

In Twentieth-Century Botany, Experimental Taxonomy, 1920-1950: Experimentalists and Naturalists

Edmund White, Eileen Myles

Abstract

It is one of the most remarkable aspects of twentieth-century biology that the creation of a wide range of highly specialized professions has occurred. The advent of neo-Darwinian evolutionary theory, dubbed the Contemporary Synthesis by Julian Huxley, was perhaps the most effective effort to repair the consequent lack of coherence in modern biology. 1 Biologists have come to an agreement in the second part of this century on the basic processes of evolution. Biologists and historians both see this Modern Synthesis as the most important event in twentieth-century biology. 2 Modern Synthesis merged two formerly distinct schools of biologists according to one generally recognized historical interpretation. There was minimal interaction between geneticists and taxonomists previous to 1940, according to adherers of the theory. Taxonomists and geneticists worked in two seemingly contradictory fields "worlds of thought 4 Due to lack of communication, disagreements about the relevance of different research questions, and misunderstandings about basic evolutionary principles, this incompatibility was further aggravated. Communal interactions The emergence of several subfields within biology in the twentieth century is notable. Contemporary Synthesis, Julian Huxley's name for the advent of neo-Darwinian evolutionary theory, is perhaps the most effective effort to repair the lack of coherence in modern biology. 1 Throughout the second part of the twentieth century, scientists have come to an agreement on the basic processes of evolution. Biologists and historians both see this Modern Synthesis as the most important event in twentieth-century biology. 2 Modern Synthesis merged two formerly distinct schools of biologists according to one generally recognized historical interpretation. Adherents claim that before 1940, experimental biologists, particularly geneticists, and naturalists, particularly taxonomists, had little in the way of communication "in their own minds." 4 To make

matters even more difficult, there was little communication, disagreements about the value of specific study questions, and misunderstandings about basic evolutionary concepts. Messages sent and received between Evolution: The Modern Synthesis, by Julian Huxley (London: Allen and

Unwin, 1942). All of the chapters in Ernst Mayr and William B. Provine, eds., *The Evolutionary Synthesis*, focus on the Modern Synthesis as a

unifying force in twentieth-century biology (Cambridge, Mass.: Harvard University Press, 1980). Three articles in Ernst Mayr's *The Evolutionary Synthesis*, both in Mayr and Provine, provide a complete presentation of this interpretation: "Prologue: Some Thoughts on the History of the Evolutionary Synthesis" and "The Role of Systematics in the Evolutionary Synthesis. Life Science in the Twentieth Century, by Garland Allen (New York: Wiley, 1975), describes "the persistent division and hostility between laboratory and field workers," on p. 19. Confusion over Classification: A Case Study in the History of Botany, by John Dean, presents a similar division between the "orthodox" and "experimental" taxonomists. Barnes and Shapin ed (Beverly Hills, Calif.: Sage, 1979). "Prologue," p. 13, by Mayr. 17(2) (Summer 1984): 249-270, *Journal of the History of Biology*. It costs \$02.20 for O022 5010/84/0172/0249. D. Reidel Publishing Company published it in 1984. CHRISTOPHER JOHNSON When they did meet, the two groups were distinguished by hatred and intolerance. Only a few "bridge builders," the key contributors to the Modern Synthesis, were able to heal the divide between experimentalists and naturalists.

Literature Review

I believe that the naturalist-versus-experimentalist dichotomy is an oversimplification of twentieth-century biologists' controversies, but I don't dispute their presence or relevance. There are many lines of historical data that back up my position in this matter. It is clear from looking back over the years that the so-called naturalists and experimenters were not a distinct community. It's impossible to categorize all the great biologists of the era using these two broad labels. In addition, a number of notable biologists took an active interest in taxonomic issues, showing that taxonomists were open to techniques and ideas from other fields. Cooperative study integrating taxonomists, ecologists, geneticists and cytologists was common in the early 20th century. To be clear, the bulk of employees in these industries were not involved in

these cooperative enterprises. While such conduct may not have been restricted to the Modern Synthesis's most prominent people, it was more widespread than previously thought. An example of inter-discipline interaction will be examined in this article. A slew of botanists between 1920 and 1950 merged tried-and-true field and herbarium procedures from taxonomy with cutting-edge cytology, ecology, and genetics approaches to great effect. Genecology, genomics and population systematics are just few of the terms that have been used to characterize the wide range of study that has taken place along these boundaries. 6 The creation of this study was a challenge. Experimental taxonomy was not just a question of adopting well-accepted notions from other fields into categorization. This was a moment of profound methodological and theoretical shifts in every subject from which experimental taxonomy drew inspiration. Naturalists and experimentalists. Their goals and approaches also differed significantly. Because experimental taxonomy was formed on the edge, there were inevitable disagreements. Rather than being the result of a fight between experimentalists and naturalists, these disagreements were much more complicated. However, experimental taxonomy has created a considerable body of research with important implications for evolutionary theory, categorization and plant breeding.

The study of ecology and the study of experimental taxonomy

The pioneering ecologist F. E. Clements was the first to investigate the possibilities of a "experimental taxonomy," not taxonomists (1874-1945). Clements claimed as early as 1905 that taxonomists had failed to develop adequate classification systems while ecology relied on categorization. A "hairsplitting" orgy had been embarked upon by taxonomists, he asserted, leading to the creation of systems that were illogical and unnatural. To fix this problem, descriptive approaches would have to be substituted by rigorous experimental procedures... It seems that Clements had little trust in the capacity of taxonomists to undertake such reforms: the idea of putting forms supposed to be species to conclusive tests by experimentation has evidently not even occurred to descriptive botanists as yet.... The ecologist's experimental techniques will give an organized taxonomy, and the recording of minor and unconnected variances will lead to a cure from the outside. 7 Most taxonomists were put off by Clements' venomous comments. Nevertheless, H. M. Hall (1874-1932), a floristic taxonomist and unofficial curator of the University of California's

herbarium, shared his zest for experimenting. Hall and Clements joined together in 1918 to launch a Carnegie Institution of Washington-sponsored research program in experimental mental taxonomy. It wasn't until 1926 that Hall took full charge of the program after years of cooperation between ecologist and taxonomist.

Trials with Organ Transplants

Hall and Clements' experimental taxonomy relied heavily on "reciprocal transplants." It was found that members of two closely related species were able to coexist in the same environment. Cloned individuals were reintroduced into several environments in a more advanced variant. Taxonomic, ecological, and evolutionary goals all guided these investigations. Changes in environment may spur adaptation and variety, but they can also produce new forms, according to Clements and Hall. 8 In 1920, these kinds of trials were nothing new. Many years earlier, Austrian botanist Anton Kerner von Marilaun (1831-1898) had established gardens in the Tyrolean Alps, Innsbruck, and Vienna with alpine and lowland species transferred from the mountains. Many morphological changes were attributed to the environment, according to Kerner. "In no case was ever noticed any permanent or hereditary alteration in shape or color," he concluded. Nevertheless. 9 Gaston Bonnier (1853-1922), who conducted comparable transplant trials in the French Alps, found very different findings. When growing lowland plants at higher elevations, Bonnier claimed to have transformed them into alpine species. Aside from clarifying the contradicting evolutionary assertions of Kerner and Bonnier, the transplant trials conducted by Hall and Clements were not very noteworthy. Clements said that Bonnier's findings were confirmed by his observations of the adaptability and morphological plasticity of the plants he investigated. Contrary to his claims, Clements never published a thorough report of the tests he conducted along an altitude transect on Pikes Peak in Colorado. 11 Hall never wrote a book on the subject of artificial species change for Experimentalists and Naturalists. In the end, three younger collaborators questioned Clements' evolutionary arguments to some extent. However, the trio of Jens Clausen (1891-1969), David Keck (1903-), and William Hiesey (1903-) continued the Clementsian mission of experimental taxonomy while refuting Clements' evolutionary findings after a decade of study. 12 The Swedish botanist GSten Turesson was working on a separate methodology at the same time that Hall and Clements were researching reciprocal transplant procedures.

Reciprocal transplants in Turesson's trials were essentially the opposite. Instead of using plants from the same family in different locations, like Hall and Clements did with their experiments, Turesson used plants from a variety of natural settings to cultivate them in a laboratory setting. Turesson observed that despite the same settings, there was still a lot of variance within each species. Each population has been hand-picked to thrive only in a certain region. Many of the characters' characteristics persisted even after they were taken out of this ideal setting. Turesson came to the conclusion that a population's qualities were not only adaptable, but also heritable. Turesson's findings were rapidly recognized as significant due to the breadth and precision of his tests. In addition, Turesson provided a fascinating theoretical framework for discussing the ecological (and subsequently ecological-genetic) aspects of intraspecific variation by establishing a set of theoretical units. 13 Turesson argued that organisms only showed a fraction of their true genetic diversity. Natural selection tended to diminish this kind of variation in the wild. However, the possibility of a species with a huge range of variation that is unconstrained by natural selection exists. As a concept, Turesson coined the word "coenospecies" to describe a species' whole ecological potential. The term "ecospecies" was coined to describe the coenospecies as it existed in nature. While this is true, Turesson's research showed that ecospecies were not homogeneous groupings; each was made up of a "ecotype." There was an ecotype of a local population that had adapted to a certain set of environmental circumstances..

His Theoretical Model

It is difficult to overestimate Turesson's theoretical framework's impact. The phrases "coenospecies," "eco species," and "ecotype" have appropriately been referred to as the "units of experimental taxonomy" in the decades after 1922. 14 For a variety of reasons, these notions had an impact. An initial benefit of Turesson's method was that it looked to apply to several branches of botany. Concepts like coenospecies and ecotypes were first offered as ecological theories, however They also utilized similar notions to explore cytology, genetics, and taxonomy characteristics of plant species in subsequent papers by Turesson or his followers In addition to this, Turesson's ideas looked to be based on solid scientific research. Turesson's followers contended that coenospecies, ecospecies, and ecotypes could be clearly defined by trials, unlike the rather ambiguous word "species." 16 When it comes to the study of plant species, Turesson supplied

botanists with an excellent heuristic tool in the time we're looking at. When combined with field investigations, the genecological technique allows students to "enter inside the species" and study it from the inside out, as highlighted by taxonomist W. B. Turril (1890-1964), "to grasp it as a living and consequently evolving population."

Research on Organ Transplantation: Its Importance

There was little direct impact on taxonomic practice from the 1920s experiments undertaken by Turesson, Hall, and Clements. For example, Hall and Clements' seminal taxonomic work, "The Phylogenetic Method in Taxonomy," omitted data from transplant trials. 18 It's ironic, since despite Clements' dismissive sentiments about descriptive taxonomy, "The Phylogenetic Method" was fundamentally a descriptive treatise. In a lengthy preface, the writers revisited Clements' initial arguments for experimental taxonomy. Other than this, the monograph focused on three taxa in the family Compositae. 19 Transplant trials have taxonomic and ecological value despite their lack of immediate effect. When it comes to their approach to experimental taxonomy, ecologist Clements and evolutionary biologist Turesson have a lot in common: Plant reactions to environmental change may now be studied quantitatively thanks to transplant studies. It was a promising field of study during the 1930s. 2° Experiments with transplanted organisms may yield diagnostic evidence for taxonomic categorization, according to Hall. He gave many instances from genera he'd examined both descriptively and experimentally to back up his claim that he was right. 21 As an example, Hall observed minor variants of *Haplopappus* that remained unique even when grown in the same garden. He claimed that the groupings merited at least subspecific rank in light of the experimental findings. Instead of two separate kinds of *Haplopappus*, Hall discovered that they are all variants of the same species. The two types were identical when grown in the same environment.

The Twenties were a decade in American history.

In the early days of transplant experiments, the limits and possibilities of applying experimental approaches into general taxonomic practice were clearly shown. The bulk of taxonomists did not have easy access to experimental methodologies. Experiments involving organ transplantation took a long period and were quite labor intensive. The

experimental program recommended by Hall and Clements was beyond the resources of the typical taxonomist without the help of a big funded body like the Carnegie Institution. Experimentation in taxonomy also need a broad knowledge of biology. As biology became more specialized in the 1920s, it became more impossible for individual biologists to acquire such extensive competence. To bring these two groups closer together, experimental and natural scientists collaborated on the project. Hall, on the other hand, who had a better understanding of taxonomy than Clements, was a lot more successful in this quest. 23 Hall advocated experimental taxonomy in the 1926 International Congress of Plant Sciences. Hall maintained that classical taxonomy and experimental botany were mutually beneficial, calling for a "sympathetic synthesis of the opinions of experts in diverse domains." 24 Evolutionary issues necessitated the use of both techniques. According to Hall, taxonomy and other biological disciplines have recently forged closer ties, and he called for further collaboration among experts. 25 Hall was able to share his thoughts on experimental taxonomy at the international conference. Aside from taxonomists, here he had access to experts from a wide range of other botanical fields. If we adopt Hall's moderate assessment of congress events, then his views were well received. To his wife, Hall wrote that even senior taxonomists who will likely never utilize experimental techniques responded well to his exposition of experimental taxonomy. 26 Furthermore, he expected that his ideas will influence the work of next generations of taxonomists. Experimental taxonomy has come a long way since Hall's time. A collaborative approach was often necessary to study the borderexperimental taxonomy in the decades after the convention in 1926. In addition, Hall, Clements, and Turesson supported novel and unproven experimental approaches that had never been used before. There were legitimate reasons for taxonomic experts to be skeptical of new methodologies, according to Hall himself. He described the systematist as a conservative. For this reason, he is awaiting the presentation of conclusive evidence since he is concerned that employees in these connected disciplines may be misled by their own excitement. 22 In fact, throughout the 1930s and 1940s, experimental taxonomy's adoption was hampered by this conflict between categorization stability and advancements in research methods. Resistance to experimental taxonomy was probably increased by the personalities of Clements and Turesson, who both got entangled in bitter arguments with taxonomy experts. Clements, in particular, had a

penchant for making sarcastic comments about descriptive botany while pleading for the adoption of experimental taxonomy. It was awful to see such vitriol exchanged. In reality, Clements' study used a mix of descriptive and experimental methods. In addition, as more moderate proponents of experimental taxonomy contended, description and experimentation were completely compatible in theory and practice. Clements, who was known for his dogmatism and dominance, was an odd ally for

SCIENTIFIC EXPERTISE IN CYTOGENETICS

As initially proposed by F. E. Clements, experimental taxonomy was an ecological approach to the study of plant interactions. However, the focus of experimental taxonomy changed toward genetics and cytology in the 1930s and 1940s. Even in the 1920s, there were prominent cases of taxonomists and geneticists working together. The importance of experimental genetics to taxonomy was highlighted, for example, by E. B. Babcock (1877-1954) in a brief remark published in 1924. 27 He believed that even the simplest breeding experiments may help resolve certain taxonomic mysteries. As a result, comparing chromosomal morphology might provide valuable taxonomic information, as well. Even experimental taxonomists were ignoring genetic and cytological approaches, according to Babcock. With all due respect to their complexity, he stated that recent technological improvements were making these procedures more accessible to the average taxonomist. The interest in taxonomy among geneticists was not limited to Babcock throughout the 1920s. One session of the 1926 International Congress of Plant Sciences was dedicated to debates between taxonomists and cytologists. "Sympathetic synthesis" of biological disciplines was the theme of Hall's opening remarks at this meeting. Following his presentation, articles and comments explored the taxonomic importance of cytology and genetics. When it comes to complicated taxonomic groups like *Rubus* and *Rosa* and *Viola*, the geneticist G. H. Shull (1874-1954) recognized that experimental genetics has already helped to clarify the relationships between them. If taxonomy research is going on, why aren't gardens for experimental taxonomy built at every institution? " Shull said in his closing remarks. 28 There were some cautionary comments made by some of the pundits. When it comes to long-lived woody plants, for example, genetic approaches may confront daunting practical difficulties. 29 Papers and critiques from both experimentalists and naturalists, notwithstanding these misgivings, do not indicate major distinctions between them. As a

result, taxonomists, cytologists, and geneticists all agreed that approaches from different fields could be used together in a productive manner. a study of the tarweeds using genetics, cytology, ecology, and comparative morphology to combine the best of these disciplines. "Experimental" is how the authors described this "synthetic technique." The study's primary goal was to investigate the potential for collaborative research. The project, despite its limitations, looked to be a success. *Hemizonia congesta*, a genus of three previously reported species, was supported by chromosomal morphology and breeding experiment data. The immediate outcomes of the partnership were more important than the *Hemizonia* monograph. In the field of experimental taxonomy, both botanists had fruitful research projects. Babcock began study on *Crepis* dandelion-like blooms at the suggestion of Hall. For the study's main goal, researchers wanted to "show the effectiveness of a combined assault by genetic, cytologic, and taxonomic methodologies on challenges of systematic categorization in a big and complex genus of plants." 3- Babcock and his colleagues devoted their two decades of study to Hall's memory, culminating in a huge book. 2 His monumental monograph of the genus *Crepis* remains to this day the foremost attempt to explain the evolutionary history of a plant group, while simultaneously considering all possible avenues of approach," says Babcock's research associate, G. Ledyard Stebbins (1906-), who worked with Babcock on his *Crepis* research. One of the most important works in the field of evolutionary genetics was "Genus *Crepis*" by Babcock. However, it was a taxonomy study that combined field observations, herbarium research, cytological investigations, and genetic experiments in a novel manner. In the meanwhile, Hall was setting the groundwork for an equally large research project. By the end of the 1920s, Hall was in control of all experimental taxonomy research at the Carnegie Institution. By ending Clement's direct engagement in experimental taxonomy via a change in administrative roles, Hall was able to separate himself from an increasingly contentious collaboration and create his own research team. A doctoral student in taxonomy named David Keck and an undergraduate named William Hiesey were employed by Hall in 1926. Jens Clausen, a Danish cytogeneticist, joined Hall's study team five years later. 4 Clausen was already a well-known experimental taxonomist when he joined Hall, having done extensive study on the genus *Viola*. As a result the team of Hall, Clausen, Keck, and Hiesey never came to fruition. By the time Clausen got to America in 1932, Hall had already died. A broad plan for study had been set up by Hall.

It was Clausen, Keck, and Hiesey who considerably enlarged and essentially fulfilled this goal with their vast investigations on the taxonomy, evolution, and environmental reactions of various families of North American plants. This work was funded by the Carnegie Institution and continues. Babcock's group at the University of California and the Carnegie Institution's group at Stanford made the San Francisco Bay region a hotspot for experimental taxonomy. A worldwide trend has emerged in experimental taxonomy, on the other hand, with this increase. Similar research organizations developed in Great Britain, Scandinavia, and the Soviet Union in the 1930s and 1940s. Despite the lack of a formal professional organization or specialist publication, strong formal links among experimental taxonomists were formed and maintained through a variety of causes. To begin, a loose network of researchers was established via mail and personal acquaintanceship. During a trip to Europe in 1928, Hall, for example, met with a number of well-known botanists. W. B. Turrill's novel transplant investigations at the British Ecological Society, Göte Turesson's experiments in Sweden, and Jens Clausen's study on *Viola* in Denmark were all on display during this tour. When Clausen joined Hall's group in 1931, it reinforced the bond between the Carnegie Institution staff and the European personnel. The Carnegie Institution group's results were widely disseminated because to Clausen's frequent interaction with European botanists. Naturalists and experimentalists Second, informal groups increased links among experimental taxonomists. As an example, scholars in the San Francisco region began meeting frequently in the mid-1930s for dinner and discussion of the latest scientific developments. For these "biosystematists," the organization was a place where ideas could be debated openly and honestly. 36 Similar but more official groups were established in Great Britain at the same period. Societe for the Study of Systematics in Relation to General Biology was founded in part to encourage scientists to communicate and work together on research projects. The group's efforts were not limited to experimental taxonomy. In broad terms, the group was fairly effective in promoting debate among taxonomists and other professionals. 37 Finally, the promotion of experimental taxonomy by wellknown botanists aided its advancement. For many years, cytogenetic and taxonomic procedures were lauded by geneticists such as Edgar Anderson (1897-1969) and E. B. Babcock as well as taxonomists like W. B. Turrill for their synergistic effects. "In every case the two views supplement each other; the cytological 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."

Cytogenetics' Taxonomic Importance.

On at least two levels, cytology and genetics had a considerable taxonomic impact. In order to create taxonomic data, one may apply both descriptive cytology and experimental genetics, even if the theoretical evolutionary implications were not considered. For instance, cytological descriptions of cell sizes and chromosome counts gave taxonomists a new set of traits. Cytological investigations, on the one hand, amounted to improved comparative morphology. As a result, some taxonomists have seen chromosomal traits as just another kind of morphological information. The importance of cytological evidence was emphasized by most experimental taxonomists, however. Anderson calls this cytological description "more fundamentally important evidence for understanding the genetic architecture of life than the genetic structure itself. 39 For Turrill, cytology and biology were essentially the same field. Taxonomists were compelled to see the study of chromosomes as more than "highpowered morphology" due to the theoretical implications of this merged field. 40 Methodology that included descriptive cytology, experimental genetics, and cytogenetic theory was powerful. It shed fresh light on a number of "important" genera, in particular. It was common for these groupings to be constituted of "species complexes" linked by polyploidy. According to Stebbins, "There's nothing intrinsically tough about them. He does not have to suffer from an inferiority feeling because of his inability to discern obvious distinctions among the many species in his study. 41 During the 1930s and 1940s, experimental taxonomists increasingly focused on studying polyploidy. There were extensive investigations by Anderson on *Iris*; Babcock and Stebbins on *Crepis*; Clausen, Keck and Hiesey on *Layia* and *Madia* that revealed the usefulness of cytogenetic analysis in solving the so-called crucial genera. Although cytogenetic analysis was not a wholly experimental procedure, it was not totally separated from traditional taxonomic techniques. If just chromosome numbers were studied, taxonomic conclusions might frequently be drawn. These descriptive statistics, albeit promising, needed additional verification. Hybridization tests were the most reliable method for determining the link between polyploids. Although conventional field and herbarium data as well as cytological and genetic data were used in many significant polyploid complex investigations, this was not the case for all. Anderson found chromosome complements of 38,

70, and 108 in three species of *Iris*. The allopolyploid descendant of *Iris setosa* ($2n = 38$) and *Iris virginica* ($2n = 70$), he concluded, was the *Iris versicolor* ($2n = 108$) he found. 42 He used a wide range of evidence, including cytology, hybridization tests, comparative morphology, geography, and ecology to tell the story of *Iris*' evolutionary connections.

Taxonomists' Reaction to Cytogenetics

The experimental taxonomy research conducted in the 1930s and 1940s generated remarkable instances of cutting-edge, collaborative study. Botanists such as Anderson and Babcock used field observation, herbarium study, and cytogenetic analysis to produce cytogenetic and taxonomy studies. Clausen, Keck, and Hiesey are examples of productive research groups that effectively blended the abilities of a wide range of experts. Historians had supposed that taxonomists and other experts had a more limited conversation. Taxonomists and geneticists were not separated from each other, as some have claimed, as this evidence shows. Despite some instances of collaboration, the introduction of new methods and concepts into taxonomy was a source of friction. During the 1930s and 1940s, both proponents and opponents engaged in verbal combat. 43 However, despite the fact that these debates shed some information on the distinctions amongst botanists, the arguments were often vague and unconnected to specific experiments. Disagreements between naturalists and experimentalists may be more clearly shown via criticisms of individual experimental research studies. A noteworthy example is A. J. Wilmott's (1888-1950) reaction to J. W. Gregor's (1900-present) experimental investigation of grasses of the genus *Phleum*, which he saw as a threat. Because of this, the debates are shown to be more complicated than they appear to be at first. Gregor was more interested in ecological genetics than taxonomy, despite his sincere enthusiasm for the subject. For his cytogenetic studies on *Phleum* he published *Delimitation of Species* in 1944. Turesson's theoretical model of plant species was used by the author to try and explain the data in the article. A coenospecies was formed between *P. pratense* and *P. alpinum* due to the restricted gene flow between them. Based on chromosomal counts, this coenospecies, *Phleum alpinum pratense*, was separated into four ecospecies: Finally, facies was used to further split each ecospecies into a slew of ecotypes. The simplicity of Gregor's quad rinomial system makes it difficult to endorse it. Nonetheless, he contended that unlike categories based on gross morphology his method effectively represented evolutionary links. In particular, Wilmott was

enraged by Gregor's claim that taxonomists rely only on gross morphology and are uninterested in evolutionary links, which Wilmott took issue with. It is unfortunate that certain taxonomists lack understanding of current genetics and cytology, but at the same time, it is regrettable that some geneticists lack knowledge of taxonomy. 46 Journal of Botany contact between Wilmott and the two botanists ensued after his response. 47 WilmottGregor seems to be a debate between a naturalist and an experimentalist at first glance. After all, a simple dichotomy between the two guys does not do justice to how they differed from one other. Gregor recognised the need for both experimental and descriptive data in order to arrive at an accurate categorization. Gregor's 1931 publication, although emphasizing cytogenetic data, also emphasized the significance of comparative morphology. It is possible that because Gregor's brief article was not an exhaustive taxonomic study of the two species of *Phleum*, his proposals illustrated the utility of Turesson's theoretical system and did not necessarily constitute a definitive reorganization of the Genus *Phleum*, as he had previously stated. In hindsight, Gregor should have made his warning clearer. Wilmott obviously considered Gregor's essay as more than an instance of a revolutionary process. Wilmott's criticism of Gregor's reclassification of *Phleum* must be seen as an argument for taxonomic stability rather than simply an attack on cytogenetic analysis per se, because Wilmott felt that Gregor was not only trying to reclassify *Phleum* on the basis of insufficient evidence, but was also advocating Turesson's units as valid taxonomic nomenclature. He had a lot of criticisms for Gregor's research. Turesson's units were an unneeded burden on the nomenclature of the past, he said in the first place. This wasn't a one-of-a-kind remark. In the field of experimental taxonomists, Turesson's approach was not universally accepted. Despite their interest in Turesson's theoretical papers, not all of them considered the genecological units to be valid taxonomic categories. On the other hand, Wilmott took issue with how much importance Gregor placed on cytogenetic data. Furthermore, he opposed the idea of altering existing categorization schemes on the basis of innovative methodologies, claiming that the more conventional taxonomic information was as flexible. 48 Wilmott also suggested that morphological and distributional variables, as well as cytogenetic criteria, contributed to the "naturalness" of species. Gregor ignored standard taxonomic data in favor of an approach that had not been well verified. Not all cytogenetic data is reliable, and Wilmott's mistrust was not reactive in nature. Cytology was a fast evolving science in the

1930s. The basic concepts of chromosomal mechanics were hotly debated by cytologists, who were themselves divided on the subject. Consider C. D. Darlington's 1932 publication, *Recent Advances in Cytology*, today considered a foundational work in the field of cytogenetic theory. 49 Taxonomists may be justified in questioning the incorporation of cytogenetic data into categorization in light of these basic disputes among top cytologists. Using the naturalist/experimentalist dichotomy to analyze the Wilmott-Gregor argument tends to misunderstand the nature of debates concerning experimental taxonomy controversy. Gregor and Wilmott's disagreements sprang from disagreements among experimental taxonomists. Many people disagreed over whether or not taxonomic theory needed to be revised. Some experimental taxonomists argued that a comprehensive revision was warranted by discoveries in cytogenetics. Taxonomic theory was resisted by those who agreed with Wilmott's concerns about taxonomic stability. Despite the naturalist vs. experimentalist debate, experimental taxonomists thought their study was perfectly consistent with conventional taxonomy. Experimental taxonomists like Gregor, who established a clear line between experimental and conventional taxonomy, were not immune to this trend.

CONCLUSION

Botanists who contributed to the development of experimental taxonomy were motivated by a wide range of reasons. Even while experimental taxonomy was never just a taxonomic endeavor, classification enhancement was clearly one of the primary goals of the study. Experimental taxonomists mostly agreed with Hall and Clements that experimental approaches provided a more objective basis for categorization. Taxonomy gained a new depth as a result of these techniques, one that field and herbarium investigations alone could not match. Traditional taxonomic approaches were never totally separated from experimental methodologies. Experimental taxonomists used both descriptive and experimental techniques in their work. The majority of scientists willingly admit that they owe a debt to classical taxonomy. It wasn't only experimentalism that made twentieth-century taxonomy more rigorous, though. Through the expanded use of numerical methodologies in specific statistics, the experimental and descriptive sides of taxonomy have both been enhanced ~ Experimental taxonomists were interested in categorization from the beginning. Many researchers, on the other hand, came to their work from disciplines other than taxonomy.

Classification was of secondary importance to these botanists, who were more interested with ecological and genetic issues. Babcock and Stebbins' 1938 investigation of *Crepis* s3 (and Babcock's final monograph on the genus, published in 1947), for example, shows no evidence that they made a clear difference between taxonomic and cytogenetic results. A series of publications, "Experiments on the Nature of Species," started by the Carnegie Institution group in 1940, included ecological and cytogenetic findings. The fact that experimental taxonomists accomplished large-scale investigations rather than just taxonomic or cytogenetic ones explains a great deal about the value of their work. Much of experimental taxonomy was driven primarily by evolutionary considerations. As early as the second decade of the twentieth century, Hall and Clements urged taxonomists to embrace a clearly evolutionary approach to study. Experimental taxonomists are likely to agree with Hall when he said, "If there be any organic evolution, then taxonomy deals with the results of evolution, which assigns to taxonomy both its highest duty and its greatest responsibility." s4 The theoretical approaches of experimental taxonomists were diverse, other from a shared interest in evolution. Researchers at Carnegie Institution for Science have a wide range of perspectives on evolution. Clements pioneered experimental taxonomy as part of his Lamarckian investigation into adaptation and speciation. It was a wide concern for evolutionary issues that prompted Hall's study. Instead than using particular evolutionary mechanisms, Hall used a generic understanding of evolutionary processes to determine phylogenetic connections. Some of his subsequent colleagues at the Carnegie Institution publicly distanced themselves from Clements' theoretical approach. Clausen, Keck, and Hiesey's neo-Darwinian interpretations of adaptation and speciation could not have been more different from Clements's. To be sure, Clements' work and that of subsequent Carnegie scientists have many commonalities despite their divergent theoretical perspectives. The first book of "Experimental Studies on the Nature of Species" continued the Clementsian study agenda in terms of research questions and methods. Clausen, Keck, and Hiesey's book sprang out of Clements's preliminary description of transplant experimentation in the early twentieth century. For the Carnegie Institution research group, the common ground with experimental taxonomists in general was not a philosophical one, but one of technique. Amidst the demise of evolutionary theory, Clements' interest in cutting-edge experimentation remained. Experimentation in taxonomy was fraught with

difficulties. During the years 1920-1950, botanical study in this region was still a hybrid. Experimental taxonomy's goals and scope were never fully specified. It is because of this that experimental taxonomists dispute on the relationship between their study and other botanical efforts. Experimental taxonomists have questioned the 'taxonomic' character of their study, even if it is closely linked to general taxonomy; However, there were still issues even if taxonomy could be defined as a subfield of this hybrid study. When new taxonomy techniques and theories started flooding the field, taxonomists were understandably dubious. The domains from which experimental taxonomists drew, from 1920 to 1950, were Experimentalists and Naturalists themselves, who were experiencing substantial theoretical and methodological changes, were not just integrating well-accepted methodologies from ecology and cytogenetics. Despite difficulties and disagreements, experimental taxonomists contributed significant categorization advancements. As a result, they made substantial advances to the study of plant ecology and the development of genetic variation. It is clear that twentieth-century botanists were not confined to naturalist and experimentalist groups. An early example of inter-specialty collaboration is the 1926 International Congress of Plant Sciences combined session of taxonomists, cytologists, and geneticists. There was no evidence of the alleged antagonism and intolerance between experimentalists and naturalists in the presentations and comments delivered at this session. They also don't imply that geneticists and taxonomists exist in separate, incompatible mental realms.. International conferences were not the only place where taxonomists and other experts could meet and discuss their work. Discussions among experts seem to have been commonplace in the 1930s. Many groups of biologists from various fields met for discussion, such as the Biosystematists and the

Society for the Study of Systematics in Relation to General Biology. Several renowned twentiethcentury botanists' diverse scientific interests are overshadowed by the naturalist-experimentalist divide. The majority of experimental taxonomists are neither naturalists nor experimentalists in the traditional sense. Some of the most well-known and well-respected traditional taxonomists of the 20th century have included Hall, Keck, and Turrill. Numerous experts from domains other than taxonomy also showed a strong interest in taxonomic issues, not only in experimental aspects.. Anderson, for example, proposed a variety of modifications to improve the statistical analysis of herbarium collections. According to this

investigation into the history of experimental taxonomy, there is a more complex link between experimentalism and taxonomy than the naturalist-versus-experimentalist opposition suggests. Experimental taxonomy was developed by F. E. Clements as a reaction to descriptive botany. In hindsight, this revolution was not fiercely fought and failed to be finished effectively. The experimental taxonomy approach to botanical study was never really experimental. Methods from classical taxonomy were frequently used by even the most enthusiastic experimentalists. Field observation and herbarium approaches may be used together in experimental taxonomy, according to moderate advocates. An amazing amount of work was produced between 1920 and 1950 in an effort to combine cytogenetics, ecology, and taxonomy into a single discipline. However, this union was neither a total rewrite of taxonomic theory of practice or a condemnation of descriptive botany.

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Refarences

1. Julian Huxley, *Evolution: The Modern Synthesis* (London: Allen and Unwin, 1942).
2. The Modern Synthesis as a unifying force in twentieth-century biology is a general theme of all the essays in Ernst Mayr and William B. Provine, eds., *The Evolutionary Synthesis* (Cambridge, Mass.: Harvard University Press, 1980).
3. This interpretation is comprehensively presented by Ernst Mayr in two articles, "Prologue: Some Thoughts on the History of the Evolutionary Synthesis" and "The Role of Systematics Evolutionary Synthesis," both of which appear in Mayr and Provine, *The Evolutionary Synthesis*. Garland Allen mentions "the longstanding separation and distrust between laboratory and field workers" in his *Life Science in the Twentieth Century* (New York: Wiley, 1975), p. 19. A somewhat similar distinction between "orthodox" and "experimental" taxonomists is presented by John Dean, "Controversy over Classification: A Case Study in the History of Botany," in *Natural Order: Historical Studies in Scientific Culture* Barry Barnes and Steven Shapin ed. (Beverly Hills, Calif.: Sage, 1979).
4. Mayr, "Prologue," p. 135. *Ibid.*, pp. 40-42.

6. I shall use the term "experimental taxonomy," since it appears to have enjoyed wide currency between 1920 and 1950. It was used as a general descriptive term referring to the use of cytological, ecological, and genetic methods for the study of systematic relationships among plants. In referring to specific botanists as experimental taxonomists, I am not necessarily implying that they themselves claimed the designation; rather, I am suggesting that they shared a particular methodology and a loose set of common objectives.

7. Frederic E. Clements, *Research Methods in Ecology* (Lincoln, Nebr.: University Publishing Co., 1905), pp. 12 - 13.

8. F. E. Clements and H. M. Hall, "Experimental Taxonomy," *Carnegie Inst. Wash. Yearb.*, 18 (1919), 334-335.

9. Anton Kerner von Marilaun, *The Natural History of Plants*, trans. F. W. Oliver (New York: Holt, 1895), pt. 2, p. 514. Emphasis in original.

10. Bonnier's experiments were flawed by methodological problems. What he claimed to be transformed lowland species may well have been related alpine species that had invaded the experimental garden. A critical analysis of Bonnier's research is provided by William M. Hiesey, "Environmental Influence and Transplant Experiments," *Bot. Rev.*, 6 (1940), 181-203.

11. Aside from brief accounts published in *Carnegie Institution of Washington Yearbook* beginning in 1918, Clements' only discussion of experimental speciation was in an article devoted primarily to experimental methodology. In the paper he deferred detailed discussion to a later report - which was, however, never published. See Frederic Clements, "Experimental Methods in Adaptation and Morphogeny," *J. Ecol.*, 17 (1929), 357-379.

12. Clements' experiments probably were marred by the same methodological problems encountered by Bonnier. Hall and his associates were unable to confirm any of Clements' experimental results. See Hiesey, "Environmental Influence," pp. 185-187.

13. Göte Turesson, "The Genotypical Response of the Plant Species to the Habitat," *Hereditas*, 3 (1922), 211-347. I have discussed the development of Turesson's ideas in greater detail in "Experimental Taxonomy, 1930-1950: The Impact of Cytology, Ecology, and Genetics on Ideas of Biological Classification" (Ph.D. diss., Oregon State University, 1982).

14. J. W. Gregor, "The Units of Experimental Taxonomy," *Chron. Bot.*, 7 (1942), 193-196; D. H. Valentine, "The Units of Experimental Taxonomy," *Acta Biotheoret.*, 9 (1949), 75-88.
15. The term "genecology" was coined by Turesson to refer to the ecological study of species. Genecology later became associated with ecological genetics. However, in his early writings Turesson made a clear distinction between genetics and ecology. S~e G6te Turesson, "The Scope and Import of Genecology," *Hereditas*, 4 (1923), 171-176.
16. Turesson's system was one of several nomenclatorial reforms proposed by experimental taxonomists. For a detailed discussion see Hagen, "Experimental Taxonomy."
17. W. B. Turrill, "The Ecotype Concept," *New Phytologist*, 45 (1946), 34-43.
18. Harvey Monroe Hall and Frederic E. Clements, "The Phylogenetic Method in Taxonomy," *Carnegie Inst. Wash. Publ. no. 326* (1923).
19. Although methodologically traditional, the monograph was controversial because Hall and Clements "lumped" a larger number of species into a few comprehensive ones. This was a direct attack on the earlier work of P. A. Rydberg, who responded to Hall and Clements in "Scylla and Charybdis," *Proc. Internat. Cong. Plant ScL* (1926), 1539-51.
20. The results of two decades of transplant experiments were compiled in 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 Inst. Wash. Publ. no. 520* (1940).
21. H. M. Hall, "Heredity and Environment - as Illustrated by Transplant Studies," *Sci. Monthly*, 35 (1932), 289-302.
22. H. M. Hall, "Significance of Taxonomic Units and Their Natural Basis from the Point of View of Taxonomy," *Proc. Internat. Cong. Plant ScL* (1926), 1571-74.
24. Hall, "Significance of Taxonomic Units."
26. H. M. Hall, "Letter to Carlotta Case Hall - August 21, 1926," H. M. Hall papers, University of California, Berkeley, Bancroft Library.
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28. George H. Shull, "Significance of Taxonomic Units and Their Natural Basis: Point of View of Genetics," *Proc. Internat. Cong. Plant Sci.* (1926), 1578- 86. Emphasis in original.
29. K. M. Wiegand, "Discussion of Dr. H. M. Hall's Paper," *Proc. Internat. Cong. Plant ScL* (1926), 1575-76.
30. Ernest Brown Babcock and Harvey Monroe Hall, "Hernizoniacongesta. A Genetic, Ecologic, and Taxonomic Study of the Hay-Field Tarweeds," *Univ. Cal. Publ. Bot.*, 13 (1924), 15-100.