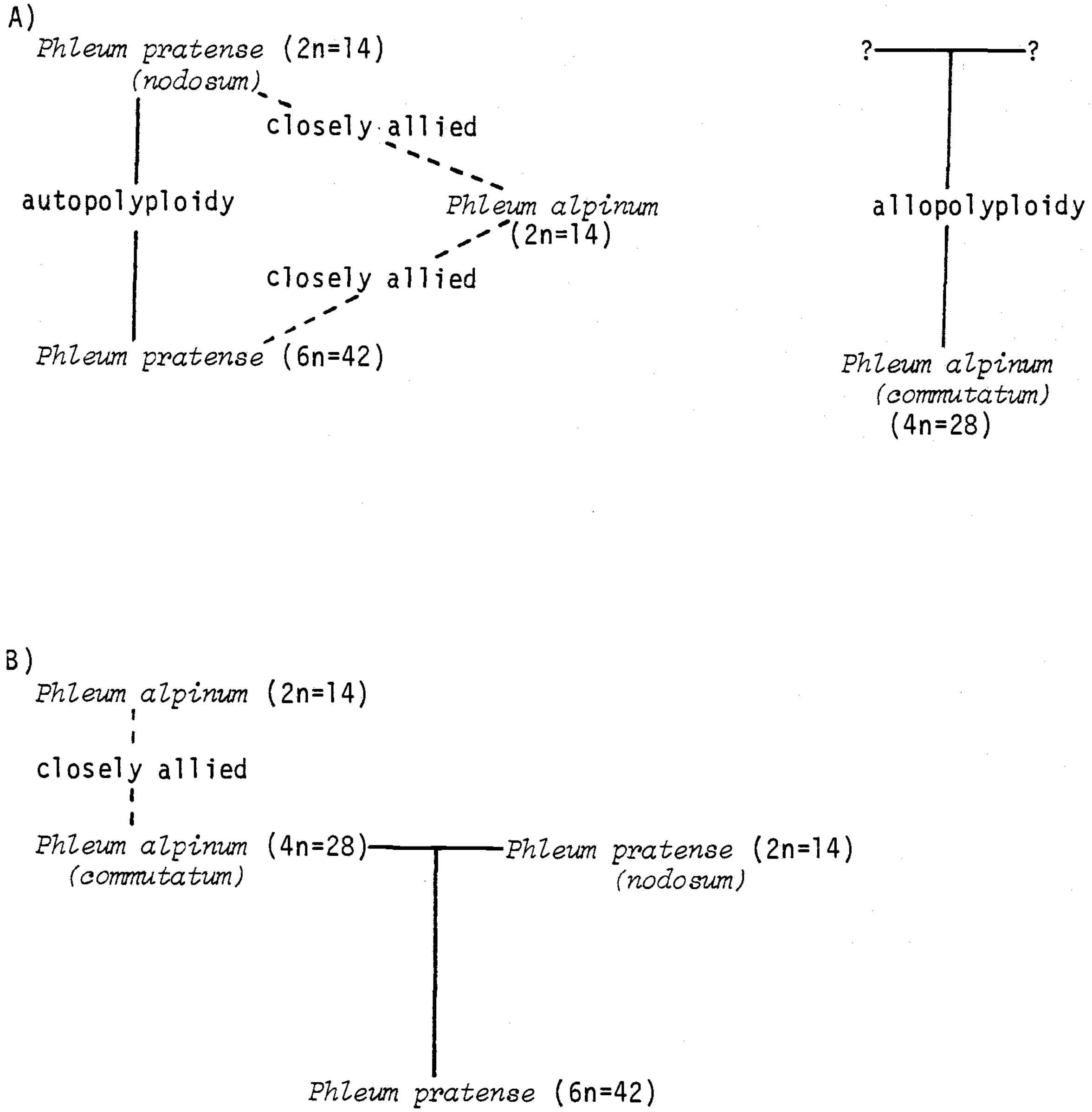
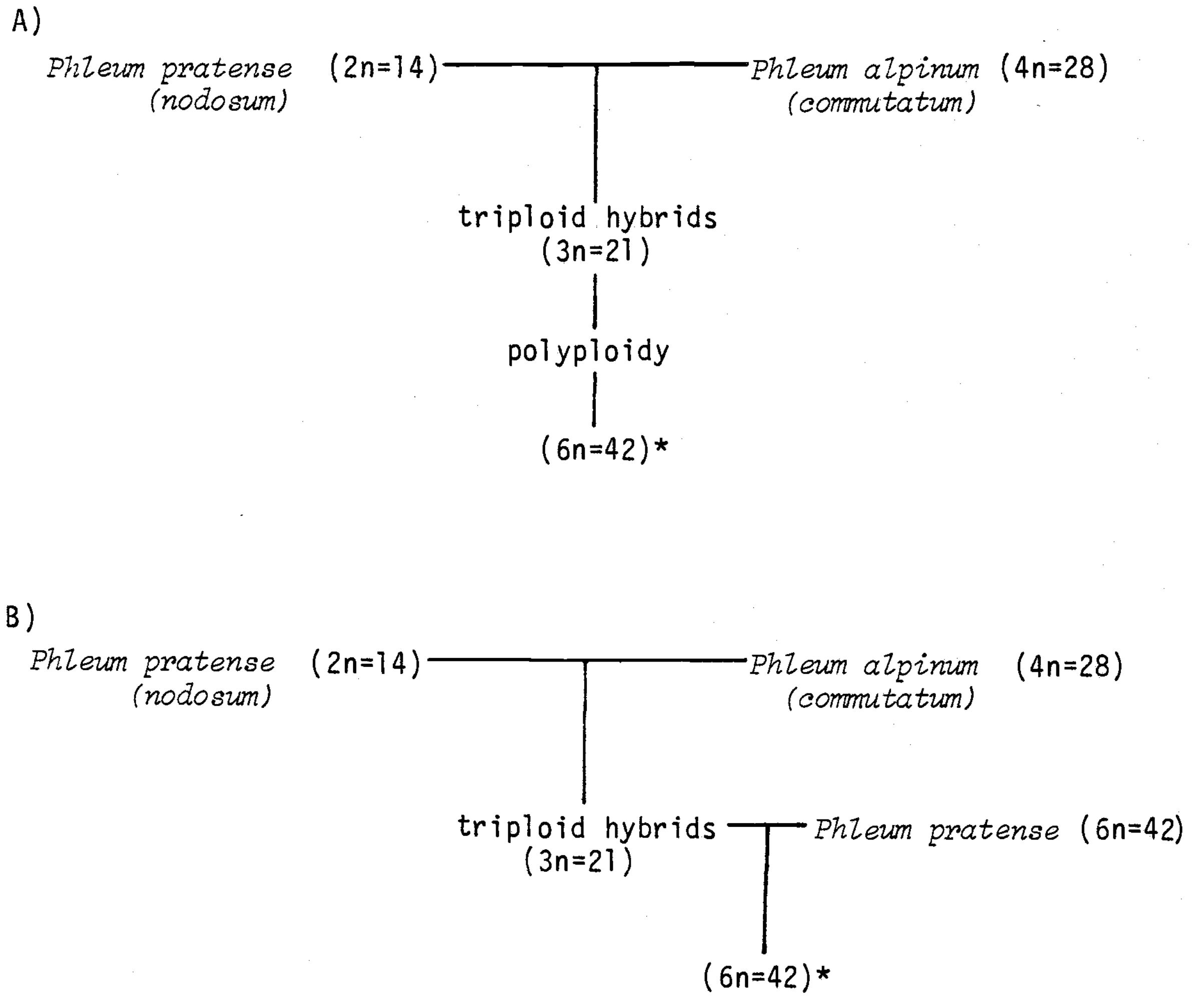


Figure 4. Hypothetical relationships among four species in the genus *Phleum*. A) According to Nordenskiöld. B) According to Gregor.

and the pairing behavior of chromosomes, Nordenskiöld concluded that the ancestral species was similar or identical to diploid *Phleum pratense* (*Phleum nodosum* in Nordenskiöld's terminology).[37] While the diploid *Phleum alpinum* was closely related to both forms of *Phleum pratense*, it was not, Nordenskiöld claimed, part of the direct lineage of the hexaploid.[38] Again, Nordenskiöld based this claim primarily on cytogenetic criteria, but also on morphological similarities and differences. In a more damaging criticism, Nordenskiöld suggested that the "artificial" hexaploid which Gregor and Sansome had produced might not have been the result of allopolyploidy.[39] Since the artificial hexaploid had been used to bridge the gap between diploid *Phleum pratense* (i.e., *Phleum nodosum*) and hexaploid *Phleum pratense*, it was of critical importance for Gregor's tentative phylogenetic scheme of the *Phleum* group. According to Gregor and Sansome, a triploid hybrid resulted from the experimental cross between diploid *Phleum pratense* (2n=14) and tetraploid *Phleum alpinum* (4n=28) (Fig. 5).[40] These triploids were generally sterile. However, when unreduced gametes produced by the hybrids combined, fertile hexaploids (6n=42) were produced. These "artificial" hexaploids were also fully fertile when crossed with the natural hexaploid *Phleum pratense*. Nordenskiöld suggested that unreduced ova produced by the triploid hybrids might have been pollinated by wild hexaploid *Phleum pratense* (Fig. 5).[41] The offspring of the contaminated triploid hybrids would in this case also be hexaploid (6n=42). Such contamination of the experimental crosses by wild pollen was likely, Nordenskiöld claimed, because the



*interfertile with *Phleum pratense* (6n=42)

Figure 5. Alternative explanations for the origin of "artificial *Phleum pratense*." A) Origin according to Gregor. B) Origin according to Nordenskiöld.

wind pollinated hexaploid *Phleum pratense* was so prevalent around the experimental gardens which Gregor and Sansome had used. According to Nordenskiöld the chromosomal behavior, crossing behavior, and appearance of the artificial hexaploid could all be better explained on the basis of her scenario rather than by Gregor's explanation.[42] Finally, tetraploid *Phleum alpinum* (*Phleum commutatum* in Nordenskiöld's terminology) was a distinct and rather ancient allopolyploid species whose parent species were unknown, although they were unlikely to be either of the diploid species studied by Gregor (Fig. 4)[43] This interpretation was evidenced by the strong intersterility demonstrated between tetraploid *Phleum alpinum* and the other three species (Fig. 6). In short, Nordenskiöld suggested that the four groups studied were less tightly related phylogenetically than Gregor had tentatively proposed.

Although Nordenskiöld disagreed with Gregor's interpretation of the phylogenetic relationships within this section of the genus *Phleum*, she agreed with Gregor that the species-complex could best be interpreted as a genecological unit (Fig. 6).[44] According to Nordenskiöld,

> The four above discussed species, which as already stated are morphologically close to one another but which genetically, cytologically, and also ecologically are distinctly separated, can thus according to TURESSON'S...terminology be regarded as good *ecospecies* belonging to one and the same *coenospecies*, constituting the whole species-complex under discussion.[45]

The recognition of this "natural" genecological unit had, according to Nordenskiöld, distinct advantages over the previous classifications of the species-complex. The *Phleum* species-complex could neither be considered a single "collective species" nor two distinct species.[46]

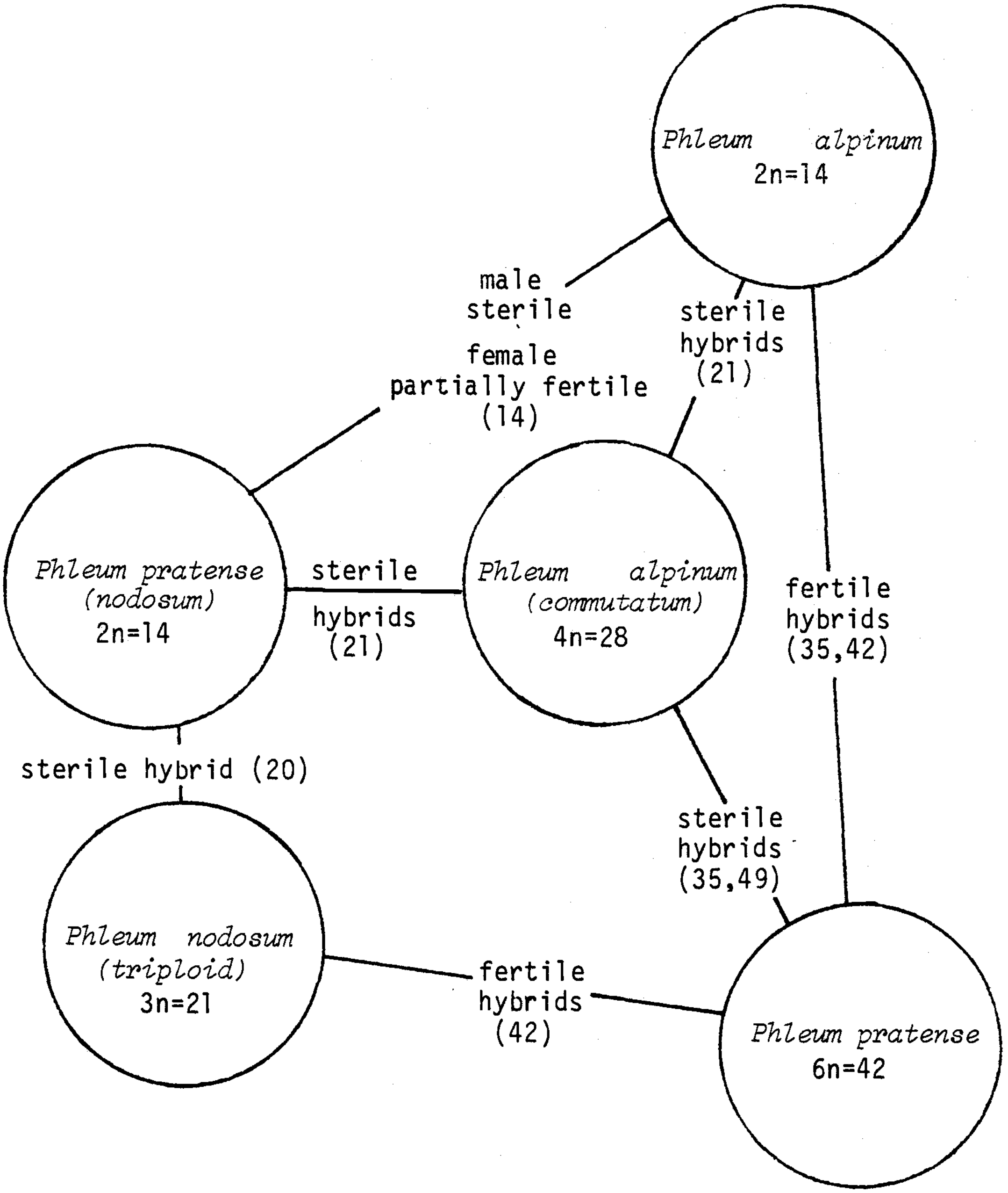


Figure 6. The Coenospecies comprising the species-complex within the genus *Phleum* as determined by Nordenskiöld. Numbers of chromosomes in experimental hybrids given in parentheses.

The use of genecological terms indicated both the close morphological and ancestral relationships within the species-complex, and also indicated the very real genetical, cytological, and ecological distinctions among the subgroups.

Much the same kind of disagreements which arose over Gregor's classification of four species in the genus *Phleum*, were raised by A.H. Sturtevant in a critique of Dobzhansky and Epling's taxonomic treatment of *Drosophila pseudoobscura*. Dobzhansky and Epling argued that Race A and Race B of *Drosophila pseudoobscura* were in fact two distinct species: *Drosophila pseudoobscura* and *Drosophila persimilis*.[47] This reclassification was based on a number of criteria including structural differences in chromosomes, sterility of male hybrids, inviability of backcross offspring of female hybrids, differences in geographic distribution, and slight statistical differences in external morphology.[48] In a critical review of this reclassification, A.H. Sturtevant argued against giving species status to the races of *Drosophila pseudoobscura*.[49]

Sturtevant was particularly critical of the morphological criteria used by Dobzhansky and Epling. One of these criteria was the "Reed's Wing Index" which involved multiplying wing area by the third power of wing length.[50] According to Dobzhansky and Epling, "In conjunction with the differences in number of teeth in the sex combs and other characters, this index is probably sufficient to discriminate between [Race] A and B on purely morphological grounds."[51] Sturtevant disagreed, stating,

> It was shown by Mather and Dobzhansky (Amer. Nat. 73:5-25; 1939) that wing length and wing width are highly correlated; this index, therefore, is nearly equivalent to the fifth power of wing length - it is, in short, a method of greatly magnifying slight differences in wing length, with no increase in the significance of such differences. It was shown by Mather and Dobzhansky (loc. cit.) that there is no consistent difference between the two races in question in wing length - the averages for the two sexes even differ in opposite directions. The index is, therefore, useless in distinguishing Race A from Race B.[52]

Sturtevant concluded,

> The name *persimilis* being of doubtful validity, and being based in part on a non-existent character difference, I shall use the older designation of Race A and Race B in this review. One advantage of this system is that it gives a name (*pseudoobscura*) to the complex made up of Race A and Race B - which is as far as one can go in identifying wild specimens without breeding from them or examining their chromosomes.[53]

Sturtevant's criticism of Dobzhansky and Epling underscores major differences over both the evaluation of data and the fundamental nature of systematics. Both Sturtevant and Dobzhansky had extensive experience in genetics and cytology. Sturtevant had been one of the original members of T.H. Morgan's genetics research group. Along with Dobzhansky, Sturtevant pioneered the use of cytological analysis of giant chromosomes for constructing phylogenetic sequences in *Drosophila pseudoobscura*.[54] In his extensive taxonomic descriptions of species in the genus *Drosophila* Sturtevant supplemented comparative morphological data with data from cytology, genetics, and ecology.[55] It can hardly be claimed, therefore, that Sturtevant was either ignorant of genetics or opposed in principle to the use of cytogenetic analysis in taxonomy. Nonetheless, he placed considerably less emphasis on this criterion than did Dobzhansky. According to Dobzhansky and

Epling, cytogenetic data was the surest way to distinguish what were, in their view, two undeniably separate species.[56] As Dobzhansky and Epling noted,

> It is certain that if any kind of structural difference had been known between *D. pseudoobscura* and *D. persimilis*, they would have been classed as species from the start. Calling them races, and designating them by the letters A and B instead of by Latin names, was an attempt to appease conservative taxonomists who continue to adhere to the purely morphological concepts of species and race.[57]

Sturtevant took quite a different view on the relative importance of different kinds of taxonomic data.

> Distinct species must be separable on the basis of ordinary preserved material. This is in order to make possible for a museum man to apply a name to his material. The necessity for such a provision seems to me to be obvious, since only in this way can effective use be made of the whole technique of taxonomy.[58]

In the 1951 edition of *Genetics and the Origin of Species* Dobzhansky criticized Sturtevant for holding a "morphological species concept."[59] By juxtaposing Sturtevant against a long list of supporters of Dobzhansky's populational conception of *speciation*, Dobzhansky implied that Sturtevant's taxonomic views were inconsistent with neo-Darwinian theory.[60] However, by equating theories of speciation with taxonomic concepts Dobzhansky missed the point of Sturtevant's emphasis on comparative morphology as the primary taxonomic criterion. Sturtevant was not arguing against the evolutionary implications of Dobzhansky's work on *Drosophila pseudoobscura*. Rather, Sturtevant argued that as *taxonomic criteria*, the kinds of evidence that Dobzhansky emphasized were difficult or impossible to apply. According to Sturtevant,

> Cross fertility between distinct species is in general absent or so slight as to make unlikely any transfer of genes from one to the other in nature. This criterion is difficult to apply, and seems to me of secondary value for that reason. Geneticists are likely to emphasize its importance, taxonomists to minimize it. It is clearly of first importance for evolutionary theory, but even in the best understood cases it is still difficult to judge how much actual transfer of genes occurs.[61]

In a footnote, Sturtevant enumerated the conditions affecting gene flow in nature. These included: the frequency with which individuals from different groups crossed, the effective population sizes of the parental groups, the fertility of the hybrids, the frequency of matings between hybrids and members of the parental groups, the fertilities of different types of backcross hybrids, ecological differences among parental types and various hybrids, and the concomitant selective pressures on different parental and hybrid types.[62] According to Sturtevant, "Each of these is difficult to evaluate, so that one will practically always have to resort to indirect evidence, or in borderline cases to poorly founded guesses."[63]

Zoogeographical criteria were also difficult to apply in the classification of *Drosophila*. According to Sturtevant,

> This criterion [geographical distribution] is one that taxonomists usually emphasize. It is clearly helpful, but can never be decisive (unless made so by artificial definition). Our knowledge of distribution areas of Drosophila is still too imperfect in most cases to make possible a rigorous use of this principle.[64]

The evaluation of data concerning *Drosophila pseudoobscura* was problematic. Dobzhansky and his colleagues had undertaken an unprecedented census and cytogenetic analysis of natural populations of fruit flies. According to Dobzhansky,

> In the course of the investigation reported in this paper, the chromosomes of considerably more than 10,000 descendants of wild parents have been studied, particular attention being paid to the third chromosomes. It is fair to say that the gene arrangement in more than 20,000 third chromosomes and a somewhat smaller number of other chromosomes has been scrutinized.[65]

A number of gene arrangements which characterized either *Drosophila pseudoobscura* or *Drosophila persimilis* had never been detected in the chromosomes of members of the other species.[66] Those gene arrangements which were shared by both species were not necessarily evidence of hybridization, but could be interpreted as the inheritance from a common ancestral group. "To summarize," wrote Dobzhansky and Epling, "although we cannot assert that *D. pseudoobscura* never hybridizes in nature with *D. persimilis*, this hybridization is certainly not enough to constitute a channel for regular gene exchange."[67] However, despite the extent of Dobzhansky's field collections and cytogenetic analyses, his methods could give only indirect evidence of gene flow between groups of *Drosophila*. According to the rigorous requirements for taxonomic data put forward by Sturtevant this evidence could not be decisive for delimitating species.

The differences between Sturtevant and Dobzhansky were deeper than mere disagreements over the relative value of different forms of taxonomic data. These differences also marked fundamental differences over the nature and purpose of taxonomy. Dobzhansky and a number of other biologists viewed classification in explicitly evolutionary terms. Lower taxa, and particularly species, were defined as evolutionary units. For example, Dobzhansky defined species as, "...that stage in the evolutionary process, 'at which the once actually or potentially interbreeding array of forms becomes segregated in two or more separate arrays which are physiologically incapable of interbreeding.'"[68]

Sturtevant's rejection of Dobzhansky's taxonomic generalizations was not due to a rejection of Dobzhansky's evolutionary ideas, many of which Sturtevant shared.[69] Rather it was due to the difficulty of explicitly applying these evolutionary principles in the practice of taxonomy. Sturtevant was much more ready than Dobzhansky to view taxonomy as a relatively autonomous field with its own guiding principles. While not denying the importance of evolutionary theory, Sturtevant could deny its relevance to the practice of classifying organisms.

Contrary to the implications of Dobzhansky, Sturtevant was not the only taxonomist to be critical of Dobzhansky's evolutionary conception of species. W.B. Turrill noted that intersterility and interfertility were very broad terms, and that in practice these phenomena could rarely be exhaustively tested.[70] According to Turrill,

> The zoologists have, in theory but not always in practice, emphasized intersterility of groups as the most important specific criterion. Cytogeneticists tend to follow this zoological lead. The botanist knows that for plants such a criterion used primarily would lead to a special classification of little or no general use.*[71]

---

*Dobzhansky complained that he and Ernst Mayr were wrongly accused of defining species in terms of "intersterility." See: Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1951; Columbia Paperback Edition, 1964), p. 262. The complaint is justified. Both Dobzhansky and Mayr discussed a number of isolating mechanisms which maintained distinct species; hybrid sterility being only one of these. See: Dobzhansky, *Genetics*

In a more specific criticism of Dobzhansky, Turrill wrote,

> Dobzhansky (132) [i.e., *Genetics and the Origin of Species*] deals with many problems in which genetics throws light on the origin and nature of species. It is, however, doubtful whether some of his conclusions can apply so widely in the plant kingdom as to make them valid biologically. This is particularly true of his conception of a species. What the plant taxonomist considers with full justification as good species - what for general botanical purposes he must accept as species - are often not nearly such discrete units genetically or cytogenetically as postulated by Dobzhansky and other zoologists for animals. The view that species must be physiologically incapable of breeding one with another to produce fertile offspring can not be maintained in practice in plants to give a generally useful classification. It could be maintained consistently to give a special classification, possibly with interesting results, but these would be of limited use.[72]

A detailed discussion of the differences between Dobzhansky and Turrill on the nature of species is well beyond the scope of this dissertation. Both biologists wrote extensively on what is commonly known as the "species problem," or as Turrill preferred, the "species problems."[73] However, these differences in conceptions of species are aspects of different perspectives that Dobzhansky and Turrill took on the nature of taxonomy in general.

Dobzhansky took an explicitly evolutionary perspective on systematics and undoubtedly agreed with Julian Huxley that the major task facing systematists was the detection of "evolution at work." Although he was active in the work of classifying *Drosophila*,

---

and the Origin, (1937), pp. 231-232; Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), pp. 247-257. Nonetheless, the distinction between "intersterility" and "isolating mechanisms" as a whole, does not significantly change Turrill's criticism of Dobzhansky's conception of species.

Dobzhansky was primarily interested in the origin of species, not in the ordering of existing species. For Dobzhansky, the taxonomic categories used by systematists were "arbitrary," "subjective," and "convenient" creations of the systematist.[74] The "objective realities" of biology were Mendelian populations. The species was the one taxonomic unit of special interest to Dobzhansky because it could be closely identified with the "real" Mendelian population. According to Dobzhansky,

> Categories of classification are constructs devised by the student for his convenience; in this sense, they are sometimes called "arbitrary" or "subjective." Mendelian populations are spatio-temporal objects, and hence can be designated as "real" or "objective." But some taxonomic groupings, particularly species and races, are, by deliberate effort of the systematists, made to coincide as closely as possible with Mendelian populations of different orders.[75]

It was for this reason that Dobzhansky could note, "Species are tangible natural phenomena."[76] Dobzhansky could not provide systematists with a "yardstick" for determining the limits of species.[77] Nonetheless, while systematists had traditionally intuited the natural limits of species, Dobzhansky claimed that his evolutionary conception of species could replace intuition with an "analytical judgment."[78]

Turrill was not uninterested in evolutionary problems. Nonetheless, his taxonomic interests primarily involved problems of classification rather than problems of the origin of species. Perhaps for this reason Turrill, like Sturtevant, was able to draw a distinction between taxonomic concepts and the conceptions of evolutionary genetics. According to Turrill, although Dobzhansky's conception of species might be important for theoretical discussions of the origin of species, it was not necessarily useful for the practicing taxonomist.[79] Turrill went even further by suggesting that genetics and taxonomy were based on fundamentally different principles.[80] Genetics, like evolutionary theory, was based on a genealogical principle while taxonomy was based on a similarity principle.[81] Therefore, what the geneticist considered a species did not necessarily coincide with what the taxonomist "with full justification" determined to be a species.[82]

Species did not have the significance in Turrill's taxonomy that they had in Dobzhansky's. As Turrill suggested, the methods of genetics were to a large extent limited to the species and to subspecific categories.[83] The taxonomist, on the other hand, had to be concerned with a wider range of categories. According to Turrill, the species was like other taxonomic terms, primarily a category constructed on the basis of similarities and differences.[84] Species were more "natural" than other taxonomic groups only in the sense that they generally contained organisms which showed the greatest correlations of similarities and differences.[85]

The differences between Turrill and Dobzhansky were not simply differences between a "practical" taxonomist and a "theoretical" taxonomist. Turrill had a well-articulated theoretical foundation for his taxonomic views.[86] Turrill considered "usefulness" to be the primary attribute of a system of classification. A system could only be justified in terms of the purposes for which it was designed. A logical corollary of this theory was that there could be no single "natural" classification system. Naturalness could only be measured in terms of the amount of information conveyed by the system. To the extent that biologists had different classificatory needs, a number of equally valid systems of classification could be devised. In putting forth the idea of multiple systems of classification Turrill was not advocating complete "subjectivity" in taxonomy. First of all, it was not so much individual taxonomists who determined the usefulness of systems, but rather groups of biologists or disciplines. Furthermore, not all systems were equally valid. For any given set of purposes some systems would prove to be more useful than others. In particular, what was known as the "orthodox" system had proved historically to be the most general and useful classification system for the majority of biologists. In this sense it was the most "natural" system of classification.

This utilitarian theory of taxonomy was important for a number of reasons.* First, advocates of the theory, particularly W.B. Turrill

---

*In describing Turrill's ideas on the basis of taxonomy as the "utilitarian theory" I am not implying a direct connection between Turrill and the nineteenth century British Utilitarians. Both Turrill and J.S.L. Gilmour cited John Stuart Mill in justification for their theory of taxonomy. However, Gilmour, the more philosophical of the two biologists, was more closely allied with W.S. Jevons and a number of twentieth century logicians than with Mill. For example, see: J.S.L. Gilmour, "A Taxonomic Problem," *Nature* 139 (1937): 1040-1042. Both Gilmour and Turrill referred to their philosophy as "logical" as opposed to "phylogenetic." This term seems misleading since a phylogenetic system can be logical. In short, the term "utilitarian" emphasizes the major points of Turrill and Gilmour's theory: every classification must have a purpose, and the justification of a system of classification can only be given in terms of its usefulness in serving this purpose.

and his sometime colleague, J.S.L. Gilmour, were influential taxonomists who disseminated their ideas widely both in print and in discussions on taxonomy.[87] Second, and more importantly, a number of other taxonomists accepted at least some of the utilitarian ideas put forward by Turrill and Gilmour.[88] Finally, the utilitarian theory of classification provided a rational defense for experimental taxonomy while maintaining the integrity of established taxonomy.

The incorporation of the results of experimental taxonomy into the established system was problematic. According to Turrill, technical improvements in such descriptive morphological methods as microscopy had not significantly altered either taxonomic theory or practice.[89] The same could not be said for the techniques of experimental taxonomy. As Turrill noted,

> During the last three decades, several branches of biology, and especially cytology, ecology, and genetics, have shown phenomenal development. Perhaps their growth is largely due to their being biological, and not merely botanical or zoological, and also to the fact that they cannot be classified as morphology or physiology, but are intimate compounds of both. Their development has certainly brought them into closer and closer contact with taxonomy. Sometimes, indeed, there has been a rather violent impact.[90]

There were, Turrill suggested, indications that taxonomy had reached a "cross-roads" in its development.[91] Undeniably, cytology, ecology, and genetics provided potentially powerful methods of taxonomic analysis. Nonetheless, as in the case of *Phleum*, there could be considerable disagreement even among experimental taxonomists over the significance of the newly acquired experimental data.

Experimental taxonomy could be reconciled with established systems of classification, according to Turrill, if the utilitarian basis of taxonomy was accepted. The "orthodox" system of classification, or "alpha taxonomy" in Turrill's terms, remained established precisely because it had proved useful for biologists in general.[92] Alpha taxonomy was a general form of classification based primarily on comparative morphology that served as a foundation for all biological research. Primarily, alpha taxonomy served as a convenient means for identifying organisms.[93] However, it also served as a repository for a large amount of information about organisms.[94] Furthermore, alpha taxonomy served to indicate gaps in biological knowledge.[95] To the extent that the biology of particular groups of organisms was incomplete alpha taxonomy remained an active area of research. Because so many inductive generalizations could be derived from a properly constructed classification, even by itself alpha taxonomy consisted of much more than simply a catalog of dead specimens.[96]

Systematics, however, consisted of more than alpha taxonomy. Not only was taxonomy the foundation for all biological research, but it was also a meeting place for other biological disciplines.[97] As a summary of knowledge about plants and animals, Turrill saw taxonomy as a broad discipline which would ideally epitomize existing biological information. This "omega" taxonomy was only in an embryonic state during the 1930s and 1940s.[98] In fact, according to Turrill, biologists were still struggling toward a "beta" taxonomy.[99] To promote development toward the omega taxonomy biologists should freely experiment with new methods of taxonomic analysis and new theoretical systems of classification. Much of this experimentation had already occurred during the 1930s and 1940s. Aside from a large amount of experimental taxonomic data, a number of new theoretical systems of classification had been developed. According to Turrill, these systems were often useful for specific purposes and ought to be maintained as subsidiary classification systems.[100] However, unless they proved to be generally useful they ought not be incorporated into the established system.[101] The established alpha taxonomy and the subsidiary systems were compatible and necessary components of the emerging omega taxonomy. According to Turrill,

> There should be continued experimentation as to how the new kinds of data can be incorporated in and used in taxonomy. This free "experimenting taxonomy" need not be bound by the traditions of alpha taxonomy of which it will represent an easily modifiable fringe, in the main advancing but always ready to evacuate positions no longer tenable. By trials and errors this "experimenting taxonomy" will enable, one hopes, orthodox relatively stabilized taxonomy to incorporate new data gradually and cautiously, because of the need for conservatism and stabilization, from an alpha position towards a far off omega perfection of the classification of all (biological) knowledge.[102]

The utilitarian theory of taxonomy was not entirely convincing. In particular, those taxonomists who argued for an explicitly evolutionary basis for systematics criticized the utilitarian ideas.[103] Even some of those who accepted the utilitarian theory noted that the case for the theory was not effectively argued in the 1930s and 1940s.[104] While Turrill and Gilmour presented a rational argument for separating alpha taxonomy from evolutionary concepts, they failed to convincingly refute the contention of evolutionists such as Dobzhansky that the most useful classification could at the same time be phylogenetic. The proper relationship between evolutionary theory and taxonomy was not settled during the 1940s.[105] However, while Turrill and Gilmour failed to put forth irrefutable arguments for a utilitarian basis for alpha taxonomy, Turrill's failure to elaborate on the evolutionary aspects of omega taxonomy is open to even greater criticism. Turrill presented taxonomy as more than simply practical classification. Omega taxonomy, as a meeting place for other biological disciplines was, according to Turrill, to become the principle focus of future biology. Nonetheless, in his discussions of omega taxonomy Turrill never presented a detailed account of how evolutionary theory was to fit into omega taxonomy. Evolutionary relationships were presented as no more than one of a number of important forms of biological relationship with which omega taxonomy would deal. Such a contention put forward without considerable elaboration could not be taken very seriously during a period when evolutionary theory was being forcefully presented as the major unifying concept in biology.

Despite these criticisms, Turrill's idea of general and subsidiary systems based on the utilitarian theory of taxonomy provided a rational justification for experimental taxonomy. This justification gave experimental taxonomists broad latitude to explore a wide range of plant and animal relationships without being restricted by the constraints of established taxonomic practice and nomenclature. At the same time the "alpha" taxonomy which served as a foundation for all biological research was protected from ephemeral modifications. This protection was particularly important in the case of a number of new experimental nomenclatures that were developed during this period. As I will argue in the next chapter, it was not always clear whether these nomenclatures were meant to replace or to simply supplement the orthodox nomenclature of established taxonomy. Much of the rather polemical discussion over the "units of experimental taxonomy" might have been avoided had utilitarian theory of taxonomy been more widely accepted.

NOTES

CHAPTER FOUR

1. F.E. Clements, *Research Methods in Ecology* (Lincoln, Nebraska: University Publishing Company, 1905), p. 13.

2. H.M. Hall, "Heredity and Environment - As Illustrated by Transplant Studies," *Scientific Monthly* 35 (1932): 289-302, p. 291.

3. Ibid.

4. Jens Clausen, David D. Keck, and William M. Hiesey, "Experimental Taxonomy," *Carnegie Institution of Washington Yearbook* 35 (1936): 208-214.

5. Ibid., p. 209.

6. W.B. Turrill, "Experimental and Synthetic Plant Taxonomy," in: J.S. Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940), p. 69.

7. For another, somewhat similar, defense of comparative morphology in taxonomy, see: Ernest Brown Babcock, *The Genus Crepis: Part One: The Taxonomy, Distribution, and Evolution of Crepis*, [*University of California Publications in Botany*, vol. 21 (1947], p. 4.

8. Turrill, "Synthetic Plant Taxonomy," p. 47.

9. W.B. Turrill, "Taxonomy and Genetics," *Journal of Botany* 76 (1938): 33-39, p. 33; W.B. Turrill, "The Expansion of Taxonomy with Special Reference to the Spermatophyte," *Biological Review* 13 (1938): 342-373, p. 367.

10. Ibid.

11. Turrill, "Expansion," pp. 346-350; W.B. Turrill, "Taxonomy and Phylogeny," *Botanical Review* 8 (1942): 247-270, 473-532, 655-707, p. 496.

12. Turrill, "Expansion," p. 349.

13. Ibid., p. 346-350.

14. Ibid., p. 348.

15. See above: p. 78.

16. Edgar Anderson and W.B. Turrill, "Biometrical Studies on Herbarium Material," *Nature* 136 (1935): 986.

17. Edgar Anderson, "The Technique and Use of Mass Collections in Plant Taxonomy," *Annals of the Missouri Botanical Garden* 28 (1941): 287-292, pp. 291-292.

18. Edgar Anderson, "Mass Collections," *Chronica Botanica* 7 (1943): 378-380, p. 379.

19. E.M. Marsden-Jones, V.S. Summerhayes, and W.B. Turrill, "Special Herbaria as Adjuncts to Modern Botanical Research," *Journal of Ecology* 18 (1930): 379-383.

20. J.W. Gregor, "Experimental Delimitation of Species," *New Phytologist* 30 (1931): 204-217, p. 204.

21. Ibid., p. 206.

22. A.J. Wilmott, "Experimental Delimitation of Species," *Journal of Botany* 70 (1932): 49-50.

23. J.W. Gregor, "Correspondence," *Journal of Botany* 70 (1932): 154-155; A.J. Wilmott, "Correspondence," *Journal of Botany* 70 (1932): 155.

24. E.J. Salisbury, "The Ecologist Appreciates and Criticizes the Taxonomist," *Journal of Ecology* 27 (1939): 402-405.

25. Gregor, "Experimental Delimitation," p. 207.

26. For example, see: J.W. Gregor, "The Units of Experimental Taxonomy," *Chronica Botanica* 7 (1942): 193-196.

27. Gregor, "Experimental Delimitation," p. 210.

28. Gregor, "Correspondence," p. 155.

29. Gregor, "Experimental Delimitation," p. 212.

30. For example, see: Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), chaps. VIII and IX; Jens Clausen, David D. Keck, and William M. Hiesey, "The Concept of Species Based on Experiment," *American Journal of Botany* 26 (1939): 103-106.

31. Ibid.

32. Wilmott, "Experimental Delimitation," p. 50.

33. Wilmott, "Correspondence," p. 155.

34. Ibid.

35. Hedda Nordenskiöld, "Cytogenetic Studies in the Genus *Phleum*," *Acta Agriculturae Svecana* 1 (1945) 1-137.

36. Ibid., p. 124.

37. Ibid.

38. Ibid.

39. Ibid., pp. 125-126.

40. Gregor, "Experimental Delimitation," p. 209.

41. Nordenskiöld, "Cytogenetic Studies," pp. 125-126.

42. Ibid., pp. 123-126.

43. Ibid., p. 124.

44. Ibid., pp. 126-128.

45. Ibid., p. 127.

46. Ibid.

47. Th. Dobzhansky and Carl Epling, *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and its Relatives*, Carnegie Institution of Washington Publication No. 554 (1944).

48. Ibid., pp. 5-6.

49. A.H. Sturtevant, "Drosophila pseudoobscura," *Ecology* 25 (1944): 476-477.

50. Dobzhansky and Epling, *Contributions*, p. 6; Sturtevant, "Drosophila pseudoobscura," p. 476.

51. Dobzhansky and Epling, *Contributions*, p. 6.

52. Sturtevant, "Drosophila pseudoobscura," p. 476.

53. Ibid.

54. Dobzhansky, *Genetics and the Origin*, (1937), pp. 92-97.

55. A.H. Sturtevant, *The North American Species of Drosophila*, Carnegie Institution of Washington Publication No. 301 (1921), chaps. II, III, IV, VII, XIII, XIV; A.H. Sturtevant, *The Classification of the Genus Drosophila with Descriptions of Nine New Species*, University of Texas Publications No. 4213 (1942), pp. 17-21.

56. Dobzhansky and Epling, *Contributions*, pp. 9-10.

57. Ibid., p. 7.

58. Sturtevant, *Classification*, p. 32.

59. Theodosius Dobzhansky, *Genetics and the Origin of Species*, 3rd edition (New York: Columbia University Press, 1951; Columbia Paperback Edition, 1964), p. 263.

60. Ibid.

61. Sturtevant, *Classification*, p. 32.

62. Ibid.

63. Ibid.

64. Ibid.

65. Dobzhansky and Epling, *Contributions*, p. 54.

66. Ibid., pp. 8-9.

67. Ibid., p. 9.

68. Dobzhansky, *Genetics and the Origin*, (1937), p. 312.

69. For example, see: A.H. Sturtevant, "Essays on Evolution. III. On the Origin of Interspecific Sterility," *Quarterly Review of Biology* 13 (1938): 333-335.

70. W.B. Turrill, "The Ecotype Concept: A Consideration with Appreciation and Criticism, Especially of Recent Trends," *New Phytologist* 45 (1946): 34-43.

71. W.B. Turrill, "Taxonomy and Phylogeny," p. 519.

72. Ibid., p. 522.

73. For Turrill's views on species see: Turrill, "Expansion," p. 352; Turrill, "Taxonomy and Genetics," p. 34; Turrill, "Taxonomy and Phylogeny," pp. 480-482, 519-524. For Dobzhansky's views on species see: Th. Dobzhansky, "A Critique of the Species Concept in Biology," *Philosophy of Science* 2 (1935): 344-355; Th. Dobzhansky, "What is a Species," *Scientia* 61 (1937) 280-286; Dobzhansky, *Genetics and the Origin of Species*, (1937), chap. X; (1941); chap. XI; (1951), chap. IX.

74. Dobzhansky, *Genetics and the Origin*, (1937), p. 306; (1951), p. 256.

75. Dobzhansky, *Genetics and the Origin*, (1951), p. 256.

76. Ibid., p. 263.

77. Ibid., p. 264.

78. Ibid.

79. Turrill, "Taxonomy and Phylogeny," p. 252.

80. Ibid., p. 253.

81. Ibid.

82. Ibid., pp. 252-253.

83. Turrill, "Expansion," p. 355; Turrill, "Taxonomy and Phylogeny," p. 519.

84. Turrill, "Taxonomy and Phylogeny," p. 480.

85. Ibid.

86. Turrill, "Expansion," pp. 345-346; Turrill, "Taxonomy and Phylogeny," pp. 676-684; J.S.L. Gilmour and W.B. Turrill, "The Aim and Scope of Taxonomy," *Chronica Botanica* 6 (1941): 217-219.

87. For example, see: Turrill, "Expansion," pp. 345-346; Turrill, "Taxonomy and Phylogeny," pp. 676-684; Gilmour and Turrill, "Aim and Scope;" J.S.L. Gilmour, "A Taxonomic Problem," *Nature* 139 (1937): 1040-1042; J.S.L. Gilmour, "Taxonomy and Philosophy," in: J.S. Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940); J.S.L. Gilmour, "The Development of Taxonomic Theory Since 1851," *Nature* 168 (1951): 400-402 [note: erratum, p. 500].

88. For example, see: J.W. Gregor, "The Units of Experimental Taxonomy," *Chronica Botanica* 7 (1942): 193-196, p. 193; J.S.L. Gilmour and J. Heslop-Harrison, "The Deme Terminology and the Units of Micro-Evolutionary Change," *Genetica* 27 (1954): 147-161, p. 148; J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: William Heinemann, Ltd., 1953); J.S.L. Gilmour and S.M. Walters, "Philosophy and Classification," in: W.B. Turrill, ed., *Vistas in Botany, Vol. 4, Recent Researches in Plant Taxonomy* (London: Pergamon Press, 1964), pp. 2-9.

89. Turrill, "Expansion," p. 344.

90. Ibid.

91. Ibid.

92. Ibid., pp. 346-350.

93. Ibid., p. 343.

94. Ibid., p. 346.

95. Ibid., p. 343.

96. Gilmour and Turrill, "Aim and Scope."

97. Turrill, "Expansion," p. 369.

98. Ibid., pp. 369-370.

99. Ibid., p. 347.

100. Turrill, "Expansion," pp. 369-370; Gilmour and Turrill, "Aim and Scope," p. 219.

101. Ibid.

102. Turrill, "Expansion," p. 370.

103. Ernst Mayr, *Principles of Systematic Zoology* (New York: McGraw-Hill Book Co., 1969), pp. 68-69. While accepting the need for several kinds of classification systems, George Gaylord Simpson argued that the phylogenetic system is not only the best but also the most practical form of classification. Furthermore, Simpson was so opposed to the utilitarian claim that usefulness could be equated with naturalness that he accused J.S.L. Gilmour of being "illogical" for suggesting this equation. See: George Gaylord Simpson, *Principles of Animal Taxonomy* (New York: Columbia University Press, 1961), pp. 25-28, 57. It should be

noted that in reference to kinds of classification systems Gilmour and Turrill suggested replacing the terms "natural" and "artificial" with the terms "general" and "special." See: Gilmour and Turrill, "Aim and Scope," p. 218.

104. R.E. Blackwelder who generally agreed with the taxonomic ideas of Turrill and Gilmour suggested that in terms of convincing large numbers of followers Turrill and Gilmour were not successful. See: R.E. Blackwelder, *Taxonomy*, (New York: John Wiley & Sons, Inc., 1967), p. 346.

105. See my discussion of the controversy over phylogeny and taxonomy in this dissertation, pp. 20-25.

Chapter Five: Experimental Systems of Classification

I have argued that a major impetus for doing experimental taxonomy was the desire to replace what were considered "subjective" traditional taxonomic methods with rigorous objective methods. Although there was considerable enthusiasm for the introduction of "objective" methods into taxonomy, the implementation of these methods was problematic. Even among taxonomists who used the same cytological, ecological, and genetic methods there was disagreement over the interpretation of data and the relative importance of different kinds of data. Equally problematic was another important aspect of experimental taxonomy: revisions in nomenclature.

Along with the claim that descriptive or observational taxonomy was not rigorously objective, a number of taxonomists felt that the established categories of taxonomic nomenclature were, themselves, imprecise and incapable of characterizing complex organismal relationships. In response to this, a number of alternative terminologies were proposed to systematize the findings of experimental taxonomic research. Despite the popularity that many of these "units of experimental taxonomy" attained with certain groups of biologists during the 1930s and 1940s, few of the new systems gained widespread acceptance.[1] Similar to the methods of experimental taxonomy, the units of experimental taxonomy faced criticism not only from critics of experimental taxonomy, but from advocates as well.

The implementation of new terminologies was complicated by a number of factors. First, the new systems were not complete revisions of the established taxonomic nomenclature. Experimental taxonomy found its greatest, some claimed its only, application at about the species level. The new systems of classification were, therefore, limited to sets of infraspecific (or at most infrageneric) categories. While some advocates of the new terminologies argued that eventually experimental taxonomy would force a complete revision of taxonomic nomenclature, critics contended that taxonomy, as a whole, was barely affected by changing conceptions of species.[2] Second, it was often not clearly stated whether the new terms employed by experimental taxonomists were to be used for "practical" classification of organisms, for theoretical discussions about population dynamics or both. One result of this confusion was rather stale arguments over the "reality" of various taxonomic units.[3] Finally, the relationship between the newly proposed units and the established nomenclature was rarely explicitly stated. It was often not clear whether advocates of the new terminologies intended to replace or simply to supplement established taxonomic categories. Underlying all of these problems was the fact that the interests of taxonomists were hardly homogeneous. Terms that some workers found tremendously useful for particular classificatory problems appeared redundant or superfluous to other biologists.

In retrospect few of the units of experimental taxonomy were successful in terms of longevity.[4] Most of the terminologies that will be discussed in this chapter have only limited currency. For example, while the term "deme" is still occasionally used by population biologists as a synonym for "population," the extended "deme" terminology which provided an exhaustive classification of different kinds of populations is apparently obsolete.[5] Even the more successful terminologies such as Turesson's genecological system exist only in rather attenuated forms.

The historical analysis of obsolete terms and concepts is problematic. Briefly, two methods of evaluation present themselves. In the past, a number of commentators have traced the conceptual lineages of currently accepted ideas about species.[6] The valid historical question that such studies attempt to answer is: "How did present biological concepts develop from those of the past?" The problem with many such studies is that they tend to ignore those ideas that were not the immediate precursors of current concepts. Such historical accounts often view past scientific activity solely from the narrow perspective of present scientific interests. A second historical method attempts to view obsolete concepts from the perspective of the problems for which they were devised as solutions. In using this method I am explicitly attempting to analyze concepts as rational attempts to solve particular problems. In evaluating the units of experimental taxonomy the question that

I pose is: "Why during the 1930s and 1940s did experimental taxonomists feel compelled to develop new taxonomic units?"

In answering the above question I stress the variety, not only of biological problems facing experimental taxonomists, but also the variety of perspectives that experimental taxonomists brought to bear on these problems. Because both the problems and the proposed solutions were so diverse, it is perhaps not surprising that few of the experimental terminologies were widely accepted. Nonetheless, even the less "successful" systems were widely discussed. As a number of taxonomists of the period noted, the outlines of future taxonomy, what W.B. Turrill called "omega" taxonomy, were not clearly visible.[7] Only by constant experimentation with new systems would a more serviceable taxonomy come into being. This sentiment was eloquently expressed by W.H. Camp, an advocate of nomenclatorial reform. In discussing what he considered to be the inadequacies of the present nomenclature Camp noted,

> Our present system of nomenclature was designed to fit a concept of static genera and species. Tinker with it as we will, we cannot re-tailor this mouldy shroud into something which will serve as an adequate nomenclatorial covering for the complex, living groups which we are now beginning to realize must be defined. No one knows exactly what this system will be; as yet one can see only a general outline, for our knowledge is too scant to permit a filling in of all the details...The new system of nomenclature will have to be cut of a different cloth from the old and tailored so as to express, in descriptive terms, a vast array of most dynamic and involved situations. The basic pattern will be as complex as life itself.[8]

Attempts to replace the "mouldy shroud" of established nomenclature with one "tailored" from the cloth of genetics, cytology, and ecology began early in the twentieth century. For example, as early as 1916 the Dutch botanist J.P. Lotsy proposed a genetic definition of species.[9] According to Lotsy, the term "species" was used, "...*to designate a group of individuals of identical constitution, unable to form more than one kind of gametes.*"[10] As such, this unit certainly did not correspond to the species which taxonomists used. Lotsy termed the taxonomic species, a "Linneon." A Linneon was, for Lotsy, a purely morphologically defined unit of similar organisms.[11] Lotsy's species definition was closely tied to his evolutionary ideas. According to Lotsy, evolution had occurred by the continual hybridization of pure species. In Lotsy's words,

> Linneons arise by crossing and are gradually exterminated by the struggle for life...All this is probably paralleled, en grand, in the appearance and extinction of the great classes. A cross between two greatly differing gametes gives rise to a great diversity of new forms which we group into families, genera, and Linneons..."[12]

Lotsy maintained the general ideas on evolution expressed in his 1916 book until his death. However, later in his career he abandoned the idea of completely homogeneous species. In an address delivered in 1930, Lotsy used the term "syngameon" to refer to a group of habitually interbreeding organisms.[13] While members of a syngameon shared a common "character-complex" they might differ in minor details.[14] The relative stability of taxonomic groups could be explained, according to Lotsy, by the habitual endogamy of the syngameons. Diversity was explained by the occasional hybridization of different syngameons, through which entirely new groups were formed.

Though Lotsy's evolutionary views were not widely accepted his conception of species apparently influenced Theodosius Dobzhansky, who approvingly cited Lotsy as a pioneer in developing the dynamic conception of species.[15] Dobzhansky and Lotsy shared little common ground concerning the mechanism of evolution. Furthermore, Lotsy's emphasis on genetic homogeneity was completely foreign to Dobzhansky's idea of genetically diverse populations. Nonetheless, Dobzhansky agreed with Lotsy's contention that species be considered in evolutionary genetic terms.

Following Sewell Wright, Dobzhansky envisioned the organic world as a sort of topographical landscape.[16] This landscape consisted of "adaptive peaks" separated by "adaptive valleys." Various gene combinations were scattered about on these hills and valleys, although the actual number of such combinations was but a miniscule fraction of the total possible combinations which, according to Wright, were more numerous than the electrons in the universe. "Furthermore," according to Dobzhansky,

> the existing gene combinations are by no means scattered at random through the entire field of the possible ones. On the contrary, the gene combinations are grouped together into more or less compact arrays, each array being attached, to use the symbolic picture of Wright, to one or to several related 'adaptive peaks' in the field. The arrays are therefore complexes of fairly similar gene combinations that make their carriers fit to survive in the environments that are encountered in nature. The 'adaptive valleys' intervening between the peaks correspond to discordant gene

> combinations, most of which would be nearly or completely inviable. A promiscuous formation of gene combinations would give mainly a mass of freaks, something like the primeval monsters in the poetic myths of Empedocles and Lucretius.[17]

Species, according to Dobzhansky, corresponded to arrays of gene combinations grouped around the adaptive peaks. The integrity of these groups was maintained both by habitual interbreeding and by natural selection against discordant gene combinations.

Dobzhansky's discussions of the nature of species were well-received by a number of biologists.[18] While Dobzhansky's emphasis on the dynamic adaptive nature of Mendelian populations was particularly appropriate for theoretical discussions on evolution, the discussions *were* theoretical. As Dobzhansky admitted, his conception of species could not provide a "yardstick" for delimiting species.[19] Although he, himself, was involved with the practical problems of classification, Dobzhansky could rather contemptuously dismiss those who, on practical grounds, were unwilling to accept his abstract notion of species. According to Dobzhansky,

> Some systematists are loath to accept the possibility that species may not be determinable in dead preserved specimens, contending that a classification based on such an assumption will cease to be convenient. A discussion of this topic is hardly necessary here; we may only remark that the decision is here contingent on whether one is or is not satisfied with a classification that serves no other purpose than that of a well-ordered catalogue.[20]

Those systematists who attempted to implement Dobzhansky's conception of species sometimes found themselves in a quagmire of fine distinctions. For example, in a widely cited paper the

American taxonomists, W.H. Camp and C.L. Gilly classified a number of different kinds of species using both morphological and genetic criteria.[21] According to these biologists the "new systematics" or "biosystematy" had demonstrated that species were not uniform units.[22] While the old taxonomic species had served well enough as part of a "filing system," the biosystematist could no longer be satisfied with a classification based solely on outward appearance. According to Camp and Gilly, biosystematy sought not only to classify, but also to study the causes of organic diversity. To a large extent biosystematy could be equated with experimental taxonomy, although Camp and Gilly emphasized that the consistent use of appropriate concepts was just as important as the use of experimental methods.[23] Modern genetics, exemplified by Dobzhansky's *Genetics and the Origin of Species*, provided a dynamic concept of species which presented species as populations.[24] The use of this concept, along with rigorous field observations and experimental methods would, according to Camp and Gilly, allow biosystematists to delimit "natural biotic units" and also to apply a nomenclature that would express the dynamic relationships within these groups.[25]

While they were satisfied with the theoretical conception of species that Dobzhansky had presented in evolutionary genetic terms, in the field, Camp and Gilly argued, twelve kinds of biological species might be encountered (Table 1).[26] The classification of

Table 1. Bisystematic Units (From Camp and Gilly).

Homogameon	A morphologically and genetically homogeneous species, all members being interfertile.
Phenon	A phenotypically homogeneous species containing some intersterile segments.
Paragameon	A species with relatively little morphological or genetic variation, but containing some aberrant individuals. All members are interfertile.
Dysploidion	A species composed of morphologically similar members of a dysploid series.*
Euploidion	A sexually reproducing species which is composed of segments making up a euploid series.**
Alloploidion	A species derived via allopolyploidy; its members are usually highly variable but interfertile.
Micton	A species, generally widely distributed, resulting from hybridization between two or more species.
Rheogameon	A "ring species" exhibiting interfertility between segments of the ring, but with marked morphological divergence along the ring.
Cleistogameon	A species which reproduces, in part, by self-fertilization.
Heterogameon	A species made up of races which produce morphologically stable populations, but whose races can cross to produce several types of viable and fertile offspring.
Apogameon	A species containing both sexually and asexually reproducing individuals.
Agameon	A species containing only asexually reproducing individuals.

*The term "disploidy" refers to a chromosome series which does not form an array of perfect multiples of a basic number.

**The term "euploidy" refers to a chromosome series which forms an array of exact multiples of a basic number.

kinds of species prepared by Camp and Gilly illustrated the generally held view that species were complex entities that defied simple definition. Plant species, in particular, appeared to be complex assemblages and the biosystematic units reflected the importance that plant taxonomists placed on polyploidy, hybridization, and various forms of asexual reproduction. It is not clear from Camp and Gilly's article whether the two botanists intended for the biosystematic units to become part of the formal taxonomic nomenclature. However, it is clear that Camp and Gilly realized the difficulties involved in nomenclatorial reform. As the two noted, their system of categories could be attacked either for placing too much emphasis on the genetic aspects of species or for placing too much stress on comparative morphology.[27] Furthermore, as Camp noted several years later, biosystematists could be criticized for cluttering the biological nomenclature with new terms.[28] Camp, however, had little sympathy for these critics; the living world was complex and a reformed nomenclature might need to be "as complex as life itself."[29]

Camp and Gilly considered the idea that species were dynamic populations to be a concept capable of unifying biosystematics. However, other biologists pointed out that the term "population" was hardly standardized and was being used imprecisely. This was particularly problematic, according to J.S.L. Gilmour and J.W. Gregor, because so much attention was being devoted to questions of microevolution and population dynamics.[30] Populations could be defined in biogeographical, ecological, or genetic terms. While conceptually these might be three overlapping aspects of populations, in practice, biologists rarely investigated the biogeographic, ecological, and genetic characteristics of populations in a single study. Therefore, it was often not clear how the general term "population" was being used.[31] The result, according to Gilmour and Gregor, was confusion in the literature.

To avoid this confusion, Gilmour and Gregor proposed a subsidiary system of classification based on the characteristics of populations. The term "deme" would be retained as a general designator for any group of closely related organisms.[32] The prefixes "gamo-," "eco-," and "topo-," would be added to this stem to designate genetically, ecologically, or geographically defined populations. In contrast to Camp and Gilly, Gilmour and Gregor explicitly denied any connection between the "deme" terminology and orthodox taxonomic nomenclature.[33] The use of this subsidiary set of terms was to be restricted to discussions in the new field of population biology.

During the 1940s and early 1950s the deme terminology was greatly expanded by Gilmour and J. Heslop-Harrison.[34] In all, the two biologists described over thirty kinds of populations. While this detailed system was discussed, and met with approval from a number of biologists, the deme system, as a whole, failed to gain widespread acceptance.[35] Evolutionary theorists, who Gilmour and his colleagues claimed ought to find the system useful, largely ignored the fine distinctions enumerated by the deme terminology.[36] In terms of conveying information about organismal groups, the deme-units were much more precise than the general term "population." However, evolutionary theorists of the 1930s and 1940s were less interested in developing a theory capable of dealing in detail with all of the complex genetic and ecological relationships categorized by Gilmour and his colleagues, than in presenting a general picture of evolutionary dynamics. Such evolutionary theorists as Sewell Wright, Theodosius Dobzhansky, and Ernst Mayr, who were particularly interested in population dynamics used the term "population" in a very general and loosely defined way.[37] Heslop-Harrison, himself, noted the different perspectives taken by biologists on the proliferation of taxonomic terms. While some experimental taxonomists were interested in classifying the complexities of organismal groups, other biologists might find this procedure futile. According to Heslop-Harrison, "Recently there has been a tendency among more radically-minded evolutionists to deplore the 'taxonomic' attitude in their science - the attitude which seeks to detect, define and classify 'types,' be they 'eco-,' 'topo-,' 'cyto-,' or of some other form, rather than study processes."[38] While Heslop-Harrison admitted to being sympathetic to the idea of taxonomy without "typification," he, along with a number of other experimental taxonomists, saw the nomenclatorial experimentation of the 1930s and 1940s as a necessary process leading to an "omega" taxonomy.[39]

Much less detailed than the extensive classification of populations proposed by Gilmour and his colleagues, was an earlier attempt to distinguish populational units by the botanist B.H. Danser. In 1929, Danser defined three new terms to express the genetic relationships within species.[40] According to Danser, a "comparium" consisted of a group of individuals having the capacity to hybridize ("Bastardierungsmöglichkeit") regardless of the fertility of the hybrid offspring.[41] A "commiscuum" was a group of individuals capable of interbreeding to produce fertile offspring ("Vermischungsmöglichkeit").[42] The smallest group which Danser recognized was the "convivium."[43] A convivium was a group of freely interbreeding individuals which was more or less isolated and morphologically distinguishable from other such groups. None of Danser's terms could be precisely equated with taxonomic species. Furthermore, although Danser's work was cited by a number of taxonomists, his categories appeared highly problematic. According to W.B. Turrill, "Detailed criticism of this scheme is difficult because the author [Danser] gives practically no actual examples of its working. The whole scheme appears very hypothetical, though from the nature of the criteria used it should be almost entirely experimental."[44] Turrill suggested that Danser's general ideas might be an important step toward the comprehensive "omega" taxonomy of the distant future. Nonetheless, he noted two major problems for the immediate implementation of Danser's system.[45] First, while two organisms could be shown to be part of the same commiscuum or comparium through hybridization experiments, negative results from such experiments would not constitute acceptable proof that the organisms were of different comparia or commiscua. Second, according to Turrill, Danser had not carefully considered the problems of self-sterility and apomixis in his system.*

Turrill may have missed the intent of Danser's system. It is not clear that Danser had envisioned his units as categories for taxonomists to use in the practical business of constructing classifications for particular groups of organisms. In a much more extensive paper written during the early 1940s, but published posthumously in 1950, Danser suggested that the terms he had introduced in 1929 might only have theoretical significance.[46] As Danser's editors lamented, the 1950 paper was a rough draft which undoubtedly would have been revised had the author lived longer.[47] Nonetheless, the editors noted, the general ideas expressed in Danser's "A Theory of Systematics" had developed much earlier in Danser's career.

According to Danser, his paper was theoretical in the sense that it was "...a speculation on the scientific foundations of systematics."[48] As such, Danser explicitly excluded from his

---

*The term "apomixis" refers, in general, to any form of asexual reproduction.

discussion any considerations of taxonomic practice. In Danser's words,

> Systematics as a science must refrain from concessions to practice which are at variance with its scientific character; at any rate this must not be considered as its scientific task...Also all applied botany lies outside systematics as a science, as well as nomenclature and other matters which in practical life are taken as belonging to systematics because they belong to the activities of the systematist.[49]

If this statement accurately describes Danser's view on systematics then his lack of examples and the difficulties in applying his categories in practice were irrelevant to his purposes. Similar to Dobzhansky, Danser was not developing categories that the working taxonomist could apply in day to day work, but rather a way of conceptualizing the group relationships found in nature. Convivia, commiscua, and comparia were not so much things to be discovered in nature, as theoretical terms used to express genetic relationships among organisms. These terms were embedded in a loosely articulated theoretical system that Danser clearly had not fully developed at his death.

According to Danser, a natural system of classification rested on two bases. The classification of groups higher than species rested on typology, or a theory of types.[50] Each group of organisms could be characterized by an abstract "ground-plan" or "type." The ground-plan for a group consisted of an "imaginary" organism that combined all of the characteristics common to that group.[51] The classification of species and subspecific groups was, on the other hand, based not on typology, but rather entirely on genetic concepts. According to Danser,

> Genetics has proved that the classification of the species to groups of higher rank is a completely different matter to classification of species to smaller units. The former is almost entirely outside genetics, the latter lies completely within its scope, at any rate it cannot to any scientific purpose be realized or explained without genetic methods.[52]

The classification of species and lower groups was to be based on the theoretical framework of gene transfer between populations, that is, in terms of convivia, commiscua, and comparia.

The relationship between the two forms of systematics proposed by Danser was never clearly delineated. While one might have concluded that the typological and genetic systems were radically different, Danser gave some hints that this was not so. Species were to be thought of in group or populational terms, but they were also, according to Danser, "metamorphoses" of the ground-plans of the higher categories.[53]

Although Danser's 1929 paper was cited by a number of experimental taxonomists and Danser himself showed an interest in experimental taxonomy, his later theoretical paper seems to have been virtually ignored.[54] Part of this lack of recognition may be due to the fact that Danser's support of "typology" was uncongenial to the views of a number of systematists of the period. The article was not only highly abstract but also obviously not in a polished final form. The highly abstract nature of the paper in itself may have seemed foreign to experimentalists. Most experimental taxonomists were not so much interested in reforming systematics as a whole, as in rigorously analyzing the lowest taxonomic categories. Finally, many experimental taxonomists wanted taxonomic units that could be readily identified with groups of organisms as they were found in the field.

The difficulty of applying a highly abstract theoretical system to the classification of groups of organisms was a problem for other experimental classification systems, as well. In the case of the "genecological" system, proposed by Göte Turesson, the units were redefined in less theoretical terms and were subsequently widely used to categorize natural groups of organisms.

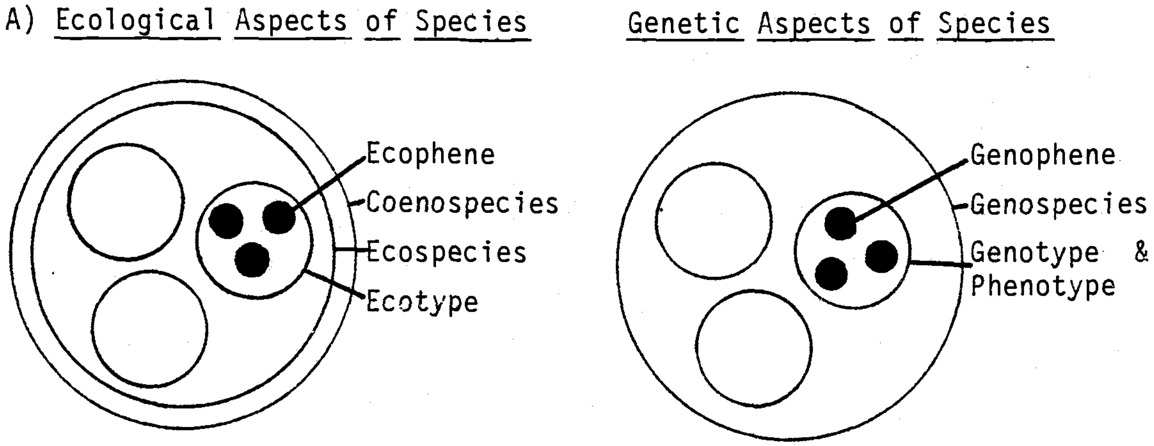
Turesson's genecological units were undoubtedly the alternative system of nomenclature used most widely by experimental taxonomists during the 1930s and 1940s. The association between Turesson's system and experimental taxonomy extended back to the very origin of the genecological terms. Turesson, himself a leading innovator in experimental botany, introduced the terms in the concluding chapter of an extended technical report which detailed the results of numerous transplant experiments.[55] The genecological terminology was used extensively by a number of prominent experimental taxonomists, including J.W. Gregor, Hedda Nordenskiöld, Jens Clausen, David Keck, and William Hiesey. The relationship between experimental taxonomy and Turesson's nomenclature was so close that at least one commentator suggested that the genecological terms were the "units of experimental taxonomy."[56] Furthermore, the terms were widely discussed both among advocates and critics of Turesson's system.[57] Even Turesson's severest critics conceded that, at the very least, the genecological terms and the concepts underlying them were a major impetus to experimental studies in taxonomy.[58]

Both the popularity of Turesson's system and the criticism that it received were due in part to the attempt to incorporate concepts from both genetics and ecology within the same system. Such a combination harmonized well with the interdisciplinary perspectives of many experimental taxonomists. Nonetheless, the integration of genetic and ecological concepts was never fully made. Furthermore, the system remained somewhat ambiguous because the definitions of terms were never fully standardized. Turesson himself used the terms in different ways during his career. This ambiguity was exacerbated by the use of the terms both for theoretical discussions of population dynamics and the practical activity of classifying specimens. Finally, the exact relationship between the genecological nomenclature and the orthodox nomenclature was never clearly made. In the writings of some experimental taxonomists the terms appeared to be synonymous with orthodox categories while in other writings the genecological units were presented as subsidiary to the established nomenclature.

When Turesson introduced his terminology in two papers published in the journal, *Hereditas*, in 1922, he made a fairly clear distinction between ecological and genetical concepts.[59] In fact, the hybrid term, "genecology," was not introduced until the following year.[60] According to Turesson, while species had been extensively studied experimentally from the perspective of genetics, the same was not true of research from an ecological perspective.[61] Geneticists had quite fruitfully worked with the conception of species as "genotype compounds."[62] However genetics could not explain the "bridgeless gaps" found between species, nor could it explain how changes in the non-living world brought about the formation of new genotype compounds. According to Turesson, the genotype compounds making up species were adaptively shaped by the selective action of the environment. This aspect of the species problem, according to Turesson, was not fundamentally genetic, but rather ecological. As Turesson stated,

> The species problem is thus seen to be in a large measure an ecological problem. As such it has hitherto remained almost unattacked from an experimental point of view. While at present the genetical side of the problem is fairly well understood, we have only to a slight extent been able to arrive at an understanding of the ecological questions involved. So much appears certain, however, that the Linnean species are units of the same importance ecologically as their constituent elements are genetically.[57]

According to Turesson species could conceptually be analyzed into genetic and ecological compounds and the separation between these aspects ought to be maintained. Since a terminology expressing the genetic aspects of species was already well-established, Turesson proposed a set of parallel ecological terms (Fig. 7).[63]



B)

Ecological Terms	Genetic Terms
Coenospecies	Genospecies
Ecospecies	
Ecotypes	Genotypes & Phenotypes
Ecophenes	Genophenes

Figure 7. Turesson's original conception of the genetic and ecological aspects of species. A) Symbolic representation of parallels between ecological and genetic aspects of species. B) Hierarchy of terms indicating parallels between ecological and genetic terms. (From Turesson).

According to Turesson, species could be envisioned as fairly discrete collections or compounds of genotypes.[64] The discreteness of these groups could be explained in terms of ecological limitations. The total range of genotype combinations could never be realized in nature because of the selective action of the environment. Ecologically, therefore, a species could be conceived as a genotype compound which had been limited and defined by its environment. This genotype compound, as it was realized in nature, Turesson termed the "ecospecies."[65]

That the ecospecies did not represent the full potential of the genotype compound could easily be demonstrated experimentally. Brought under cultivation, wild plants showed a wide range of previously unexpressed variation, much of which was demonstrably heritable. This variation could be further enhanced by artificially hybridizing naturally distinct groups. This evidence, according to Turesson, indicated that the ecospecies, unfettered by natural restraints, was a potentially much more varied entity than that found in the field.[66] Under a range of hypothetical habitats the ecospecies could express a great deal of hidden variation. The sum total of the genetic possibilities of a species Turesson termed a "genospecies."[67] A parallel ecological entity, the "coenospecies," represented all the potential manifestations of the genospecies.[68] It ought to be stressed that both of these entities were theoretical in the sense that neither could be completely determined empirically or experimentally.

Below the level of ecospecies Turesson recognized a number of more concrete genetic and ecological units. The environmental conditions that defined the limits of the ecospecies were rarely homogeneous. Therefore, most ecospecies were broken up into what could vaguely be referred to as varieties. A more concrete ecological expression for these subunits was the "ecotype," which Turesson defined as, "...the product arising as a result of the genotypical response of an ecospecies to a particular habitat..."[69] Ecotypic differentiation was illustrated by the dramatic differences which Turesson claimed he had found in conspecific plants that were growing in very different habitats. These differences were, according to Turesson, due to the selective molding of particular genotypes by specific sets of environmental conditions. Apparently influenced by Lotsy's conception of genetically homogeneous small species, Turesson, in 1922, pictured each ecotype paralleled by a particular genotype. Nonetheless, it seems questionable whether he envisioned either genotypes or ecotypes in static or "typological" terms as later critics claimed.[70] Although Turesson stressed the distinctness of different ecotypes and did not recognize the "intergroup variation" or "clines" that later biologists emphasized, he was aware of individual variation. As Turesson pointed out in his 1922 paper, each genotype was capable of producing a variety of reactions or "genophenes" under different conditions.[71] Similarly, ecotypes, under extreme habitat conditions were capable of responding with adaptive modifications that Turesson called "ecophenes."[72]

Turesson again emphasized the ecological perspective of his system in a slightly later paper entitled "The Scope and Import of Genecology."[73] According to Turesson, genecology was to be a distinct subdivision of ecology. Neither autecology, the study of the relationship between the plant and environment, nor synecology, the study of plant communities, adequately studied the species as an ecological unit. According to Turesson,

> From the point of view of genecology the Linnean species represents a genetically complex community, the distribution and the composition of which is largely determined by ecological factors and the genotypical constitution of the individuals composing the species-community. The Linnean species represents as such a much important ecological unit, to which the name *ecospecies* has been given by the present writer. The hereditary variation within the ecospecies and the relation of this variation to habitat conditions furnished one of the most important problems in genecology.[74]

While Turesson had emphasized the distinction between the ecological and genetic aspects of species, already by 1923 this distinction was becoming blurred in his writings. First of all, genecology, in contrast to autecology, was to consider only *heritable* variation. Second, genecology, as a basically experimental science, was to utilize breeding experiments as well as transplant experiments.

In his later discussion of genecology Turesson placed little, if any, emphasis on the distinction between the genetic and ecological aspects of species. Consequently, the units which Turesson had originally described in ecological terms were, by

1930, defined in a combination of ecological and genetic terms. Some of the units were, in fact, defined primarily in genetic terms. For example, Turesson described the ecospecies as "...an amphimict-population the constituents of which in nature produce vital and fertile descendants with each other giving rise to less vital or more or less sterile descendants in nature, however, when crossed with constituents of any other population."*[75] According to Turesson the ecospecies could, in some cases, be identified with taxonomic species.

Turesson also made a major modification in his conception of the coenospecies. The coenospecies had been originally presented as a theoretical entity representing the total ecological potentials of a given genotype-compound. By 1930, however, Turesson defined the coenospecies as a much more concrete entity. According to Turesson, a coenospecies represented "...a population-complex the constituents of which group themselves in nature in species units of lower magnitude on account of vitality and sterility limits having all, however, a common origin so far as morphological, cytological or experimental facts indicate such an origin."[76] As in the case of ecospecies, coenospecies could, in some cases, be identified with taxonomic species or groups of species.

The changes Turesson made in his genecological system were

---

*The term "amphimixis" refers to sexual reproduction or more specifically, to crossbreeding.

significant. In their modified form the genecological units were widely discussed and used by experimental taxonomists. While experimental taxonomists occasionally mentioned Turesson's earlier definitions, the later definitions were the ones almost universally referred to.[77] Turesson's genecological system, as defined in 1929, appealed to experimental taxonomists for a number of reasons. First, by minimizing the abstract theoretical aspects of the genecological units, Turesson presented experimental taxonomists with what they considered to be a more "precise" set of definitions.[78] Coenospecies and ecospecies were no longer "hypothetical" units but rather "real" entities.[79] More importantly, Turesson's later emphasis on genetic criteria made his units more readily amenable to experimental delimitation. The "sterility-fertility" criterion, testable by breeding experiments, was emphasized by a number of experimental taxonomists.[80] Finally, by making his units more concrete Turesson presented experimental taxonomists with a set of what appeared to be rigorously determinable counterparts to such traditional taxonomic units as species and subspecies.[81]

Those experimental taxonomists who followed Turesson tended to put an increasing amount of emphasis on gene exchange, determined experimentally by breeding tests, as the prime criteria for genecological units. For example, J.W. Gregor defined the ecospecies as "...a population with an inherently low capacity for exchanging genes with other populations of its coenospecies."[82] A coenospecies was, for Gregor, "...a population which is incapable of exchanging genes with other populations, even when given the opportunity."[83]

While the later modifications in Turesson's system made the genecological units more "precise" in the sense that they were more amenable to experimental delimitation, implementation of the genecological system remained problematic for a number of reasons. First, the relationship between the genecological units and traditional taxonomic units remained unclear. Second, the units continued to be modified by later workers and the differences in usage led to some confusion. Third, the units which, according to their advocates, referred only to experimentally defined groups at times were applied to groups that had not been thoroughly studied by the methods of experimental taxonomy. Finally, while a number of biologists, mainly botanists, found the genecological terms useful, another group of biologists, mainly zoologists, found the terms difficult to apply.

In 1929 Turesson, himself, had suggested that genecological units could, in some cases, correspond with taxonomic species.[84] Later experimental taxonomists who used the genecological terminology also stressed the parallels between the experimentally determined units and such taxonomic groups as species and subspecies. For example, Jens Clausen, David Keck and William Hiesey argued that the ecospecies of the experimental taxonomist corresponded closely to the species of the "moderately conservative" taxonomist.[85] Furthermore, the other two genecological units recognized by Clausen, Keck, and Hiesey, the coenospecies and the ecotype, corresponded to the species-complex and the subspecies, respectively.[86] While some experimental taxonomists could argue that the genecological units were rigorously defined counterparts of traditional taxonomic categories, the argument could also be made that genecological units were simply redundant. For example, Theodosius Dobzhansky, who had developed his own dynamic conception of species considered genecological units superfluous, difficult to apply, and misleading in their evolutionary implications.[87] Even J.W. Gregor who was a strong supporter of genecology during the 1930s and early 1940s, noted that coenospecies and ecospecies were essentially equivalent to the conceptions of species outlined by such evolutionists as Ernst Mayr and Theodosius Dobzhansky.[88] The only defense for maintaining the prefixes coeno- and eco-, according to Gregor, was that they indicated groups which had been experimentally delimitated.[89]

Although Turesson and other experimental taxonomists modified the definitions of coenospecies and ecospecies to emphasize genetical criteria, the ecotype remained an essentially ecological term. Nonetheless, although the definition remained largely unchanged, a number of problems arose when ecotypes were identified with actual groups of organisms. Those who tried to identify ecotypes in the field discovered the complexity of the concept. According to experimental taxonomists, ecotypes could be recognized as responses to edaphic factors, climatic factors (climatypes), biotic factors (synecotypes), or geographic distribution (topotypes).[90] In many cases more than one factor could be responsible for the formation of an ecotype, the discovery of which led to such unwieldy terms as "geoclimatype."[91] Furthermore, J.W. Gregor suggested that the ecotype concept might fruitfully be used in the recognition of agricultural plants. Rather than confuse ecotypes, which were products of natural selection, with artificially selected agricultural forms, Gregor suggested the term "agroecotype" to cover the latter.[92]

The proliferation of terms associated with the ecotype concept, in itself, made for an unwieldy system. More troublesome however, was the rather arbitrary and inconsistent way that the terms could be used. For example, the term "ecotype" was at times used as a general term encompassing all the more specialized terms, but was also used specifically to refer to edaphic ecotypes.[93] The arbitrary use of terms was even more insidious if biologists identified ecotypes without sufficient evidence.[94] For example, J.W. Gregor warned against the danger of calling a population an "alpine ecotype" simply because it was found at a high elevation. In order to use the term "ecotype," the ecologically significant characteristics of the group had to be investigated experimentally.

Potentially the most damaging criticism leveled against the use of the ecotype concept was the claim that ecotypes were mere artifacts created by improper sampling methods. For example, critics claimed that Turesson had selected from very different populations of plants while ignoring intermediate populations. Even J.W. Gregor noted, "...one wonder[s] whether some at least of Turesson's edaphic ecotypes are not just prominent reference points between stretch arrays of less distinct ecotypic populations that by their exclusion from ecotypic status tend to throw into relief the more conspicuously differentiated populations."[95] This form of criticism was not limited to Turesson's field work. Critics suggested that the same overemphasis of ecotypic distinctness had been made by other experimental taxonomists and might be an inherent problem in genecological classification.*[96] Much of the force of

---

*Ernst Mayr went so far as to claim that the ecotype concept was a manifestation of Platonic "essentialism" or "typological thinking." See: Ernst Mayr, "Evolutionary Significance of the Systematic Categories," in O. Hedberg, ed., *Systematics To-Day* (Uppsala, Sweden: A.B. Lundequistska Bokhandeln, 1958), pp. 14, 20. This charge against Turesson's units has recently been repeated. See: G. Ledyard Stebbins, "Botany and the Synthetic Theory of Evolution," in: Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge: Harvard University Press, 1980), p. 141. The characterization of the ecotype concept as "typological" seems questionable. Mayr claimed that typologists viewed variation as "unreal" or something to be "ignored." He also equated typological thinking with a static species concept. See: Mayr, "Evolutionary Significance," p. 14. Clearly, Turesson's entire research program was directed at analyzing the nature of hereditary variation. Furthermore, as Jens Clausen pointed out in response to Mayr's remarks, Turesson viewed species, not as static entities, but as dynamic, adaptive this criticism would have been blunted had the distinctness of ecotypes not been so emphasized and if the concept had not been so directly used in classifying natural groups of plants. Experimental taxonomists such as J.W. Gregor, Jens Clausen, David Keck, and William Hiesey pointed out that where smooth ecological gradients occurred distinct ecotypes would be difficult or impossible to delimit except in statistical terms.[97] In such situations, Gregor suggested, the ecotype ought to be considered simply a range on an "ecocline." However, as Gregor noted there were examples of discontinuous ecological gradients and along these gradients distinct ecotypes could be defined.[98]

While a number of critics pointed to the ambiguities in the genecological units, some also criticized the fundamental basis of Turesson's system. Turesson and his followers developed the genecological system to clarify the relationships between hereditary variation and specific local environmental characters. Both the methods and the terminology employed by Turesson were designed for

---

units. See remarks of Jens Clausen: Ibid., p. 20. While Turesson overemphasized the distinctness between ecotypes, his followers were well-aware of the intergrades between ecotypes and the problems these posed for the genecological system. For example see: J.W. Gregor, "The Ecotype," *Biological Review* 19 (1944): 20-30, pp. 27-29; Jens Clausen, David D. Keck, and William M. Hiesey, *Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants*. Carngie Institution of Washington Publication No. 520 (1940), p. 415.

botanical studies. Furthermore, not even all plant groups appeared amenable to genecological study and explanation. While some commentators noted the limitations of genecology, both supporters and critics of the system often treated it as though it were a general system of classification.

Zoologists in particular were critical of the genecological terms. Although some zoologists occasionally employed the terms, the entire thrust of genecology was somewhat foreign to the study of adaptation in animals.[99] First, sedentary plants were much more susceptible to local environmental conditions than were most animals. Not suprisingly, therefore, botanists pioneered the detailed analytical study of relationships between organism and environment.[100] Second, the experimental techniques employed by Turesson and his followers were much more applicable to plants than animals. In particular, transplant experiments, which were absolutely essential for determining ecotypes, were almost totally impossible to apply in zoological studies. Finally, the genecological units which for many botanists were valuable concepts, however problematic, seemed inapplicable and redundant to many zoologists.

The ambivalence of zoologists to Turesson's system was illustrated by Theodosius Dobzhansky's critical evaluation of the genecological terms. In the second edition of *Genetics and the Origin of Species*, Dobzhansky presented a rather detailed account of experimental taxonomic research. Impressed as he was with this research, Dobzhansky found the ecotype concept difficult to apply. According to Dobzhansky,

> It seems virtually certain that geographical races in general are adapted to the environment in which they have developed and in which they live, and hence are ecotypes by Turesson's definition. Nevertheless, gaining an insight into the adaptive significance of many of the characteristics distinguishing geographical races is a highly vexatious problem. What, for example, is the adaptive value of the eye colors or the nose shapes distinguishing human races?[101]

A rather similar evaluation of Turesson's concepts was presented by Ernst Mayr. Along with a number of other zoologists and some botanists, Mayr was committed to a geographical conception of species and subspecies. Amplifying on the *Rassenkreis* theory of Bernard Rensch, Mayr envisioned species as being made up of interlocking groups of geographic races.[102] This "polytypic species concept" was not necessarily in opposition to the genecological conception of species, since geography and environmental variables were so tightly linked. As Mayr noted, "I know of no definition by which such ecological races, the true ecotypes, could be distinguished from typical subspecies or at least from microsubspecies. For example, should we call a mountain race, which has differentiated from a lowland race, an ecological race or a geographic race?"[103] Nonetheless, according to Mayr, zoologists who defined races ecologically tended to place too much emphasis on the correlation between environmental variables and taxonomic characters.[104]

Zoologists were not the only ones critical of the genecological system. Turesson's system, while developed for botanical research, did not work equally well for all groups of plants. Furthermore, some plant taxonomists argued that genecology placed undue emphasis on a very limited number of characteristics.[105] In principle, genecology was a joint genetic and ecological approach to studying plants. However, especially after 1930, sterility and fertility became the primary criteria for making genecological distinctions. The definitions of the ecospecies and the coenospecies, in particular, emphasized these two criteria. Sterility and fertility criteria had great appeal for experimentalists because they seemed to give the taxonomist a clear, experimentally verifiable basis for classifying groups of organisms. Furthermore, the genecological conception of species had a great deal of heuristic power. As W.B. Turrill noted, "The genecological method does seem to enable the student 'to get inside the species,' to study it from within, and, in combination with field-studies, to understand it as a living, and therefore, changing, population."[106] Nonetheless, Turrill feared that the importance of field studies was too often minimized by those who followed Turesson. According to Turrill, "One may fairly say, however, that there has been an increasing tendency in theory to emphasize the sterility-fertility criteria at the expense of geographical-ecological [ones]..."[107]

Turrill's ambivalence toward genecology is indicative of the ambiguous position of Turesson's system. In his own taxonomic research Turrill found only limited use for the genecological units.

"Nevertheless," Turrill noted, "the writer, in common with many other taxonomists, is in very wide agreement with the genecologist's standpoint, and especially with the original [ecological] viewpoint of Turesson and with the extended methods of later workers."[108] More graphically than any other example, Turesson's system illustrates the problematic nature of the "units of experimental taxonomy." The genecological system was widely used by experimental taxonomists. The criteria by which the genecological units were defined appeared to be, at least potentially, open to experimental testing. Advocates of genecology argued that the system had value not only for classification of organisms but also for explanation of evolutionary, ecological, and genetic relationships among related groups of organisms. Furthermore, the genecological system had undeniable heuristic value. A number of extensive field and experimental research projects were at least partly inspired by Turesson's conceptual scheme. Nonetheless, there were major problems for general implementation of the genecological system. The criteria emphasized by genecologists could not be readily applied in many groups of organisms. The genecological terms were never fully standardized and were therefore somewhat ambiguous. Furthermore, a number of biologists were opposed to genecology on conceptual grounds. Finally, the relationship between the genecological system and the established taxonomic nomenclature was never clearly stated.

Problems such as these, that surrounded the units of experimental taxonomy were never satisfactorily resolved. However, one attempted resolution that received fairly widespread support among experimental taxonomists was the utilitarian distinction between general and subsidiary classification systems. According to the utilitarian theory of taxonomy articulated by W.B. Turrill and J.S.L. Gilmour, the units of experimental taxonomy constituted special or subsidiary systems of classification.[109] These systems were useful for particular biological problems. Occasionally an experimental scheme would cast new light on a problematic group of organisms, in which case the results would be incorporated into the established general system of classification. However, for the most part, the subsidiary systems did not provide generally useful classification schemes. By maintaining subsidiary systems distinct from established taxonomic classification two ends were served. The integrity of the established system was protected, thus providing biologists with a stable foundation for research. Secondly, experimental taxonomists were not bound by the orthodoxy of established taxonomy and were free to experiment with new systems of classification. The free experimentation with subsidiary systems coupled with the stability of the established system would, according to Turrill and Gilmour, result in an orderly transition from the limited taxonomy of the 1930s and 1940s to the more comprehensive "omega" taxonomy of the future. While the utilitarian theory of taxonomy was not accepted by a majority of taxonomists, a number of taxonomists saw the distinction between general and subsidiary systems of classification as a sound justification for continued work in experimental taxonomy.[110]

NOTES

CHAPTER FIVE

1. The phrase "units of experimental taxonomy" has been used by at least two commentators on experimental taxonomy. See: J.W. Gregor, "The Units of Experimental Taxonomy," *Chronica Botanica* 7 (1942): 193-196; D.H. Valentine, "The Units of Experimental Taxonomy," *Acta Biotheoretica* 9 (1949): 75-88.

2. For example, see: Arthur Cronquist, "The Old Systematics," in C.A. Leone, ed., *Taxonomic Biochemistry and Serology* (New York: The Ronald Press Co., 1964); P.H.A. Sneath and R.R. Sokal, *Numerical Taxonomy* (San Francisco: W.H. Freeman & Co., 1973), pp. 16-17.

3. For critical commentaries on these arguments, see: J.R. Gregg, "Taxonomy, Language, and Reality," *American Naturalist* 84 (1950): 419-435; J.S.L. Gilmour and S.W. Walters, "Philosophy and Classification," in: W.B. Turrill, ed., *Vistas in Botany, Vol. 4, Recent Researches in Plant Taxonomy* (London: Pergamon Press, 1964), p. 6.

4. For a list of commonly used infraspecific terms, see: A.E. Emerson, "Species: Biology," *Encyclopedia Brittanica* 14th edition (revised, 1973).

5. See: Ernst Mayr, *Animal Species and Evolution* (Cambridge: Harvard University Press, Belknap Press, 1963), pp. 136-137, 357-358; Emerson, "Species: Biology."

6. For example, see: Ernst Mayr, "Species Concepts and Definitions," in: Ernst Mayr, ed., *The Species Problem*, American Association for the Advancement of Science Publication No. 50 (1957); John R. Beaudry, "The Species Concept: Its Evolution and Present Status," *Revue Canadienne de Biologie* (Montreal) 19 (1960): 219-240; David L. Hull, "The Effect of Essentialism on Taxonomy - Two Thousand Years of Stasis," *British Journal for the Philosophy of Science* 15 (1965): 314-326; 16 (1966): 1-18; David L. Hull, "The Metaphysics of Evolution," *British Journal for the History of Science* 3 (1967): 309-337.

7. For example, see: W.B. Turrill, "The Expansion of Taxonomy with Special Reference to Spermatophyta," *Biological Review* 13 (1938): 342-373, pp. 369-370; W.H. Camp, "Biosystematy," *Brittonia* 7 (1951): 113-127, pp. 125-127; J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: William Heinemann, 1953), p. 122; J.S.L. Gilmour, "The Species: Yesterday and Tomorrow," *Nature* 181 (1958): 379-380.

8. Camp, "Biosystematy," pp. 125-126.

9. J.P. Lotsy, *Evolution by Means of Hybridization* (The Hague: Martinus Nijhoff, 1916).

10. Ibid., p. 27.

11. Ibid.

12. Ibid., p. 159.

13. J.P. Lotsy, "On the Species of the Taxonomist in its Relation to Evolution," *Genetica* 13 (1931): 1-16.

14. Ibid.

15. Theodosius Dobzhansky, *Genetics and the Origin of Species* (New York: Columbia University Press, 1937), p. 311.

16. Ibid., pp. 307-308.

17. Ibid.

18. For example, see: F.W.S., "*Genetics and the Origin of Species*," *Nature* 141 (1938): 310; A.E. Emerson, "The Origin of Species," *Ecology* 19 (1938): 152-154. For a list of biologists who Dobzhansky felt shared his conception of species, see: Theodosius Dobzhansky, *Genetics and the Origin of Species*, 3rd edition (New York: Columbia University Press, 1951; Columbia Paperback Edition, 1964), p. 263.

19. Dobzhansky, *Genetics and the Origin* (1937), p. 312.

20. Ibid., p. 316.

21. W.H. Camp and C.L. Gilly, "The Structure and Origin of Species," *Brittonia* 4 (1943): 323-385.

22. Ibid., p. 324.

23. Ibid., p. 326-331.

24. Ibid.

25. Ibid.

26. Ibid., pp. 334-355.

27. Ibid., pp. 379-382.

28. Camp, "Biosystematy," p. 113.

29. Ibid., p. 126.

30. J.S.L. Gilmour and J.W. Gregor, "Demes: A Suggested New Terminology," *Nature* 144 (1939): 333.

31. Ibid.

32. Ibid.

33. Ibid.

34. J.S.L. Gilmour and J. Heslop-Harrison, "The Deme Terminology and the Units of Micro-Evolutionary Change," *Genetica* 27 (1954): 147-161.

35. For a list of biologists who approved of the general outlines of the system developed by Gilmour, Gregor, and Heslop-Harrison, see: Ibid., p. 148.

36. For example, Mayr considered the term "deme" a superfluous synonym for "population." See: Mayr, *Animal Species*, pp. 136-137, 357-358.

37. For example, see: Sewell Wright, "Statistical Consequences of Mendelian Heredity," in: J.S. Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940), pp. 161-162; Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), p. 24; Theodosius Dobzhansky, *Genetics and the Origin*, (1951), p. 15.

38. Heslop-Harrison, *New Concepts*, p. 122.

39. Ibid.

40. B.H. Danser, "Ueber die Begriffe Komparium, Kommiskuum, und Konvivium und ueber die Entstehungsweise der Konvivium." *Genetica* 11 (1929): 399-450.

41. Ibid., p. 400.

42. Ibid., p. 401.

43. Ibid., pp. 403-405.

44. Turrill, "Expansion," p. 356.

45. Ibid., pp. 356-357.

46. B.H. Danser, "A Theory of Systematics," *Bibliotheca Biotheoretica* 4 (1950): 117-180.

47. See the editors' note preceeding Danser's article, Ibid., p. 116.

48. Ibid., p. 117.

49. Ibid., pp. 117-118.

50. Ibid., pp. 124-125.

51. Ibid.

52. Ibid., p. 173.

53. Ibid., p. 141.

54. For example, see discussions of Danser's system in: Gilmour, "Species"; J.S.L. Gilmour, "Taxonomy," in: A.M. Macleod and L.S. Cobley, eds., *Contemporary Botanical Thought* (Chicago: Quadrangle Books, 1961), p. 41; Heslop-Harrison, *New Concepts*, pp. 95-97.

55. Göte Turesson, "The Species and Variety as Ecological Units," *Hereditas* 3 (1922): 100-113; Göte Turesson, "The Genotypical Response of the Plant Species to the Habitat," *Hereditas* 3 (1922): 211-347.

56. Valentine, "Units of Experimental Taxonomy."

57. For example, see: E.C. Barton-Wright, *Recent Advances in Botany* (Philadelphia: P. Blakiston's Son & Co., Inc., 1932), chap. III; Gregor, "Units of Experimental Taxonomy"; J.W. Gregor, "The Ecotype," *Biological Review* 19 (1944): 20-30; W.B. Turrill, "The Ecotype Concept: A Consideration with Appreciation and Criticism, Especially of Recent Trends," *New Phytologist* 45 (1946): 34-43; G. Ledyard Stebbins, *Variation and Evolution in Plants* (New York: Columbia University Press, 1950), chap. II.

58. Ernst Mayr, *Animal Species and Evolution* (Cambridge: Belknap Press, Harvard University Press, 1963), pp. 351-352.

59. Turesson, "Genotypical Response," pp. 341-347.

60. Göte Turesson, "The Scope and Import of Genecology," *Hereditas* 4 (1923): 171-176.

61. Turesson, "Genotypical Response," p. 344.

62. Ibid., pp. 341-347.

63. Ibid., pp. 344-348.

64. Ibid.

65. Ibid.

66. Ibid.

67. Ibid.

68. Ibid.

69. Ibid., p. 345.

70. For example, see: Ernst Mayr, "The Evolutionary Significance of the Systematic Categories," in: O. Hedberg, ed., *Systematics To-Day* (Uppsala, Sweden: A.B. Lundequistska Bokhandeln, 1958), pp. 14, 20; G. Ledyard Stebbins, "Botany and the Synthetic Theory of Evolution," in: Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis: Perspectives on the Unification of Biology* (Cambridge: Harvard University Press, 1980), pp. 140-142.

71. Turesson, "Genotypical Response," p. 346.

72. Ibid., p. 346.

73. Turesson, "Scope and Import."

74. Ibid., p. 172.

75. Göte Turesson, "Zur Natur und Begrenzung der Artenheiten," *Hereditas* 12 (1929): 323-334, p. 333; Göte Turesson, "Genecological Units and their Classificatory Value," *Svensk Botanisk Tidskrift* 24 (1930): 511-518.

76. Ibid.

77. For example, see: J.W. Gregor, "Experimental Delimitation of Species," *New Phytologist* 30 (1931): 204-217, pp. 206-207; Gregor, "Ecotype," pp. 21-22; Jens Clausen, David D. Keck, and William M. Hiesey, "The Concept of Species Based on Experiment," *American Journal of Botany* 26 (1939): 103-106; Jens Clausen, David D. Keck, and William M. Hiesey, *Experimental Studies on the Nature of Species. I. Effect of Varied Environments on Western North American Plants*, Carnegie Institution of Washington Publication No. 520 (1940), p. vii; Valentine, "Units of Experimental Taxonomy," pp. 75-76.

78. Valentine, "Units of Experimental Taxonomy," p. 75.

79. Heslop-Harrison, *New Concepts*, pp. 95-96. See also: Turrill, "Ecotype Concept," pp. 37-38.

80. Heslop-Harrison, *New Concepts*, p. 97.

81. Clausen, Keck, and Hiesey, "Concept of Species."

82. J.W. Gregor, "Experimental Taxonomy. IV. Population Differentiation in North American and European Sea Plantains Allied to *Plantago maratima* L.," *New Phytologist* 38 (1939): 291-322, p. 321.

83. Ibid.

84. Turesson, "Genecological Units," p. 515.

85. Clausen, Keck, and Hiesey, "Concept of Species," p. 104.

86. Ibid.

87. Dobzhansky, *Genetics and the Origin*, (1951), pp. 147, 272-273.

88. Gregor, "Ecotype," p. 23.

89. Ibid.

90. Gregor, "Units of Experimental Taxonomy," pp. 194-195; Gregor, "Ecotype," pp. 24-26.

91. Ibid.

92. J.W. Gregor, "The Ecotype Concept in Relation to the Registration of Crop Plants," *Annals of Applied Botany* 20 (1933): 205-219, p. 214.

93. Gregor, "Units of Experimental Taxonomy," p. 194.

94. Ibid., p. 195.

95. Gregor, "Ecotype," p. 25.

96. W.B. Turrill, "Experimental Attacks on Species Problems," *Chronica Botanica* 7 (1942): 281-283, p. 283; Stebbins, *Variation*, pp. 43-44.

97. Clausen, Keck, and Hiesey, *Effect of Varied Environments*, p. 415; Gregor, "Ecotype," pp. 27-29.

98. Gregor, "Experimental Taxonomy IV," p. 321; Gregor, "Ecotype," p. 28.

99. For example, see: Dobzhansky, *Genetics and the Origin*, (1951), pp. 272-273; Richard B. Goldschmidt, "Ecotype, Ecospecies, and Macroevolution," reprinted in: Leonie K. Piternick, ed., *Richard Goldschmidt: Controversial Geneticist and Creative Biologist* (Boston: Birkhäuser Verlag, 1980).

100. Theodosius Dobzhansky noted that botanical studies of this problem were more detailed and extensive than zoological counterparts. See: Dobzhansky, *Genetics and the Origin* (1941), p. 202.

101. Ibid., p. 199.

102. Mayr, *Systematics*, chap. V, especially pp. 111, 120.

103. Ibid., pp. 194-195.

104. Ibid., p. 195.

105. Turrill, "Ecotype Concept," pp. 39-43.

106. Ibid., p. 37.

107. Ibid., p. 39.

108. Ibid., p. 41.

109. See: J.S.L. Gilmour, "A Taxonomic Problem," *Nature* 139 (1937): 1040-1042; Turrill, "Expansion," pp. 369-370; J.S.L. Gilmour and W.B. Turrill, "The Aim and Scope of Taxonomy," *Chronica Botanica* 6 (1942): 217-219.

110. For example, see: Gregor, "Units of Experimental Taxonomy," p. 193; Heslop-Harrison, *New Concepts*, pp. 110-111; J.S.L. Gilmour and S.M. Walters, "Philosophy and Classification," p. 12.

CONCLUSION

The developments in experimental taxonomy between 1930 and 1950 were characteristic of a more general renewal of interest and activity in systematics that has commonly been referred to as the "new systematics." To an even greater extent than experimental taxonomy, the new systematics was a broad, diversifying movement that cannot easily be characterized as a unified school of thought. Both the ideas expressed in Huxley's *New Systematics*, the book that initially popularized the term "new systematics," and the aims and activities of the Association for the Study of Systematics in Relation to General Biology, the group that published Huxley's anthology, were diverse. For example, the expressed aims of the Association ranged from practical matters of lobbying for more research positions in taxonomy and preparing handbooks of British flora and fauna, to sponsoring symposia on the theoretical and philosphical foundations of taxonomy. The diversity of aims of the Association mirrors the variety of activities of taxonomists, in general. Systematists of the first half of the twentieth century were involved with a wide range of innovative concerns. In terms of methodology, systematists of this period stressed the significance of extensive field collections and statistical analyses of taxonomic data. Systematists were showing a keen interest both in the methods and theories of other biological disciplines including cytology, ecology, and genetics. Theoretical systematists continued and expanded the traditional taxonomic ties with evolutionary theory. Notably, a number of taxonomists contributed to the rise of modern neo-Darwinian theory. Other theoretically inclined systematists who were less interested in evolutionary theory attempted to reconcile taxonomic theory with developments in modern logic and philosophy of science.

All of these diverse strands of taxonomic activity were represented in the various essays published in Huxley's *New Systematics*. In general, the theme that unified this book was an optimism about the future of taxonomy. More than in the past, according to the "new systematists," the discipline of taxonomy was a growing and important focus of biological activity. W.B. Turrill termed this change in systematics the "expansion of taxonomy." It was this expansion of taxonomic theory and practice that formed the essence of the new systematics.

One important aspect of the new systematics was the introduction of cytological, ecological, and genetic techniques and ideas into taxonomy. Experimental taxonomy, which incorporated parts of all three of these disciplines, illustrates clearly both the possibilities and the problems involved in the "expansion of taxonomy." The biological disciplines from which experimental taxonomists borrowed seemed to offer the means for significantly improving biological classification. At the very least, cytological, ecological, and genetic methods opened up a wealth of previously unexplored taxonomic characteristics. For example, cytological determinations of chromosomal numbers and morphology provided taxonomists with what appeared to be highly stable and specific characteristics of taxonomic groups.

Furthermore, the cytogenetic implications of chromosomes as "genetic systems" so eloquently elaborated by cytologists such as C.D. Darlington, convinced a number of taxonomists that the structural characteristics of chromosomes were more significant than gross morphological structures. Perhaps of even greater importance, however, the biological fields from which experimental taxonomists borrowed appeared to provide a set of rigorous techniques for testing taxonomic relationships. While taxonomy had traditionally been a descriptive science, and hence according to some, a subjective activity, the introduction of experimental methods from such fields as genetics appeared to provide objective testable criteria for determining the limits of taxonomic groups.

Despite the enthusiasm for experimental taxonomy, the incorporation of techniques and ideas from other biological disciplines was problematic. In the first place, taxonomists who turned to cytology, ecology, and genetics were not borrowing from fully developed fields. Even during the 1930s and 1940s all of these fields were undergoing major theoretical and methodological changes. For example, C.D. Darlington's *Recent Advances in Cytology*, now seen as an important early statement of cytogenetic theory, was quite controversial when it was first published in 1932. Similarly, while the principles of Mendelian genetics were well-established by 1930, other areas of genetics, notably population genetics, were only beginning to be explored. As a consequence, even among taxonomists who used the same experimental techniques there could be major disagreements over the significance of particular data.

Another problem that experimental taxonomists faced was the difficulty of assimilating complex techniques and ideas from other highly technical fields. It was virtually impossible for a single biologist to have expertise in taxonomy and also in cytology, ecology, and genetics. This "problem" had two salutory effects on the new systematics. First, it was a stimulus for discussions among taxonomists and specialists from other biological fields. For example, the Association for the Study of Systematics in Relation to General Biology promoted symposia on the reciprocal relationships between taxonomy and other biological disciplines. In addition to discussions, cooperative taxonomic research projects were undertaken by groups of biologists with different biological backgrounds. For example, the highly successful experimental taxonomists Jens Clausen, David Keck, and William Hiesey employed a team approach to research. Clausen's main interest was in cytogenetics, Hiesey concentrated on transplant experimentation, while Keck was primarily involved with systematic and nomenclatorial problems. Despite the cooperation among taxonomists and other specialists, the influx of new techniques was a source of some controversy among systematists. The methods employed in experimental taxonomic research were largely limited to the species level or below. Furthermore, many of the "taxonomists" whose training came in other fields were primarily interested in the ecological, genetic, and evolutionary relationships among species and populations. Taxonomists could, with some justification, complain that their field was being infiltrated by biologists with limited understanding of or interest in general taxonomy.

Controverises over the legitimacy of experimental taxonomy could be rather bitter. Both critics and advocates of experimental taxonomy were guilty of rather intemperate outbursts. In a recent article, John Dean has emphasized these controversies in drawing a sharp distinction between experimental taxonomists and orthodox herbarium and museum taxonomists.[1] According to Dean, these taxonomists formed two opposing schools of thought based largely on incompatible beliefs about the nature and purposes of taxonomy. Orthodox taxonomists followed the taxonomic methodology inherited from the Linnean tradition that defined groups in terms of gross morphological differences. Experimental taxonomists, primarily biologists with cytogenetic training, generally studied the dynamics of populations defined in terms of gene exchange.

In a general way, the dichotomy presented by Dean is a model of two different modes of taxonomic research. However, this model breaks down when it is applied to actual historical situations. First, a number of influential taxonomists cannot be adequately characterized as either experimental or orthodox taxonomists. Taxonomists such as W.B. Turrill and Edgar Anderson were actively involved both in herbarium research and in experimental research. Both taxonomists proposed innovations in herbarium techniques that would make herbarium collections more useful to experimentalists. Although Turrill's primary research was in "orthodox" taxonomy, he wrote extensively on the relationships between taxonomy and other biological discplines. Second, by emphasizing the controversies between experimentalists and orthodox taxonomists, the controveries within these groups are obscured. For example, the cytogenetic data used in the classification of *Phleum* were open to a number of different interpretations. While J.W. Gregor's original experimental classification of *Phleum* was criticized by the "orthodox" taxonomist, A.J. Wilmott, it was also criticized, perhaps in a more damaging way, by the experimentalist, Hedda Nordenskiöld. Finally, by emphasizing the controversial aspects of experimental taxonomy, the dichotomy obscures the fact that a number of taxonomists saw experimental and orthodox taxonomies as compatible enterprises. These included taxonomists such as W.B. Turrill and J.S.L. Gilmour, whose interests were not primarily experimental, but also strong advocates of experimental taxonomy such as J.W. Gregor and J. Heslop-Harrison. Particularly after 1940, Gregor, who continued to draw a sharp distinction between the two forms of taxonomic research, emphasized the potential harmony between experimental and orthodox taxonomies. According to Gregor

> While the primary responsibility of the orthodox taxonomist is to supply the reference points for the general biologist, the experimental taxonomist feels himself in no way bound by such practical considerations. He is therefore free to contemplate the theoretical aims of taxonomy and in particular the dynamics of population arrangement. It does not follow, however, that on this account his researches are necessarily divorced from those of the practical taxonomist; on the contrary both systems, though basically different, ought to be regarded as mutually helpful.[2]

Gregor's evaluation of the relationship between experimental and orthodox taxonomies represents the more restrained view of experimentalists who had come to see the limitations as well as the strengths of their enterprise. During the early 1930s enthusiastic claims about reforming general taxonomy through the use of experimental methods were made. Nonetheless, even the most enthusiastic advocates of experimental taxonomy acknowledged the importance of comparative morphology as a foundation for their research. More moderate advocates, such as W.B. Turrill, pointed out that in practice "experimental taxonomy" did not rely entirely on experimental methods. Experimental taxonomy entailed a blend of "orthodox" methods and innovative methods, both experimental and descriptive.

Both in theory and in practice it became increasingly clear during the 1930s and 1940s that experimental taxonomy was a limited, albeit important, subdivision of general systematics. Theoretically, most experimental taxonomists were inclined toward the study of populations and species. Relatively few of these biologists had any serious interest in reforming higher taxonomic categories. While some experimentalists claimed that experimental methods would eventually force a restructuring of the general system of classification, no concrete formula for bringing about such a reform was ever presented. The innovations in nomenclature developed by experimental taxonomists were almost entirely limited to the species level. The methods employed by most experimental taxonomists also precluded the development of a general experimental taxonomy. As J. Heslop-Harrison noted, "...[experimental taxonomy's]'ceiling' is the level at which genetical experimentation becomes impossible, so that in actuality no chance of producing an all-embracing classification based upon experimental methods exists at all."[3]

Even at the species level, the application of experimental methods was rather limited. The groups of organisms that experimentalists studied were generally chosen *because* they were amenable to experimental manipulation. In the plant kingdom, relatively little experimental taxonomy was undertaken on woody plants. In the animal kingdom, experimental taxonomy comparable to that innitiated by botanists was very limited. Important sections of the animal kingdom, notably birds, were particularly unsuited for cytogenetic study. Only in such groups as *Drosophila* was extensive "experimental taxonomy" completed.*

Despite its limitations the significance of experimental taxonomy ought not be underestimated. The introduction of repeatable experimental methods added a rigor to taxonomic practice that herbarium and museum taxonomy, however exacting, could not match. Cytogenetic analysis, along with adding a new set of taxonomic characters, provided a methodology for unraveling previously intractable taxonomic problems. In plants, both taxonomic and evolutionary relationships were

---

*John Dean points out that characteristically experimental taxonomists received their training in fields other than taxonomy. It ought to be noted that a number of geneticists, including, Theodosious Dobzhansky, J.T. Patterson, and A.H. Sturtevant became interested in taxonomic problems in *Drosophila*. Nonetheless, training in genetics did not necessarily lead to an "experimentalist" perspective on taxonomy. Although he included cytological and genetic data in his descriptions of species, A.H. Sturtevant considered comparative morphology the primary criterion for distinguishing species in the genus *Drosophila*. A rigid adherence to the dichotomy between experimental and orthodox taxonomists would, therefore, necessitate categorizing Sturtevant as an "orthodox" taxonomist, despite his experimental training.

confused by the effects of hybridization and polyploidy. Cytology and genetics provided both the theory and the techniques for analyzing hybrid and polyploid groups. In animals, cytogenetics was also a powerful, though extremely limited, tool. For example, in *Drosophila*, the analysis of giant salivary chromosomes seemed to provide a "magic key" for unlocking all taxonomic problems.[4] This tool was effectively used by Theodosius Dobzhansky to detect subtle differences between the "sibling species" *Drosophila pseudoobscura* and *Drosophila persimilis*. Finally, experimental taxonomists contributed an impressive body of basic biological research. This research emphasized previously unexplored problems of infraspecific variation, adaptive responses of populations to local habitats, and the evolutionary and genetic dynamics of populations.

The extent to which this body of research could be considered "taxonomic" was a question that even some experimental taxonomists raised.[5] In terms of general classification, or "alpha" taxonomy, a number of taxonomists were leery of the wholesale assimilation of experimental results. However, these taxonomists agreed that this research was an important component of the developing "omega" taxonomy that would more clearly reflect the totality of knowledge about biological relationships. Moderate advocates of both "orthodox" and experimental taxonomies voiced this opinion. For example, using a metaphor from genetics, the orthodox taxonomist Arthur Cronquist noted,

> The biosystematists emphasize questions of the structure, origin, and maintenance of breeding populations, a perfectly legitimate

> field of inquiry, born of the union of taxonomy and genetics. A backcross of biosystematics to classical taxonomy gives us the modified classical taxonomy of the future, receptive to data of all sorts, and chiefly concerned, as in the past, with the general system, evolutionary relationships, and the definition of taxa at all ranks.[6]

Using a similar metaphor, W.B. Turrill noted,

> There would be reciprocal advantage if experimentalists and their herbarium colleagues frequently consulted one another. This would, by introgressive hybridization of methods and ideas, produce hybrid vigour in plant taxonomy.[7]

Experimental taxonomy could not claim title to the general system of classification. Nonetheless, in its own right, experimental taxonomy was a viable biological enterprise. Furthermore, although its ties to general taxonomy at times appeared tenuous, experimental taxonomy formed an important element in the expansion of taxonomy that characterized the new systematics.

This historical study of experimental taxonomy indicates a different relationship between experimentalism and descriptive biology than that traditionally portrayed by the "naturalist-experimentalist" dichotomy. During the early years of experimental taxonomy a number of advocates of this form of taxonomic research did see themselves taking part in what the historian Garland Allen refers to as the "revolt from morphology."[8] Yet, this revolt was not vigorously waged and was never completed. Even the most enthusiastic practitioners of experimental taxonomy admitted their debt to descriptive comparative morphology. Critics pointed out that all experimental taxonomic research relied on some comparative morphological techniques, however refined. Furthermore, the integration of different experimental techniques was itself a complicated and never entirely satisfactory process. Between 1930 and 1950 cytology, ecology, and genetics were all developing into highly complex technical fields. Combining methods and theories from these fields with those of taxonomy, itself a rather technical discipline, involved a good deal more than replacing "subjective" descriptive techniques with a unified body of rigorously "objective" experimental techniques. Attempts to fuse cytology, ecology, and genetics with taxonomy produced an impressive body of research that has been termed "experimental taxonomy." However, this fusion constituted neither a repudiation of descriptive comparative morphology nor a complete revision of general taxonomic theory and practice.

NOTES

CONCLUSION

1. John Dean, "Controversy over Classification: A Case Study from the History of Botany," in: Barry Barnes and Steven Shapin, eds., *Natural Order: Historical Studies of Scientific Culture* (Beverly Hills, California: Sage Publications, Inc., 1979).

2. J.W. Gregor, "The Units of Experimental Taxonomy," *Chronica Botanica* 7 (1942): 193-196, p. 193.

3. J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: William Heinemann Ltd., 1953) p. 110.

4. The term "magic key" was used in this context by M.J.D. White. See: M.J.D. White, *Animal Cytology and Evolution* (Cambridge: Cambridge University Press, 1945), p. 313.

5. See: Heslop-Harrison, *New Concepts*, p. 122.

6. Arthur Cronquist, "The Old Systematics," in: C.A. Leone, ed., *Taxonomic Biochemistry and Serology* (New York: The Ronald Press, Co., 1964), p. 11.

7. W.B. Turrill, "Foreward," in: Heslop-Harrison, *New Concepts*, p. vi.

8. Garland Allen, *Life Science in the Twentieth Century* (New York: John Wiley & Sons, Inc., 1975), p. 19.

SELECTED BIBLIOGRAPHY

Secondary Sources

Allen, Garland. *Life Sciences in the Twentieth Century*. New York: John Wiley & Sons, Inc., 1975.

__________. *Thomas Hunt Morgan: The Man and His Science*. Princeton: Princeton University Press, 1978.

Allen, Marshall W. "J.H. Woodger and the Emergence of Supra-Empirical Orders of Discussion in Early Twentieth Century Biology." Master's Thesis, Oregon State University, 1975.

Arkell, W.J. "Species and Species." in *The Species Concept in Paleontology* ed. by P.C. Sylvester Bradley. London: The Systematics Association, 1956.

Beaudry, Jean R. "The Species Concept: Its Evolution and Present Status." *Revue Canadienne de Biologie* 19 (1960): 219-240.

Benson, Keith R. "Problems of Individual Development: Descriptive Embryological Morphology in America at the Turn of the Century." *Journal of the History of Biology* 14 (1981): 113-146.

Blackwelder, Richard E. *Taxonomy*. New York: John Wiley & Sons, Inc., 1967.

Cain, A.J. "Logic and Memory in Linnaeus' System of Taxonomy." *Proceedings of the Linnean Society of London* 169 (1957): 144-163.

__________. "The Post-Linnean Development of Taxonomy." *Proceedings of the Linnean Society of London* 170 (1958): 234-244.

__________. "Deductive and Inductive Methods in Post-Linnean Taxonomy." *Proceedings of the Linnean Society of London* 170 (1959): 185-217.

Carlson, Elof A. *The Gene: A Critical History*. Philadelphia: W.B. Saunders Co., 1966.

Carson, Hampton. "Cytogenetics and the Neo-Darwinian Synthesis." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

Clausen, Jens. "The Function and Evolution of Ecotypes, Ecospecies, and Other Natural Entities." in *Systematics To-day* ed. by O. Hedberg. Uppsala: A.B. Lundequistska Bokhandeln, 1958.

Cravens, Hamilton. *The Triumph of Evolution.* Philadelphia: University of Pennsylvania Press, 1978.

Cronquist, Arthur. "The Old Systematics." in *Taxonomic Biochemistry and Serology* ed. by Charles A. Leone. New York: The Ronald Press Co., 1964.

____________. *The Evolution and Classification of Flowering Plants.* Boston: Houghton Mifflin Co., 1968.

Darlington, C.D. "The Evolution of Genetic Systems: Contributions of Cytology to Evolutionary Theory." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

Dean, John. "Controversy over Classification: A Case Study from the History of Botany." in *Natural Order: Historical Studies in Scientific Culture* ed. by Barry Barnes and Steven Shapin. Beverly Hills: Sage Publications, 1979.

Dunn, L.C. *A Short History of Genetics.* New York: McGraw-Hill Book Co., 1965.

Emerson, A.E. "Species." *Encyclopedia Brittanica* 14th edition (revised 1973).

Farber, Paul Lawrence. "The Type-Concept in Zoology During the First Half of the Nineteenth Century." *Journal of the History of Biology* 9 (1976): 93-119.

____________. "A Historical Perspective on the Impact of the Type Concept on Insect Systematics." *Annual Review of Entomology* 23 (1978): 91-99.

Gilmour, J.S.L. "The Species: Yesterday and To-morrow." *Nature* 181 (1958): 379-380.

____________. "Taxonomy." in *Contemporary Botanical Thought* ed. by A.M. Macleod and L.S. Cobley. Chicago: Quadrangle Books, 1961.

Gilmour, J.S.L. and S.M. Walters. "Philosophy and Classification." in *Vistas in Botany, Vol. 4, Recent Researches in Plant Taxonomy* ed. by W.B. Turrill. London: Pergamon Press, 1964.

Goldschmidt, R.B. "Fifty Years of Genetics." *American Naturalist.* 89 (1950): 313-339.

Grant, Verne. "The Plant Species in Theory and Practice." in *The Species Problem* ed. by Ernst Mayr. American Association for the Advancement of Science Publication No. 50, 1957.

Gregg, J.R. "Taxonomy, Language, and Reality." *American Naturalist* 84 (1950): 419-435.

___________. *The Language of Taxonomy. An Application of Symbolic Logic to the Study of Classificatory Systems.* New York: Columbia University Press, 1954.

Gregg, J.R. and F.T.C. Harris, eds., *Form and Strategy in Science.* Dordrecht-Holland: D. Reidel Publishing Co., 1964.

Hecht, Max K. and William C. Steere, eds., *Essays in Evolution and Genetics in Honor of Theodosium Dobzhansky.* New York: Appleton-Century-Crofts, Meredith Corp., 1970.

Hedberg, Olov, ed., *Systematics To-Day.* Uppsala: A.B. Lundequistska Bokhandeln, 1958.

Heslop-Harrison, J. *New Concepts in Flowering-Plant Taxonomy.* London: William Heinemann Ltd., 1953.

Hubbard, C.E. "William Bertram Turrill." *Royal Society of London: Biographical Memoirs* 17 (1971): 689-712.

Hull, David L. "The Effect of Essentialism on Taxonomy - Two Thousand Years of Stasis." *British Journal for the Philosophy of Science* 15 (1965): 314-326; 16 (1965): 1-18.

___________. "The Metaphysics of Evolution." *British Journal for the Philosophy of Science* 3 (1967): 309-337.

___________. "A Matter of Individuality." *Philosophy of Science* 45 (1978): 335-360.

Leone, Charles A., ed., *Taxonomic Biochemistry and Serology.* New York: The Ronald Press Co., 1964.

Levine, Howard, Lee Ehrman, and Rollin Richmond. "Theodosius Dobzhansky up to Now." in *Essays in Evolution and Genetics in Honor of Theodosius Dobzhansky* ed. by M.K. Hecht and W.C. Steere. New York: Appleton-Century-Crofts, Meredith Corp., 1970.

Marsden-Jones, E.M. and W.B. Turrill. *The Bladder Campions.* London: Adlard & Son, Ltd., 1957.

Mayr, Ernst. "Species Concepts and Definition." in *The Species Problem* ed. by Ernst Mayr. American Association for the Advancement of Science Publication No. 50, 1957.

___________. "The Evolutionary Significance of the Systematic Categories." in *Systematics To-Day* ed. by O. Hedberg. Uppsala: A.B. Lundequistska Bokhandeln, 1958.

___________. *Animal Species and Evolution.* Cambridge: Harvard University Press, Belknap Press, 1963.

___________. "The New Systematics." in *Taxonomic Biochemistry and Serology* ed. by C.A. Leone. New York: The Ronald Press Co., 1964.

___________. *Principles of Systematic Zoology.* New York: McGraw-Hill Book Co., 1969.

___________. "Prologue: Some Thoughts on the History of the Evolutionary Synthesis." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

___________. "The Role of Systematics in the Evolutionary Synthesis." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

Mayr, Ernst and William B. Provine, eds. *The Evolutionary Synthesis: Perspectives on the Unification of Biology.* Cambridge: Harvard University Press, 1980.

Provine, William B. *The Origins of Theoretical Population Genetics.* Chicago: University of Chicago Press, 1971.

___________. "Francis B. Sumner and the Evolutionary Synthesis." *Studies in the History of Biology* 3 (1979): 211-240.

Simpson, George G. *Principles of Animal Taxonomy.* New York: Columbia University Press, 1961.

Sneath, Peter H.A. and Robert R. Sokal. *Numerical Taxonomy.* San Francisco: W.H. Freeman and Co., 1973.

Stebbins, G. Ledyard. "Botany and the Synthetic Theory of Evolution." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

Sturtevant, A.H. *A History of Genetics*. New York: Harper & Row, Publishers, Inc., 1965.

Sylvester-Bradley, P.C., ed., *The Species Concept in Paleontology*. London: The Systematics Association, 1956.

Turrill, W.B. *Pioneer Plant Geography*. The Hague: Martinus Nijhoff, 1953.

__________. "John Christopher Willis." *Royal Society of London: Biographical Memoirs* 4 (1958): 353-357.

__________. "Plant Taxonomy, Phytogeography and Plant Ecology." in *Vistas in Botany, Vol. 4, Recent Researches in Plant Taxonomy* ed. by W.B. Turrill. London: Pergamon Press, 1964.

Turrill, W.B., ed., *Vistas in Botany, Vol. 4, Recent Researches in Plant Taxonomy*. London: Pergamon Press, 1964.

Waddington, C.H. *The Evolution of an Evolutionist*. Ithaca: Cornell University Press, 1975.

Walters, S.M. "The Shaping of Angiosperm Taxonomy." *New Phytologist* 60 (1961): 74-84.

Wettstein, Alexander. "Cytology in the T.H. Morgan School." in *The Evolutionary Synthesis: Perspectives on the Unification of Biology* ed. by Ernst Mayr and William B. Provine. Cambridge: Harvard University Press, 1980.

Primary Sources

"Age and Area Hypothesis, The." *American Journal of Botany* 11 (1924): 541-578.

Aldrich, J.M. "The Limitations of Taxonomy." *Science* 65 (1927): 381-385.

Allan, H.H. "Wild Species-Hybrids in the Phanerogams." *Botanical Review* 3 (1937): 593-615.

__________. "The Nomenclature of Hybrids." *Chronica Botanica* 5 (1939): 205-209.

__________. "Natural Hybridization in Relation to Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Anderson, Edgar. "The Concept of the Genus: A Survey of Modern Opinion." Bulletin of the Torrey Botanical Club 67 (1940): 363-369.

Anderson, Edgar. "The Problem of Species in the Northern Blue Flags, *Iris versicolor* L. and *Iris virginica* L." *Annals of the Missouri Botanical Garden* 15 (1928): 241-333.

__________. "The Distribution of *Iris versicolor* in Relation to the Post-Glacial Great Lakes." *Rhodora* 35 (1933): 154-160.

__________. "Hybridization in American Tradescantias." *Annals of the Missouri Botanical Garden* 23 (1936): 511-525.

__________. "The Species Problem in *Iris*." *Annals of the Missouri Botanical Garden* 23 (1936): 457-509.

__________. "Cytology in its Relation to Taxonomy." *Botanical Review* 3 (1937): 335-350.

__________. "Supra-specific Variation in Nature and in Classification from the View-point of Botany." *American Naturalist* 71 (1937): 223-235.

__________. "The Technique and Use of Mass Collections in Plant Taxonomy." *Annals of the Missouri Botanical Garden* 28 (1941): 287-292.

__________. "Mass Collections." *Chronica Botanica* 7 (1943): 378-380.

Anderson, Edgar and W.B. Turrill. "Biometrical Studies on Herbarium Material." *Nature* 136 (1935): 986.

Arkell, W.J. and J.A. Moy-Thomas. "Paleontology and the Taxonomic Problem." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

"Aspects of the Species Problem." *American Naturalist* 42 (1908): 217-281.

"Association for the Study of Systematics in Relation to General Biology." *Nature* 140 (1937): 163-164.

"Association for the Study of Systematics in Relation to General Biology. Annual Report. II. (1938-40)." *Proceedings of the Linnean Society of London* 152 (1941): 399-403.

__________. "Annual Report. III. (1940-41)." *Proceedings of the Linnean Society of London* 153 (1941): 309-310.

__________. "Annual Report. IV. (1941-42)." *Proceedings of the Linnean Society of London* 156 (1944): 246-247.

__________. "Annual Report. V. (1942-46)." *Proceedings of the Linnean Society of London* 157 (1946): 223-224.

Babcock, E.B. "Genetics and Plant Taxonomy." *Science* 59 (1924): 327-328.

__________. "Cytogenetics and the Species Concept." *American Naturalist* 65 (1931): 5-18.

__________. *The Genus Crepis: Part One: The Taxonomy, Phylogeny, Distribution, and Evolution of Crepis; Part Two: Systematic Treatment.* [part of *University of California Publications in Botany*, Vol. 21, 22 (1947)].

Baker, F.C. "On Genus and Species Making." *Science* 72 (1930): 37-39.

Balfour-Browne, J. "The Species Problem." *Report of the British Association for the Advancement of Science* (1935): 63-78.

Barton-Wright, E.C. *Recent Advances in Botany.* Philadelphia: P. Blakiston's Son and Co., Inc., 1932.

Bateson, William. "Area of Distribution as a Measure of Evolutionary Age." *Nature* 111 (1923): 39-43.

Bather, F.A. "Biological Classification, Past and Future." *Quarterly Journal of the Geological Society* 83 (1927): lxii-civ.

__________. "The Shifting Diagnosis." *Paleobiologica* 1 (1928): 51-54.

__________. "Zoological Nomenclature." *Encyclopedia Brittanica* 14th edition.

Belling, John. "Critical Notes on C.D. Darlington's 'Recent Advances in Cytology'." *University of California Publications in Botany* 17 (1933): 75-110.

Bremekamp, C.E.B. "The Principles of Taxonomy and the Theory of Evolution." *Pamphlet of the South African Biological Society* 4 (1931): 1-8.

__________. "Phylogenetic Interpretations and Genetic Concepts in Taxonomy." *Chronica Botanica* 5 (1939): 398-403.

Calman, W.T. "The Taxonomic Outlook in Zoology." *Science* 72 (1930): 279.

Calman , W.T. "A Museum Zoologist's View of Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Camp, W.H. "Biosystematy." *Brittonia* 7 (1951): 113-127.

Camp, W.H. and C.L. Gilly. "The Structure and Origin of Species." *Brittonia* 4 (1943): 323-385.

Clausen, Jens. *Stages in the Evolution of Plant Species*. Ithaca, New York: Cornell University Press, 1951.

Clausen, Jens, David D. Keck, and William M. Hiesey. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 31 (1932): 201-205.

____________. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 32 (1933): 192-196.

____________. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 34 (1935): 201-206.

____________. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 35 (1936): 208-214.

____________. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 36 (1937): 204-214.

____________. "The Concept of Species Based on Experiment." *American Journal of Botany* 26 (1939): 103-106.

____________. *Experimental Studies on the Nature of Species I. Effect of Varied Environments on Western North American Plants*. Washington: Carnegie Institution of Washington Publication No. 520, 1940.

____________. "Regional Differentiation in Plant Species." *American Naturalist* 75 (1941): 231-250.

Clements, F.E. *Research Methods in Ecology*. Lincoln, Nebraska: The University Publishing Co., 1905.

Clements, F.E., H.M. Hall, W.T. Penfold, and H.L. Mason. "Transplant Experiments." *Carnegie Institution of Washington Yearbook* No. 24 (1925): 314-315.

Cockayne, L. and H.H. Allan. "The Bearing of Ecological Studies in New Zealand on Botanical Taxonomic Conceptions and Procedure." *Journal of Ecology* 15 (1927): 234-277.

"Concept of Genus, The." *Bulletin of the Torrey Botanical Club* 67 (1940): 349-389.

"Concept of Species from the Time of Linnaeus to the Present, The." *Proceedings of the Linnean Society of London* 150 (1938): 225-247.

Crampton, H.E. *Studies on the Variation, Distribution, and Evolution of the Genus Partula. The Species Inhabiting Tahiti.* Washington: Carnegie Institution of Washington Publication No. 228, 1916.

___________. *Studies on the Variation, Distribution, and Evolution of the Genus Partula. The Species of the Marina Islands, Guam and Saipan.* Washington: Carnegie Institution of Washington Publication No. 228A, 1925.

___________. *Studies on the Variation, Distribution, and Evolution of the Genus Partula. The Species Inhabiting Moorea.* Washington: Carnegie Institution of Washington Publication No. 410, 1932.

Crane, M.B. "The Origin and Behavior of Cultivated Plants." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Danser, B.H. "Ueber die Beguffe Komparium, Kommiskuum, und Konvivium und ueber die Entstehungsweise der Konvivium." *Genetica* 11 (1929): 399-450.

___________. "A Theory of Systematics." *Bibliotheca Biotheoretica* 4 (1950): 117-180.

Darlington, C.D. *Recent Advances in Cytology.* Philadelphia: P. Blakiston's Son and Co., Inc., 1932; 2nd edition, 1937.

___________. *The Evolution of Genetic Systems.* Cambridge: Cambridge University Press, 1939.

___________. "Taxonomic Species and Genetic Systems." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

De Beer, Gavin, ed., *Evolution.* Oxford: Clarendon Press, 1938.

De Beer, Gavin. "Embryology and Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

"Differences in the Systematics of Plants and Animals and their Dependence on Differences in Structure, Function, and Behavior in the Two Groups." *Proceedings of the Linnean Society of London* 153 (1941): 272-287.

"Discussion on Genetics and Taxonomy." *Report of the British Association for the Advancement of Science* (1937): 426-428.

"Discussion on Phylogeny and Taxonomy, A." *Proceedings of the Linnean Society of London* 152 (1940): 234-255.

Diver, C. "The Measurement of Ecological Factors of Use in Taxonomy." *Journal of Ecology* 27 (1939): 421-424.

___________. "The Problem of Closely Related Species Living in the Same Area." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Dobzhansky, Theodosius. "Geographical Variation in Lady-Beetles." *American Naturalist* 67 (1933): 97-126.

___________. "On the Sterility of Interracial Hybrids in *Drosophila pseudoobscura*." *Proceedings of the National Academy of Sciences* 19 (1933): 397-402.

___________. "A Critique of the Species Concept in Biology." *Philosophy of Science* 2 (1935): 344-355.

___________. "Genetic Nature of Species Differences." *American Naturalist* 71 (1937): 404-420.

___________. *Genetics and the Origin of Species*. New York: Columbia University Press, 1937; 2nd edition, 1941; 3rd edition, 1951; Columbia Paperback Edition, 1964.

___________. "What is a Species?" *Scientia* 61 (1937): 280-286.

___________. "Studies on the Genetic Structure of Natural Populations." *Carnegie Institution of Washington Yearbook* No. 38 (1939): 287-289.

___________. "Speciation as a Stage in Evolutionary Divergence." *American Naturalist* 74 (1940): 312-321.

Dobzhansky, Th. "Studies on the Genetic Structure of Natural Populations." *Carnegie Institution of Washington Yearbook* No. 39 (1940): 244-247.

____________. "Chromosomal Differences Between Races and Species of *Drosophila*." *University of Pennsylvania Bicentennial Conference in Cytology, Genetics, and Evolution.* Philadelphia: University of Pennsylvania Press, 1941.

____________. "Genetic Structure of Natural Populations." *Carnegie Institution of Washington Yearbook* No. 40 (1941): 271-276.

____________. "The Race Concept in Biology." *Scientific Monthly* 52 (1941): 161-165.

____________. "Studies on the Genetic Structure of Natural Populations." *Carnegie Institution of Washington Yearbook* No. 41 (1942): 228-234.

____________. "The Species Concept." *Revista de Agricultura* (Piracicaba, Brazil) 18 (1943): 441-442.

____________. "Genetic Structure of Natural Populations." *Carnegie Institution of Washington Yearbook* No. 43 (1944): 120-127.

____________. "On Species and Races of Living and Fossill Man." *American Journal of Physical Anthropology* 2 (1944): 251-265.

____________. "Mendelian Populations and their Evolution." *American Naturalist* 84 (1950): 401-417.

Dobzhansky, Th. and R.D. Boche. "Intersterile Races of *Drosophila pseudoobscura* Frol." *Biologische Zentralblatt* 53 (1933): 314-330.

Dobzhansky, Th. and Carl Epling. *Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and its Relatives*. Washington: Carnegie Institution of Washington Publication No. 544, 1944.

Dobzhansky, Th. and P.C. Koller. "An Experimental Study of Sexual Isolation in *Drosophila*." *Biologische Zentralblatt* 58 (1939): 589-607.

Du Rietz, G.E. "The Fundamental Units of Biological Taxonomy." *Svensk Botanisk Tidskrift* 24 (1930): 333-428.

Elton, Charles. *Animal Ecology.* New York: Macmillan Co., 1927; reprint edition, 1935.

____________. "Animal Ecology." *Encyclopedia Brittanica* 14th edition.

____________. "Preface to the Paperback Edition." in *Animal Ecology* by Charles Elton. London: Methuen & Co., Ltd., and Science Paperbacks, 1927; reprint edition, 1966.

Emerson, A.E. "The Origin of Species." *Ecology* 19 (1938): 152-154.

____________. "Taxonomic Categories and Population Genetics." *Entomological News* 56 (1945): 14-15.

Epling, Carl. "Scylla, Charybdis, and Darwin." *American Naturalist* 72 (1938): 547-561.

____________. "An Approach to Classification." *Scientific Monthly* 49 (1939): 1-8.

____________. "Taxonomy and Genonomy." *Science* 98 (1943): 515-516.

"Experimental Populations." *American Naturalist* 71 (1937): 5-68.

Faegri, K. "The Species Problem." *Nature* 136 (1935): 954-955.

____________. "Some Fundamental Problems of Taxonomy and Phylogenetics." *Botanical Review* 3 (1937): 400-423.

Ford, E.B. "Polymorphism and Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Gadow, Hans. *The Wanderings of Animals.* New York: G.P. Putnam's Sons, 1913.

Gause, G.F. *The Struggle for Existence.* New York: Williams & Wilkins Co., 1934; Dover Reprint Edition, 1971.

"Genetics and the Origin of Species." *Nature* 141 (1938): 310.

"Genetics and the Origin of Species." *Quarterly Review of Biology* 13 (1938): 211-212.

"Genetics and the Origin of Species." *Quarterly Review of Biology* 17 (1942): 73.

"Geographical Isolation as a Factor in Species Formation." *Proceedings of the Linnean Society of London* 150 (1938): 253-292.

Gilmour, J.S.L. "Whither Taxonomy?" *Report of the British Association for the Advancement of Science* (1936): 417.

___________. "A Taxonomic Problem." *Nature* 139 (1937): 1090-1042.

___________. "Taxonomy and Philosophy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

___________. "The Development of Taxonomic Theory Since 1851." *Nature* 168 (1951): 400-402. [note: erratum p. 500].

___________. "The Development of Taxonomy Since 1851." *Advancement of Science* (1952): 70-74.

Gilmour, J.S.L. and J.W. Gregor. "Demes: a Suggested New Terminology." *Nature* 144 (1939): 333.

Gilmour, J.S.L. and J. Heslop-Harrison. "The Deme Terminology and the Units of Micro-Evolutionary Change." *Genetica* 27 (1954): 147-161.

Gilmour, J.S.L. and W.B. Turrill. "The Aim and Scope of Taxonomy." *Chronica Botanica* 6 (1941): 217-219.

Gleason, H.A. "Age and Area from the Viewpoint of Phytogeography." *American Journal of Botany* 11 (1924): 541-546.

Goldschmidt, R. "Cynips and Lymantria." *American Naturalist* 71 (1937): 508-514.

___________. "Ecotypes, Ecospecies and Macroevolution." in *Richard Goldschmidt: Controversial Geneticist and Creative Biologist*. Boston: Birkhaüser Verlag, 1980.

Gregor, J.W. "Experimental Delimitation of Species." *New Phytologist* 30 (1931): 204-217.

___________. "Correspondence." *Journal of Botany* 70 (1932): 154-155.

Gregor , J.W. "The Ecotype Concept in Relation to the Registration of Crop Plants." *Annals of Applied Biology* 20 (1933): 205-219.

____________. "Experimental Taxonomy. IV. Population Differentiation in North American and European Sea Plantains Allied to *Plantago maritima* l." *New Phytologist* 38 (1930): 291-322.

____________. "Towards the New Systematics." *Nature* 146 (1940): 42-43.

____________. "The Units of Experimental Taxonomy." *Chronica Botanica* 7 (1942): 193-196.

____________. "The Ecotype." *Biological Review* 19 (1944): 20-30.

____________. "Ecotypic Differentiation." *New Phytologist* 45 (1946): 254-270.

Gregor, J.W., V. Davey, and J.M.S. Lang. "Experimental Taxonomy. I Experimental Garden Technique in Relation to the Recognition of Small Taxonomic Units." *New Phytologist* 35 (1936): 323-350.

Gregor, J.W. and F.W. Sansome. "Experiments on the Genetics of Wild Populations. I. Grasses." *Journal of Genetics* 17 (1927): 349-364.

____________. "Experiments on the Genetics of Wild Populations. II. *Phleum pratense* L. and the Hybrid *P. pratense* L. x *P. alpinum* L." *Journal of Genetics* 22 (1930): 373-387.

Haldane, J.B.S. "Heredity." *Encyclopedia Brittanica* 14th edition.

Hall, H.M. "Significance of Taxonomic Units and Their Natural Basis from the Point of View of Taxonomy." *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1571-1589.

____________. "Heredity and Environment - as Illustrated by Transplant Studies." *Scientific Monthly* 35 (1932): 289-302.

Hall, H.M. and Associates. "Experimental Taxonomy." *Carnegie Institution of Washington Yearbook* No. 25 (1926): 345-346.

Hall, H.M. and F.E. Clements. *The Phylogenetic Method in Taxonomy.* Washington: Carnegie Institution of Washington Publication No. 326, 1923.

Harland, S.C. "The Genetical Conception of the Species." *Biological Review* 11 (1936): 83-112.

Heilborn, O. "Significance of Taxonomic Units and Their Natural Basis from the Point of View of Cytology." *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1571-1589.

Hiesey, W.M. "Environmental Influence and Transplant Experiments." *Botanical Review* 6 (1940): 181-203.

Hindle, E. "Dr. G.C. Robson." *Nature* 156 (1945): 75.

Hogben, L.T. "Cytology." *Encyclopedia Brittanica* 14th edition.

____________. "Problems of the Origins of Species." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Huxley, J.S. "Natural Selection and Evolutionary Progress." *Report of the British Association for the Advancement of Science.* (1936): 81-100.

____________. "Clines: an Auxiliary Taxonomic Principle." 142 (1938): 219-221.

____________. "Species Formation and Geographical Isolation." *Proceedings of the Linnean Society of London* 150 (1938): 253-264.

____________. "Ecology and Taxonomic Differentiation." *Journal of Ecology* 27 (1939): 908-919.

____________. "Introductory: Towards the New Systematics." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

____________. "Evolution in Action." *Nature* 151 (1943): 347-348.

____________. *Evolution: The Modern Synthesis.* New York: Harper & Brothers, Publishers, 1943.

Huxley, J.S., ed., *The New Systematics*. London: Oxford University Press, 1940.

Jepsen, Glenn L., George G. Simpson, and E. Mayr, eds., *Genetics, Paleontology, and Evolution*. Princeton: Princeton University Press, 1949.

Kellogg, Vernon L. *Darwinism To-day*. New York: Henry Holt and Co., 1907.

Kinsey, A.C. *The Origin of Higher Categories in Cynips*. Indiana University Publication, Science Series No. 4 (1936).

____________. "Supraspecific Variation in Nature and in Classification from the Viewpoint of Zoology." *American Naturalist* 71 (1937(: 206-222.

Lotsy, J.P. *Evolution By Means of Hybridization*. The Hague: Martinus Nijhoff, 1916.

____________. "On the Species of the Taxonomist in its Relation to Evolution." *Genetica* 13 (1931): 1-16.

Marsden-Jones, E.M., V.S. Summerhayes, and W.B. Turrill. "Special Herbaria as Adjuncts to Modern Botanical Research." *Journal of Ecology* 18 (1930): 379-383.

Mather, K. and Th. Dobzhansky. "Morphological Differences between the 'Races' of *Drosophila pseudoobscura*." *American Naturalist* 73 (1939): 5-25.

Mayr, Ernst. "Speciation Phenomena in Birds." *American Naturalist* 74 (1940): 249-278.

____________. *Systematics and the Origin of Species*. New York: Columbia University Press, 1942.

____________. "The Bearing of the New Systematics on Genetical Problems: The Nature of the Species." *Advances in Genetics* 2 (1948): 205-237.

____________. "Speciation and Systematics." in *Genetics, Paleontology, and Evolution* ed. by G.L. Jepsen, E. Mayr, and G.G. Simpson. Princeton: Princeton University Press, 1949.

____________. "Speciation in Birds." *Proceedings of the Tenth International Ornithological Congress* (1950): 91-131.

Muller, H.J. "Bearing of the 'Drosophila' Work on Systematics." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Müntzing, A., O. Tedin, and G. Turesson. "Field Studies and Experimental Methods in Taxonomy." *Hereditas* 15 (1931): 1-12.

Nordenskiöld, H. "Cytogenetic Studies in the Genus *Phleum*." *Acta Agriculturae Suecana* 1 (1945): 1-137.

Patterson, J.T. "Drosophila and Speciation." *Science* 95 (1942): 153-159.

"Phylogeny in Relation to Classification." *Nature* 167 (1951): 503-505.

Ramsbottom, J. "Taxonomic Problems in Fungi." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

"Relation of Genetics to Geographical Distribution and Speciation, The." *American Naturalist* 74 (1940).

Rensch, B. *Das Prinzip Geographischer Rassenkreise und das Problem der Artbildung*. Berlin: Begrüder Barntraeger, 1929.

____________. "Some Problems of Geographical Variation and Species Formation." *Proceedings of the Linnean Society of London* 150 (1938): 275-285.

Richards, O.W. "The Formation of Species." in *Evolution* ed. by G.R. De Beer. Oxford: Clarendon Press, 1938.

____________. "The Use of Ecological Data in Taxonomy." *Journal of Ecology* 27 (1939) 406-408.

Richards, O.W. and G.C. Robson. "The Species Problem and Evolution." *Nature* 177 (1926): 345-347, 382-384.

Robson, G.C. "A Note on the Species as a Gene-Complex." *Annals and Magazine of Natural History* 11 (1923): 111-115.

____________. *The Species Problem*. London: Oliver and Boyd, 1928.

Robson, G.C. "Species: Biological Species." *Encyclopedia Brittanica* 14th edition.

Robson, G.C. and O.W. Richards. *The Variation of Animals in Nature.* New York: Longmans, Green and Co., 1936.

Salisbury, E.J. "Plants: Distribution and Ecology." *Encyclopedia Brittanica* 14th edition.

___________. "The Ecologist Appreciates and Criticizes the Taxonomist." *Journal of Ecology* 27 (1939): 402-405.

___________. "Ecological Aspects of Plant Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Sansome, F.W. and J. Philp. *Recent Advances in Plant Genetics.* Philadelphia: P. Blakiston's, Son & Co., Inc., 1932.

Shull, G.H. "Significance of Taxonomic Units and Their Natural Basis from the Viewpoint of Genetics." *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1578-1586.

"Significance of Taxonomic Units and Their Natural Basis." *Proceedings of the International Congress of Plant Sciences* (Ithaca, 1926) (1929): 1571-1589.

Simpson, G.G. "Supra-specific Variation in Nature and in Classification from the View-point of Paleontology." *American Naturalist* 71 (1937): 236-267.

___________. "Criteria for Genera, Species, and Subspecies in Zoology and Paleontology." *Annals of New York Academy of Sciences* 44 (1943): 145-178.

Sinnott, Edmund W. "The 'Age and Area' Hypothesis and the Problem of Endemism." *Annals of Botany* 31 (1917): 209-216.

Small, James. "The Age and Area Law: A Fundamental Law of Geographic Distribution." *Science Progress* 12 (1918): 439-449.

Smith, William Wright. "Some Aspects of the Bearing of Cytology on Taxonomy." *Proceedings of the Linnean Society of London* 145 (1933): 151-181.

"Speciation." *American Naturalist* 74 (1940).

"Species Concept, The." *American Naturalist* 75 (1941): 193-263.

Sprague, T.A. "Taxonomic Botany with Special Reference to the Angiosperms." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Stebbins, G. Ledyard Jr. *Variation and Evolution in Plants.* New York: Columbia University Press, 1950.

Sturtevant, A.H. *The North American Species of Drosophila.* Washington:Carnegie Institution of Washington Publication No. 301, 1921.

____________. "Essays on Evolution. III. On the Origin of Interspecific Sterility." *Quarterly Review of Biology* 13 (1938): 333-335.

____________. *The Classification of the Genus Drosophila, with Descriptions of Nine New Species.* University of Texas Publication No. 4213, 1942.

____________. "*Drosophila pseudoobscura.*" *Ecology* 25 (1944): 476-477.

Sturtevant, A.H. and Dobzhansky, Th. "Observations on the Species Related to New Forms of Drosophila affinis, with Descriptions of Seven." *American Naturalist* 70 (1936): 574-584.

Summerhayes, V.S. and W.B. Turrill. "Ecology and Taxonomy: the Taxonomist's Viewpoint." *Journal of Ecology* 27 (1939): 424-428.

"Supraspecific Variation in Nature and in Classification." *American Naturalist* 71 (1937): 206-276.

"Symposium on the Reciprocal Relationship of Ecology and Taxonomy, A." *Journal of Ecology* 27 (1939): 401-435.

"Systematics and the Origin of Species." *Quarterly Review of Biology* 18 (1943): 270.

"Systematics Association, The. Annual Report. VI. (1946-47)." *Proceedings of the Linnean Society of London* 160 (1948): i-iv.

"Systematics Association, The. Annual Report VII. (1947-48)." *Proceedings of the Linnean Society of London* 161 (1949): i- iv.

___________. "Annual Report. VIII. (1948-49)." *Proceedings of the Linnean Society of London* 162 (1951): i-iii.

___________. "Annual Report. IX. (1949-50)." *Proceedings of the Linnean Society of London* 162 (1951): iv-vi.

"Systematics in Relation to General Biology." *Nature* 140 (1937): 211-212.

Tansley, A.G. "A Symposium on the Reciprocal Relationship of Ecology and Taxonomy: Introduction." *Journal of Ecology* 27 (1939): 401-402.

Thacker, A.G. "The Dynamics of Distribution." *Science Progress* 17 (1923): 474-477.

Thorpe, W.H. "Ecology and the Future of Systematics." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Timofeef-Ressovsky, N. "Mutations and Geographical Variation." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Turesson, Göte. "The Species and Variety as Ecological Units." *Hereditas* 3 (1922): 100-113.

___________. "The Genotypical Response of the Plant Species to the Habitat." *Hereditas* 3 (1922): 211-347.

___________. "The Scope and Import of Genecology." *Hereditas* 4 (1923): 171-176.

___________. "The Plant Species in Relation to Habitat and Climate." *Hereditas* 3 (1925): 147-236.

___________. "Zur Natur and Begrenzung der Artenheiten." *Hereditas* 12 (1929): 323-334.

___________. "Genecological Units and their Classificatory Value." *Svensk Botanisk Tidskrift* 24 (1930): 511-518.

Turrill, W.B. "Species." *Journal of Botany* 63 (1925): 359-366.

Turrill, W.B. "Investigation of Plant Species." *Proceedings of the Linnean Society of London* 147 (1935): 104-105.

____________. "Contacts between Plant Classification and Experimental Botany." *Nature* 137 (1936): 563-566.

____________. "The Association for the Study of Systematics in Relation to General Biology." *Chronica Botanica* 4 (1938): 5-7.

____________. "The Expansion of Taxonomy With Special Reference to Spermatophyta." *Biological Review* 13 (1938): 342-373.

____________. "Taxonomy and Genetics." *Journal of Botany* 76 (1938): 33-39.

____________. "Principles of Plant Geography." *Kew Bulletin* (1939): 208-237.

____________. "Experimental and Synthetic Plant Taxonomy." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

____________. "The New Systematics." *Chronica Botanica* 6 (1940): 1-3.

____________. "Experimental Attacks on Species Problems." *Chronica Botanica* 7 (1942): 282-283.

____________. "Taxonomy and Phylogeny." *Botanical Review* 8 (1942): 247-270, 473-532, 655-707.

____________. "The Ecotype Concept: A Consideration with Appreciation and Criticism Especially of Recent Trends." *New Phytologist* 45 (1946): 34-43.

"Utility of the Species Concept, The." *American Journal of Botany* 10 (1923): 221-244.

Valentine, D.H. "The Units of Experimental Taxonomy." *Acta Biotheoretica* 9 (1949): 75-88.

Vavilov, N.I. "The New Systematics of Cultivated Plants." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Waddington, C.H. *An Introduction to Modern Genetics*. London: Allen and Unwin, 1939.

Wheeler, William Morton. *Essays in Philosophical Biology*. Cambridge: Harvard University Press, 1939.

__________. "Present Tendencies in Biological Theory." in *Essays in Philosophical Biology* by W.M. Wheeler. Cambridge: Harvard University Press, 1939.

White, M.J.D. *Animal Cytology and Evolution*. Cambridge: Cambridge University Press, 1945.

__________. "Chromosomes of the Vertebrates." *Evolution* 3 (1949): 379-381.

Williams, C.B. "On 'Type' Specimens." *Annals of the Entomological Society of America* 33 (1940): 621-624.

Willis, J.C. *Age and Area*. London: Cambridge University Press, 1922.

__________. *The Course of Evolution*. London: Cambridge University Press, 1940.

Wilmott, A.J. "Experimental Delimination of Species." *Journal of Botany* 70 (1932): 49-50.

__________. "Correspondence." *Journal of Botany* 70 (1932): 155.

Woodger, J.H. *Biological Principles*. New York: Harcourt, Brace and Co., 1929.

Worthington, E.B. "Geographical Differentiation in Fresh Waters with Special Reference to Fish." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

Wright, Sewell. "Statistical Consequences of Mendelian Heredity in Relation to Speciation." in *The New Systematics* ed. by J.S. Huxley. London: Oxford University Press, 1940.

__________. "The 'Age and Area' Concept Extended." *Ecology* 22 (1941): 345-347.