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

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One of the striking features of twentieth-century biology has been the development of diverse, highly specialized fields. Perhaps the most successful attempt to remedy the resulting lack of unity in modern biology has been the rise of neo-Darwinian evolutionary theory, termed by Julian Huxley the Modern Synthesis.[1] During the second half of this century a consensus has developed among biologists concerning the primary mechanisms of evolution. This Modern Synthesis has been hailed by biologists and historians alike as the primary integrative event in twentieth-century biology.[2]

According to one widely accepted historical interpretation, the Modern Synthesis unified two previously isolated groups of biologists. Its adherents argue that prior to about 1940 there was little exchange between experimental biologists, notably geneticists, and naturalists, notably taxonomists.[3] Geneticists and taxonomists worked within two apparently incompatible "conceptual worlds."[4] This incompatibility was exacerbated by lack of communication, disagreement over the significance of various research problems, and misconceptions concerning fundamental evolutionary principles. Exchanges between

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 in the 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. 13.

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the two groups, when they did occur, were marked by intolerance and hostility. The rift between experimentalists and naturalists was resolved only through the efforts of a few "bridge builders," the major contributors to the Modern Synthesis.[5]

Without denying either the existence or the significance of controversies among twentieth-century biologists, I contend that the naturalist-versus-experimentalist dichotomy is an oversimplification. My contention rests upon a number of lines of historical evidence. First, examination of scientific activity between 1920 and 1950 indicates that the so-called naturalists and experimentalists were far from discrete groups. There are many important biologists of the period who cannot be adequately characterized by either of these broad designations. In addition, among taxonomists there was considerable interest in methods and ideas from other disciplines, and a number of important biologists took an active interest in taxonomic problems. Indeed, between 1920 and 1950 where were several notable examples of cooperative research involving taxonomists, ecologists, geneticists, and cytologists. To be sure, such cooperative ventures did not involve a majority of workers in any of these fields. But such activity was more prevalent than has been supposed and was certainly not limited only to the major figures in the Modern Synthesis.

In this article I shall analyze one episode of interaction among biologists from various disciplines. Between 1920 and 1950 a number of botanists combined traditional field and herbarium methods from taxonomy with innovative techniques from cytology, ecology, and genetics. The diverse body of research that developed along the borders of these fields has been described variously as synthetic taxonomy, genecology, genonomy, population systematics, biosystematics, and experimental taxonomy.[6] The development of this body of research was problematic. Experimental taxonomy was not merely a matter of incorporating into classification well-accepted ideas from other areas. All of the fields from which experimental taxonomy borrowed were undergoing major methodological and theoretical changes at this time.

5. 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.

Furthermore, their aims and methods were not entirely compatible. Since experimental taxonomy developed on the borderlines, conflicts inevitably arose. These conflicts were complex and cannot be interpreted as merely the product of competing experimentalist and naturalist paradigms. Despite the disagreements, experimental taxonomy produced an impressive body of research with significant implications for evolutionary theory, classification, plant breeding, and ecology.

ECOLOGY AND EXPERIMENTAL TAXONOMY

The possiblities for an "experimental taxonomy" were first explored not by taxonomists, but by the pioneer ecologist F. E. Clements (1874–1945). As early as 1905 Clements argued that while ecology depended upon classification, taxonomists had failed to provide adequate classification systems. Rather, he claimed, taxonomists had embarked upon an orgy of "hair-splitting," producing systems that were subjective, artificial, and impractical. To remedy this situation, descriptive techniques would have to be replaced by rigorous experimental methods. Clements obviously had little faith in taxonomists' ability to initiate such reform:

> The thought of subjecting forms presumed to be species to conclusive test by experiment has apparently not even occurred to descriptive botanists as yet. . . The remedy will come from without through the application of experimental methods in the hands of the ecologist, and the cataloguing of slight and unrelated differences will yield to an ordered taxonomy.[7]

Clements' caustic attacks undoubtedly alienated him from most taxonomists. Nonetheless, his enthusiasm for experimentation was shared by H. M. Hall (1874–1932), a floristic taxonomist and unofficial curator of the herbarium at the University of Claifornia. In 1918 Hall joined Clements in initiating a research program in experimental taxonomy sponsored by the Carnegie Institution of Washington. This collaboration between ecologist and taxonomist lasted until 1926, when Hall gained complete control over the program.

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

Transplant Experiments

Experimental taxonomy as practiced by Hall and Clements primarily involved "reciprocal transplants." A member of a given species was transplanted into the habitat occupied by a member of a closely related species, and vice versa. In a more sophisticated variation clones of a single individual were transplanted into a variety of habitats. The objectives of these experiments were taxonomic, ecological, and evolutionary. According to Clements and Hall, their aim was "to determine the effect of changed and measured habitats in causing adaptation and variation and in producing new forms."[8]

Such experiments were not new in 1920. Several decades earlier the Austrian botanist Anton Kerner von Marilaun (1831–1898) had transplanted various alpine and lowland species into gardens located in the Tyrolean Alps, Innsbruck, and Vienna. Kerner reported numerous morphological modifications attributable to the environment. Nonetheless, he concluded, "*in no instance was any permanent or hereditary modification in form or colour observed*."[9] Quite different results were reported by Gaston Bonnier (1853–1922), who completed similar transplant experiments in the French Alps. Bonnier claimed to have converted numerous lowland species to alpine species by planting them at a higher elevation.[10]

While Hall and Clements' transplant studies were significant (for reasons to be discussed), they did little to clarify the conflicting evolutionary claims of Kerner and Bonnier. Greatly impressed by the adaptability and morphological plasticity of the plants that he studied, Clements claimed confirmation of Bonnier's results. Despite his claims that species had been experimentally transformed along an altitudinal transect on Pikes Peak in Colorado, Clements never published a detailed account of these experiments.[11] Hall never committed himself in print

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.

on the question of artificial transformation of species. Eventually three of his younger associates cast considerable doubt on Clements' evolutionary claims. Ironically, while the team of Jens Clausen (1891–1969), David Keck (1903–), and William Hiesey (1903–) perpetuated the Clementsian program of experimental taxonomy and perfected his transplant techniques, they effectively refuted the evolutionary conclusions of a decade of Clements' research.[12]

While Hall and Clements were developing reciprocal transplant methods, a quite different technique was being perfected by the Swedish botanist Göte Turesson. Turesson's experiments were essentially the inverse of reciprocal transplants. Whereas Hall and Clements placed related plants in contrasting environments, Turesson brought plants from a range of natural habitats into cultivation in a controlled experimental garden. Despite uniform conditions, Turesson discovered that considerable intraspecific variation was maintained. Each population had been selected for existence in a particular local habitat. Even when removed from this optimum environment, many of the characteristics remained. Turesson concluded that the characteristics of a population were not only adaptive, they were hereditarily stable.

Because his experiments were extensive and quantitative, Turesson's results were quickly recognized as important. More significantly, Turesson placed these results in a provocative theoretical framework by formulating a set of theoretical units that could be used to discuss the ecological (later ecological-genetic) aspects of intraspecific variation.[13] According to Turesson, a species exhibited only part of its potential variability. In nature this variability was generally reduced by natural selection. One could, however, conceive of an enormously variable species unfettered by natural selection. Such a conceptual entity, encompassing the total ecological potential of the species, Turesson termed the "coenospecies." The coenospecies as it actually

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).

existed in nature was designated the "ecospecies." However, as Turesson believed his experiments demonstrated, ecospecies were not homogeneous groups; each was composed of an array of ecological races, or "ecotypes." The ecotype was a local population adapted to a particular set of environmental conditions.

Turesson's Theoretical System

The influence of Turesson's theoretical scheme can hardly be overestimated. During the decades following 1922 his conception of plant species was so widely discussed that the terms "coenospecies," "ecospecies," and "ecotype" justifiably have been referred to as the "units of experimental taxonomy."[14]

These concepts were influential for a number of reasons. First, Turesson's system appeared to be applicable in a variety of botanical fields. Originally coenospecies, ecospecies, and ecotypes were proposed as ecological concepts.[15] In later writings Turesson and his followers used these concepts to discuss cytological, genetic, and taxonomic aspects of plant species as well. Second, Turesson's concepts appeared to have a firm experimental basis. Unlike the seemingly nebulous term "species," Turesson's followers argued that coenospecies, ecospecies, and ecotypes could be rigorously delimited through experiments.[16] Finally, Turesson provided botanists with a dynamic model of plant species, a model that had great heuristic value during the period we are considering. As the taxonomist W. B. Turril (1890–1964) 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."[17]

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. See Göte 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.

The Significance of Transplant Experiments

The experimental studies conducted during the 1920s by Turesson, Hall, and Clements did not immediately influence taxonomic practice. For example, Hall and Clements themselves did not include data from transplant experiments in their major taxonomic publication, "The Phylogenetic Method in Taxonomy."[18] Ironically, despite Clements' condescending remarks concerning descriptive taxonomy, "The Phylogenetic Method" was essentially a descriptive work. In an extended introduction the authors reiterated the arguments for experimental taxonomy originally put forward by Clements in 1905. Beyond this, the monograph was a fairly traditional discussion of three genera in the family Compositae.[19]

Despite the lack of immediate impact, transplant experiments did have taxonomic as well as ecological significance. Both Clements and Turesson approached experimental taxonomy primarily as ecologists interested in adaptation. The transplant experiments provided a method for quantitatively studying the responses of plants to environmental changes. Such studies continued to be a fruitful area of research throughout the 1930s.[20] Hall, primarily interested in taxonomic problems, argued that in certain cases transplant experiments could provide diagnostic evidence for classification. To bolster this contention, he cited several examples from genera that he had studied both descriptively and experimentally.[21] For example, in the genus *Haplopappus* Hall discovered minor varieties that remained morphologically distinct even when raised under similar garden conditions. Given this experimental evidence, he argued that the groups deserved at least subspecific status. Conversely, Hall found that two apparently distinct forms of *Haplopappus* were environmental modifications of

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 Sci.* (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.

a single species. When raised under similar conditions, the two forms were identical.

The Decade of the Twenties

The early transplant experiments illustrate the limitations as well as the potential involved in incorporating experimental methods into general taxonomic practice. Experimental methods were not readily available to the majority of taxonomists. Transplant experiments were laborious and time-consuming. Without the support of a major funding organization such as the Carnegie Institution, the experimental program advocated by Hall and Clements was a luxury beyond the means of the average taxonomist. In addition, experimental taxonomy implied expertise in more than one biological discipline. By the 1920s biology was becoming sufficiently specialized that such broad expertise was increasingly difficult for individual biologists to attain. Consequently, experimental taxonomy often required a team approach to research. Finally, the experimental methods advocated by Hall, Clements, and Turesson were relatively new and untested. As Hall himself noted, taxonomists had rational grounds for questioning the validity of the new methods. "The systematist is a conservative," he said. "He is fearful that workers in these related fields may be self-deceived by their own enthusiasm, and hence he awaits presentation of final proofs."[22] Indeed, this tension between stability of classification and innovation in research techniques continued to pose problems for the acceptance of experimental taxonomy during the 1930s and 1940s.

The reluctance to accept experimental taxonomy was undoubtedly exacerbated by the personalities of Clements and Turesson, both of whom became embroiled in acrimonious exchanges with taxonomists. Clements in particular tended to combine appeals for the acceptance of experimental taxonomy with condescending remarks about descriptive botany. Such polemics were unfortunate. In actual practice Clements used a combination of descriptive and experimental techniques in his research. Furthermore, as more moderate advocates of experimental taxonomy argued, both in theory and in practice, description and experimentation were entirely compatible.

Dogmatic and overbearing, Clements was an unlikely agent for

22. H. M. Hall, "Significance of Taxonomic Units and Their Natural Basis from the Point of View of Taxonomy, " *Proc. Internat. Cong. Plant Sci.* (1926), 1571–74.

bringing the two groups together. Hall, who was in substantial agreement with Clements on taxonomic matters, was much more successful in this endeavor.[23] At the 1926 International Congress of Plant Sciences, Hall presented two papers advocating experimental taxonomy. Calling for a "sympathetic synthesis of the viewpoints of specialists in different fields," Hall argued that traditional taxonomy and experimental botany were mutually supportive.[24] Both approaches were required for the solution of fundamental evolutionary problems. Noting with approval "recent *rapprochements*" between taxonomy and other biological disciplines, Hall concluded with an appeal for further cooperation among specialists.[25]

The international congress was an excellent forum for Hall to present his thinking on experimental taxonomy. Here he was able to address not only the world's leading taxonomists, but also authorities from a number of other botanical disciplines. If we can accept Hall's own modest appraisal of events at the congress, his ideas met with general approval. In a letter to his wife Hall noted that his discussion of experimental taxonomy had been received sympathetically even by older taxonomists who would themselves probably never use experimental methods.[26] Furthermore, he predicted that his suggestions would have an impact on the research of younger taxonomists. Hall's view of the future of experimental taxonomy was quite accurate. During the decades following the 1926 congress, research on the borderlines between taxonomy and other biological disciplines flourished.

CYTOGENETICS AND EXPERIMENTAL TAXONOMY

Experimental taxonomy as originally envisioned by F. E. Clements was to be an ecological approach to the study of plant relationships. However, during the 1930s and 1940s much of the emphasis in experimental taxonomy shifted toward genetics and cytology. Even during the 1920s there were notable examples of the mutual interest

23. Although Hall may have had little sympathy for Clements' evolutionary views, he shared Clements' fundamental assumptions about taxonomy. Both men favored grouping small species, both supported an explicitly phylogenetic basis for classification, and both argued that the use of experimental methods would make classification more "objective."

24. Hall, "Significance of Taxonomic Units."

25. Ibid.

26. H. M. Hall, "Letter to Carlotta Case Hall – August 21, 1926," H. M. Hall papers, University of California, Berkeley, Bancroft Library.

of taxonomists and geneticists. For example, in a short note published in 1924 E. B. Babcock (1877–1954) outlined the significance of experimental genetics for taxonomy.[27] He felt that even the simplest breeding experiments could clarify certain taxonomic relationships. In addition, comparative chromosomal morphology could yield significant taxonomic information. Babcock noted that even experimental taxonomists had neglected genetic and cytological methods. While admitting the laboriousness of these methods, he suggested that recent technical advances were bringing them within reach of the general taxonomist.

Babcock was not the only geneticist interested in taxonomy during the 1920s. At the 1926 International Congress of Plant Sciences an entire session was devoted to discussions among cytologists, geneticists, and taxonomists. Hall opened this session with his call for a "sympathetic synthesis" of biological disciplines. His presentation was followed by papers and commentaries outlining the taxonomic significance of cytology and genetics. For example, the geneticist G. H. Shull (1874–1954) noted that experimental genetics had already clarified relationships within such taxonomically complex genera as *Rubus, Rosa*, and *Viola*. Shull left his audience with the rhetorical question, "Why should there not be *gardens for experimental taxonomy* established at every institution in which research in taxonomy is in progress?"[28] Cautionary remarks were submitted by some commentators. For example, it was pointed out that the application of genetic techniques might face formidable practical problems when applied to long-lived woody plants.[29] Despite such reservations, neither the papers nor the commentaries reveal radical differences between experimentalists and naturalists. Rather, taxonomists, cytologists, and geneticists agreed that methods from various disciplines could be fruitfully combined.

While botanists discussed the advantages of cooperative research, such work was already under way. In 1924 Babcock and Hall, who were close friends, published a study of California hayfield tarweeds in the genus *Hemizonia*.[30] They gave a unified taxonomic and phylogenetic

27. E. B. Babcock, "Genetics and Plant Taxonomy," *Science, 59* (1924), 327–328.

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 Sci.* (1926), 1575–76.

30. Ernest Brown Babcock and Harvey Monroe Hall, "*Hemizonia congesta*. A Genetic, Ecologic, and Taxonomic Study of the Hay-Field Tarweeds," *Univ. Cal. Publ. Bot., 13* (1924), 15–100.

account of the tarweeds, combining methods from genetics, cytology, ecology, and comparative morphology. As the authors noted, this synthetic approach was itself "experimental." A major aim of the study was to explore the possibilities of cooperative research. Though limited in scope, the experiment appeared successful. Chromosomal morphology and data from breeding experiments strengthened Hall's taxonomic claim that three previously described species formed a single complex group, *Hemizonia congesta*.

More significant than the monograph on *Hemizonia* were the indirect results of the collaboration. Both botanists developed successful research programs in experimental taxonomy. On the suggestion of Hall, Babcock initiated research on dandelionlike flowers in the genus *Crepis*. The principal objective of this study was to "demonstrate the value of a combined attack by genetic, cytologic, and taxonomic methods on problems of systematic classification in a large and complex group of plants."[31] The massive monograph that eventually culminated from two decades of research by Babcock and his coworkers was dedicated to Hall's memory.[32] According to Babcock's research associate, G. Ledyard Stebbins (1906–), "His monumental monograph of the genus *Crepis* remains to this date the foremost attempt to explain the evolution of a genus of plants primarily on a genetic basis, while considering at the same time all other possible avenues of approach."[33] Babcock's "Genus *Crepis*" was without question a major contribution to the literature of evolutionary genetics. However, it was equally an innovative taxonomic study combining field observation, herbarium research, cytological studies, and genetic experimentation.

While Babcock was pursuing his research, Hall was laying the foundation for an equally ambitious program. By the late 1920s Hall was in complete charge of the Carnegie Institution's research in experimental taxonomy. An administrative shuffle that ended Clement's direct involvement with experimental taxonomy not only freed Hall from an increasingly controversial partnership, but allowed him to design his own research team. In 1926 Hall hired David Keck, a graduate student majoring in taxonomy, and William Hiesey, an undergraduate

31. E. B. Babcock, "Investigations in the Genus *Crepis*," *Carnegie Inst. Wash. Yearb.*, *25* (1926), 316–317.

32. Ernest Brown Babcock, "The Genus *Crepis*," *Univ. Cal. Publ. Bot.*, *21*, *22* (1947), 1–1030.

33. G. Ledyard Stebbins, "Ernest Brown Babcock," *Biog. Mem. Nat. Acad. Sci.*, *32* (1968), 50–66.

at the University of California. Five years later Hall completed his research group with the hiring of Danish cytogeneticist Jens Clausen.[34] Having done considerable research on the genus *Viola*, Clausen was already a recognized experimental taxonomist when he joined Hall.

Unfortunately, the team of Hall, Clausen, Keck, and Hiesey never became a reality. Clausen had barely arrived in the United States when Hall unexpectedly died in 1932. In a general way Hall had sketched the outline of an extensive research program. This program, which the Carnegie Institution continued to fund, was greatly expanded and largely fulfilled by Clausen, Keck, and Hiesey, with their extensive studies on the taxonomy, evolution, and environmental responses of several groups of North American plants.

Thanks largely to Babcock's group at the University of California and the Carnegie Institution group at Stanford, the area around San Francisco Bay became the hotbed of experimental taxonomy. However, the growth of experimental taxonomy was an international phenomenon. During the 1930s and 1940s similar research groups flourished in Great Britain, Scandinavia, and the Soviet Union. While experimental taxonomy never became an autonomous discipline with a formal professional organization or specialized journal, strong informal ties among experimental taxonomists developed and were maintained by a number of factors.

First, through correspondence and personal aquaintance an informal network was formed among researchers. In 1928 Hall, for instance, traveled throughout Europe and met with prominent botanists. During this trip he was able to observe the newly established transplant studies of the British Ecological Society directed by W. B. Turrill, the experimental gardens of Göte Turesson in Sweden, and Jens Clausen's research on *Viola* in Denmark. This cohesiveness of the Carnegie Institution team and European workers was strengthened when Clausen joined Hall's group in 1931. Clausen's extensive correspondence with European botanists was a valuable means of disseminating the findings of the Carnegie Institution group.[35]

34. According to Stebbins, Clausen hired Keck and Hiesey after Hall's death. See Stebbins' "Botany and the Synthetic Theory of Evolution" in Mayr and Provine, *The Evolutionary Synthesis*. However, Keck and Hiesey were coauthors with Hall on research reports dating back to 1927, four years before Clausen joined the group. See "Experimental Taxonomy," *Carnegie Inst. Wash. Yearb.*, *26* (1927), 311–312.

35. Stebbins, "Botany and the Synthetic Theory," notes Clausen's frequent correspondence with the Scottish botanist J. W. Gregor. In response to my

Second, ties among experimental taxonomists were strengthened through informal organizations. For example, beginning in the mid-1930s researchers in the San Francisco area regularly met for dinner and discussion of current research. These "biosystematists" were apparently quite frank with one another, and the group served as an important forum for debating ideas.[36] A similar though more formal group was founded at about the same time in Great Britain. Taxonomists, ecologists, geneticists, and other specialists formed the Society for the Study of Systematics in Relation to General Biology, primarily to stimulate discussion and cooperation among biologists. Experimental taxonomy was but one focus of the group's activities. Nonetheless, in a general way the society was quite successful in stimulating discussions among taxonomists and other specialists.[37]

Finally, the development of experimental taxonomy was undoubtedly stimulated by the promotional writings of prominent botanists. Geneticists such as Edgar Anderson (1897–1969) and E. B. Babcock, and taxonomists such as W. B. Turrill, cogently argued the benefits of combining cytogenetic and taxonomic methods. Though marked by hyperbole, Anderson's view of the relationship between cytology and taxonomy is typical of these writings: "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."[38]

The Taxonomic Significance of Cytogenetics

Cytology and genetics were taxonomically significant on at least two levels. Without considering the theoretical evolutionary implications,

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questions on this matter, David Keck suggested the importance of Clausen's correspondence with European botanists.

36. Among the prominent early members of the biosystematists were E. B. Babcock, Jens Clausen, Lincoln Constance, Richard Goldschmidt, William Hiesey, David Keck, Herbert Mason, and G. Ledyard Stebbins. When questioned, Constance, Hiesey, Keck, and Stebbins all remarked on the usefulness of this discussion forum.

37. Perhaps the major contribution of this group was the publication of a widely read set of essays: Julian Huxley, ed., *The New Systematics* (London: Oxford University Press, 1940). In addition, the group sponsored several symposia on the relation of taxonomy to various other disciplines.

38. Edgar Anderson, "Cytology in its Relation to Taxonomy," *Bot. Rev., 3* (1937), 335–350.

both descriptive cytology and experimental genetics could be used to generate taxonomic data. For example, cytological descriptions of sizes, and numbers of chromosomes provided taxonomists with a new set of characteristics. On one level, such cytological studies were merely refined comparative morphology. Indeed, some taxonomists considered chromosomal characteristics as simply another form of morphological data. However, most experimental taxonomists stressed the special significance of cytological data. In the words of Anderson, cytological description "is evidence as to the architecture of the very germplasm itself and is, therefore, of more fundamental importance than the mere architecture erected by that germplasm.[39] Similarly, Turrill noted that cytology and genetics were effectively a single discipline. The theoretical implications of this combined discipline obliged taxonomists to consider the study of chromosomes as more then "high-powered morphology."[40]

The combination of descriptive cytology, experimental genetics, and cytogenetic theory proved to be a potent methodology. In particular, it cast new light on several "critical" genera. These groups, which defied satisfactory classification, were often composed of "species complexes" related through polyploidy. As Stebbins noted, "The difficulty of these genera is intrinsic. The systematist need have no inferiority complex about his failure to find clear differences between species in them."[41] Analysis of polyploid groups became a major preoccupation of experimental taxonomists during the 1930s and 1940s. Extensive studies by Anderson on *Iris*; by Babcock and Stebbins on *Crepis*; and by Clausen, Keck, and Hiesey on *Layia* and *Madia* demonstrated that cytogenetic analysis could provide a rational explanation for the complexity of the so-called critical genera.

It should be stressed that cytogenetic analysis was not a purely experimental technique, nor was it completely divorced from traditional taxonomic methods. Taxonomic deductions could often be derived from a descriptive study of chromosomal numbers alone. Though suggestive, these descriptive data required further confirmation. Hybridization experiments provided the most trustworthy test for relationship among putative polyploids. However, most of the major studies on polyploid complexes included traditional field and herbarium

39. Ibid.

40. W. B. Turrill, "The Expansion of Taxonomy with Special Reference to Spermatophyta," *Biol. Rev.*, *13* (1938), 342–373.

41. G. Ledyard Stebbins, Jr., "The Significance of Polyploidy in Plant Evolution," *Amer. Nat.*, *74* (1940), 54–66.

data as well as cytological and genetic data. In three species of *Iris*, for example, Anderson discovered chromosomal complements of 38, 70, and 108. He deduced that *Iris versicolor* ($2n$ = 108) was the allopolyploid derivative of *Iris setosa* ($2n$ = 38) and *Iris virginica* ($2n$ = 70).[42] Anderson's account of evolutionary relationships in *Iris* was particularly compelling because he combined a wealth of data from descriptive cytology, hybridization experiments, comparative morphology, biogeography, and ecology.

The Reception of Cytogenetics by Taxonomists

During the 1930s and 1940s experimental taxonomy produced notable examples of innovative and cooperative research. The combination of field observation, herbarium research, and cytogenetic analysis at the hands of botanists such as Anderson and Babcock resulted in studies of cytogenetic and taxonomic significance. Productive research units such as Clausen, Keck, and Hiesey successfully combined the talents of a variety of specialists. Furthermore, it appears that discussions between taxonomists and other specialists were more widespread than historians have assumed. This evidence militates against the claim that taxonomists and geneticists were isolated in incompatible conceptual worlds.

Despite examples of cooperation, the influx into taxonomy of new techniques and ideas was a source of some conflict. Proponents and opponents engaged in rhetorical skirmishes throughout the 1930s and 1940s.[43] While such polemics cast some light on the differences among botanists, the arguments tended to be rather diffuse and unrelated to particular experimental studies. Better evidence for substantive disagreements between experimentalists and naturalists would come from critiques of specific experimental research projects. A good example is the response of A. J. Wilmott (1888–1950) to J. W. Gregor's (1900–) experimental analysis of grasses in the genus *Phleum*. Their acrimonious exchange illustrates the complexity of the controversies.

Despite a genuine interest in taxonomy, Gregor was primarily concerned with ecological genetics rather than with classification. However, in 1931 he published a short paper entitled "Experimental

42. Edgar Anderson, "The Species Problem in *Iris*," *Ann. Mo. Bot. Graden, 23* (1936), 457–509.

43. Dean, "Controversy over Classification," cites a number of these conflicts as evidence for a dichotomy between herbarium taxonomists and experimental taxonomists.

Delimitation of Species,"[44] in which he briefly summarized previously published results of his cytogenetic research on *Phleum*. What made the article noteworthy was the author's attempt to fit this data into Turesson's theoretical model of plant species. Gregor claimed that *P. alpinum* and *P. pratense* constituted a single coenospecies, because limited gene flow occurred between them. This coenospecies, *Phleum alpinum-pratense*, was divided into four ecospecies on the basis of chromosomal numbers. Finally, each ecospecies was subdivided into several ecotypes primarily on the basis of facies. Gregor's complex system of quadrinomials could hardly be recommended on the basis of simplicity. Nonetheless, he argued that unlike classifications based on gross morphology his system accurately reflected evolutionary relationships.

Gregor's paper elicited a heated response from Wilmott,[45] who was particularly incensed by Gregor's implications that taxonomists relied exclusively on gross morphology and that they were unconcerned with evolutionary relationships. In an angry rebuke Wilmott wrote, "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."[46] Wilmott's rejoinder was followed by a caustic exchange between the two botanists in the correspondence section of the *Journal of Botany*.[47] Superificially, the Wilmott-Gregor dispute might appear to be a confrontation between a naturalist and an experimentalist. Polemics aside, however, the differences between the two men were more complicated than such a dichotomy would indicate.

Gregor acknowledged that a satisfactory classification required both experimental and descriptive evidence. While he placed strong emphasis upon cytogenetic data, Gregor noted the importance of comparative morphology throughout his 1931 paper. Perhaps because his brief article was not an exhaustive taxonomic study of *Phleum alpinum* and *P. pratense*, Gregor cautioned that his proposals illustrated the utility of Turesson's theoretical system and did not necessarily constitute a definitive reorganization of the genus *Phleum*. In retrospect, Gregor might have made his cautionary note more explicit.

44. J. W. Gregor, "Experimental Delimitation of Species," *New Phytologist, 30* (1931), 204–217.

45. A. J. Wilmott, "Experimental Delimitation of Species," *J. Bot., 70* (1932), 49–50.

46. Ibid.

47. J. W. Gregor, "Correspondence," *J. Bot., 70* (1932), 154–155; A. J. Wilmott, "Correspondence," ibid., 155.

Wilmott certainly viewed Gregor's article as more than an illustration of a novel methodology. He felt that Gregor not only was attempting to reclassify *Phleum* on insufficient evidence, but was advocating Turesson's units as valid taxonomic nomenclature, Wilmott's critique must be viewed as an argument for taxonomic stability rather than simply an attack on cytogenetic analysis per se. He criticized Gregor's study on a number of counts. First, he argued that Turesson's units were an unnecessary encumbrance on traditional nomenclature. This was not a unique comment. Even among experimental taxonomists there was considerable disagreement over the legitimacy of Turesson's system. While nearly all of them expressed interest in Turesson's theoretical writings, not all viewed the genecological units as acceptable taxonomic categories. Wilmott was also critical of Gregor's emphasis on cytogenetic data. Primarily, he argued against revising established classification schemes on the basis of a novel methodology, believing that cytogenetic data were as open to various interpretations as the more traditional taxonomic data.[48] Furthermore, Wilmott argued that the "naturalness" of species depended on morphological and distributional factors as well as on cytogenetic criteria. Gregor was not only placing undue emphasis on a relatively untested methodology, he was ignoring traditional taxonomic data.

Wilmott's skepticism toward cytogenetic data was not necessarily reactionary. During the 1930s cytology was a rapidly developing field. Cytologists themselves disagreed over fundamental principles of chromosomal mechanics. For example, C. D. Darlington's *Recent Advances in Cytology*, now recognized as a seminal statement of cytogenetic theory was immensely controversial when it appeared in 1932.[49] Given these fundamental disagreements among leading cytologists, taxonomists could rationally question the wholesale incorporation of cytogenetic data into classification.

Analyzing the Wilmott-Gregor dispute from the perspective of the

48. Indeed, during the two decades following 1931 cytogeneticists demonstrated that the relationships among polyploid groups in *Phleum* were considerabley more complex than Gregor had proposed. For a brief dicussion of cytogenetic research on *Phleum* see G. Ledyard Stebbins, Jr., *Variation and Evolution in Plants* (New York: Columbia University Press, 1950), p. 333.

49. C. D. Darlington, *Recent Advances in Cytology* (Philadelphia: Blakiston's 1932). For brief discussions of the reception of Darlington's text see Hampton Carson, "Cytogenetics and the Neo-Darwinian Synthesis," and C. D. Darlington, "The Evolution of Genetic Systems: Contributions of Cytology to Evolutionary Theory," both in Mayr and Provine, *The Evolutionary Synthesis.*

naturalist-versus-experimentalist dichotomy tends to distort the nature of controversies surrounding experimental taxonomy. The disagreements between Gregor and Wilmott concerned matters over which experimental taxonomists did not agree among themselves. For example, there was considerable argument over the extent to which taxonomic theory ought to be reformed. Some experimental taxonomists felt that a complete overhaul was justified by developments in cytogenetics.[50] Others shared Wilmott's concern for taxonomic stability and argued against radical changes in taxonomic theory. The naturalist-versus-experimentalist dichotomy also obscures the fact that many experimental taxonomists believed that their research was completely compatible with traditional taxonomy. This was true even of experimental taxonomists such as Gregor who drew a sharp distinction between experimental and traditional taxonomy.[51]

CONCLUSION

Experimental taxonomy was a diverse area of research, and botanists who helped develop it were motivated by a variety of concerns. While experimental taxonomy was never totally a taxonomic enterprise, improvement in classification was certainly one major motivation behind the research. Hall's and Clements' belief that experimental methods added more objectivity to classification was almost universally accepted by experimental taxonomists. Such methods did add a new dimension to taxonomy – a dimension that field and herbarium studies, however rigorous, could not duplicate. Nonetheless, experimental techniques were never completely divorced from traditional taxonomic methods. In practice, all experimental taxonomists employed a combination of descriptive and experimental methods. Most researchers freely acknowledged a debt to traditional taxonomy. Furthermore, the greater rigor of twentieth-century taxonomy was not due entirely

50. For example, in a presidential address to the American Society of Plant Taxonomists, W. H. 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 nomenclatural covering for the complex, living groups which we are now beginning to realize must be defined." See W. H. Camp, "Biosystematy," *Brittonia*, 7 (1951), 113–127.

51. Gregor, in "Units of Experimental Taxonomy," noted that while they were basically different, experimental taxonomy and orthodox taxonomy were "mutually helpful."

to experimentalism. Both the experimental and descriptive aspects of taxonomy were improved by the increased use of quantitative methods, particularly statistics.[52]

From the beginning, a number of experimental taxonomists were interested primarily in classification. But many approached their research from fields other than taxonomy. These botanists were concerned primarily with ecological and genetic problems rather than with classification. There is little indication that they drew a sharp distinction: for example, taxonomic and cytogenetic conclusions were interwoven in Babcock and Stebbins' 1938 study of *Crepis*[53] (this was even more true of Babcock's final mongraph on the genus, published in 1947). Similarly, the extensive series of monographs, "Experimental Studies on the Nature of Species," initiated by the Carnegie Institution group in 1940 combined ecological, cytogenetic, and taxonomic conclusions. Indeed, the significance of the major projects completed by experimental taxonomists was largely due to the fact that they were comprehensive studies rather than strictly taxonomic or cytogenetic.

In a general sense, the primary motivation behind much of experimental taxonomy was evolutionary. Beginning in the second decade of the century Hall and Clements exhorted taxonomists to take an explicitly evolutionary perspective on research. Hall undoubtedly spoke for the majority of experimental taxonomists when he stated, "If there be anything at all to organic evolution, then taxonomy is dealing with the products of evolution and it is this that gives to taxonomy both its highest mission and its greatest responsibility."[54]

Aside from a common interest in evolution, however, the theoretical orientations of experimental taxonomists were varied. This diversity is strikingly illustrated by the evolutionary views of members of the

52. Statistical analysis cannot be considered merely an adjunct to experimental biology. Indeed, it appears that field biologists and taxonomists were among the leading advocates of statistical methods. This was true of zoologists as well as botanists. For example, G. C. Robson and O. W. Richards reviewed numerous examples of statistical field studies ("population analysis") in *The Variation of Animals in Nature* (London: Longmans, 1936), p. 15. Similar suggestions for combining statistics and taxonomy are found in Edgar Anderson and W. B. Turrill, "Biometrical Studies on Herbarium Material," *Nature, 136* (1935), 986.

53. E. B. Babcock and G. L. Stebbins, Jr., "The American Species of *Crepis* – Their Interrelationships and Distribution as Affected by Polyploidy and Apomixis," *Carnegie Inst. Wash. Publ.* no. 504 (1938).

54. Hall, "Heredity and Environment."

Carnegie Institution research group. Experimental taxonomy was initiated by Clements as one aspect of his Lamarckian study of adaptation and speciation. In contrast, Hall's research was inspired by a broad concern for evolutionary problems. Hall rarely referred to specific evolutionary mechanisms; rather, he applied a general conception of evolutionary processes to deduce phylogenetic relationships. His later associates at the Carnegie Institution explicitly dissociated themselves from Clements' theoretical framework. The neo-Darwinian interpretations of adaptation and speciation presented by Clausen, Keck, and Hiesey could hardly have been more different than those of Clements. However, this major shift in theoretical orientation should not obscure significant similarities between the research of Clements and later Carnegie workers. In terms of research problems and methodology, the first volume of "Experimental Studies on the Nature of Species" was an extension of the Clementsian research program. Clausen, Keck, and Hiesey's monograph was the mature discussion of transplant experimentation that Clements had very tentatively initiated during the first decades of the twentieth century. The bond that linked the members of the Carnegie Institution research group to experimental taxonomists in general was one of shared methodology rather than common theoretical orientation. While Clements' evolutionary views were eventually repudiated, his enthusiasm for innovative experimental methods was shared by later workers.

The development of experimental taxonomy faced significant problems. During the period 1920–1950 this area of botanical research remained a hybrid discipline. The aims and scope of experimental taxonomy were never articulated in a completely unified manner. Consequently, even among experimental taxonomists, there were disagreements over the relation of their research to other botanical endeavors. Even though experimental taxonomy had close ties with general taxonomy, a number of experimental taxonomists questioned the "taxonomic" nature of their research.[55] Even to the extent that this hybrid discipline could be identified as a branch of taxonomy, problems arose. Taxonomists, as we have seen, were justifiably skeptical of what appeared to be a rapid influx of untested methods and ideas. Experimental taxonomists were not merely incorporating well-accepted methods from ecology and cytogenetics; during the period 1920–1950 the fields from which experimental taxonomists borrowed were

55. J. Heslop-Harrison, *New Concepts in Flowering-Plant Taxonomy* (London: Heinemann, 1953), p. 122.

themselves undergoing major theoretical and methodological changes. Despite problems and conflicts, experimental taxonomists did contribute improvements to classification. Furthermore, they made significant contributions to plant ecology and evolutionary genetics.

The development of experimental taxonomy indicates that twentieth-century botanists were not necessarily isolated in naturalist and experimentalist camps. The joint session of taxonomists, cytologists, and geneticists at the 1926 International Congress of Plant Sciences indicates communication among specialists fairly early in the century. The papers and commentaries presented during this session do not reveal the hostility and intolerance that supposedly characterized encounters between experimentalists and naturalists. Nor do they suggest incompatible conceptual worlds separating geneticists and taxonomists.

Discussions between taxonomists and other specialists were not limited to a single international congress. Particularly during the 1930s discussions among specialists appear to have been fairly widespread. Groups such as the Biosystematists and the Society for the Study of Systematics in Relation to General Biology served as forums for discussion among biologists from a variety of disciplines. The naturalist-experimentalist dichotomy tends to obscure the broad research interests of a number of prominent twentieth-century botanists. Most of the experimental taxonomists cannot be characterized adequately as either naturalists or experimentalists. Traditionally trained taxonomists such as Hall, Keck, and Turrill throughout their careers participated in both experimental and herbarium research. And a number of specialists in fields other than taxonomy took an active interest in taxonomic problems, not necessarily limited to experimental aspects. For example, Anderson suggested a number of innovations to make herbarium collections more amenable to statistical analysis.

This historical study of experimental taxonomy indicates a different relationship between experimentalism and taxonomy than that portrayed by the naturalist-versus-experimentalist dichotomy. F. E. Clements originated experimental taxonomy as a revolt against descriptive botany. In retrospect, this revolution was not vigorously waged and was not successfully completed. Experimental taxonomy was never an entirely experimental approach to botanical research. Even the most ardent advocates of experimentalism relied heavily on methods inherited from traditional taxonomy. Moderate exponents of experimental taxonomy stressed the compatibility of experimental methods, field observation, and herbarium techniques. Attempts to fuse cytogenetics, ecology, and taxonomy during the period 1920–1950 resulted in an impressive body of research. However, this fusion constituted neither a repudiation of descriptive botany nor a complete revision of taxonomic theory of practice.

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