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The Invisible Subject: Zoology and the Evolutionary Synthesis

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Abstract

Although the subject of botany and the evolutionary synthesis has been explored by historians, the counterpart subject of zoology and the evolutionary synthesis has received little or no significant discussion. Following a historical assessment of the evolutionary synthesis, the paper engages in a comparative study between the contributions of botany and zoology to the synthesis. It then highlights some of the major contributions made by zoologists and directs readers to further areas for historical inquiry. The argument is made that zoology and the synthesis are considered to be so closely synonymous that the two are frequently equated, so much so, that the subject has been rendered invisible.

Introduction

The invitation to contribute a paper on the subject of "zoology and the evolutionary synthesis" took me by surprise for at least two reasons. For one thing, although I have studied the wider evolutionary synthesis as a historian, I am presently concentrating more narrowly on the role that botanists have played in twentieth century evolutionary science. I am presently writing a biography of the late George Ledyard Stebbins, one of the pioneers of plant evolutionary biology and the botanical architect of the evolutionary synthesis. For another thing, the subject is so enormous, as I hope I will convince you in this presentation, that it would be impossible to address it properly in a hefty scholarly volume, let alone compress it in any substantive manner for a 20-25 minute presentation. As I reflected on the proposed topic, however, I realized that the subject was so rich that it really deserved an opening discussion in a forum exactly like the International Congress of Zoology.

The topic becomes more intriguing still when we realize that only very recently has it even been acknowledged as a topic at all. It has received only the most brief consideration in the form of a personal memoir/recollection in the form of an interview with the German biologist Wolf Herre (Hossfield 1999). Though the brief article is titled "Zoologie und Synthetische Theorie," it concentrates primarily on the personal reflections of Herre concerning the German context of the evolutionary synthesis and does not address zoology and the synthesis directly.

Far more revealing of "zoology and the evolutionary synthesis" is the coverage given to it in the most impressive scholarly work on the evolutionary synthesis to date. This is a collection of papers that appeared in 1980 that is edited by Ernst Mayr and William B. Provine and titled *The Evolutionary Synthesis. Perspectives on the Unification of Biology.* A new printing was recently made available in 1998 with a brief new preface by Mayr. Despite the fact that the volume has a significant essay written by Stebbins on "botany and the evolutionary synthesis," there is no formal comparable essay on zoology and synthesis; and nowhere in the volume is the subject directly addressed. Although key zoologists who contributed to the synthesis are noted, cited heavily, and their contributions are acknowledged, their common field remains unrecognized. Included here are individuals like Theodosius Dobzhansky, Julian Huxley, Ernst Mayr, Bernhard Rensch and G. G. Simpson among others. Even more revealing is the fact that "Part One" of the book titled, "Different Biological Disciplines and the Synthesis" lists the following disciplines as playing a vital role in the synthesis: genetics, cytology, embryology, systematics, botany, paleontology, and morphology, but once again there is no mention of zoology. More revealing still, is the index to volume. Although there is an entry under "botany," which sends interested readers to the essay by Stebbins, there is no comparable entry under zoology.

It may seem ironic indeed that the topic has never been addressed—almost rendered invisible— given that the history of evolution has been dominated by the presence of Ernst Mayr, one of the great zoologists of the twentieth century and the foremost historians of the evolutionary synthesis. My sense, however, is that it is not an accident that the subject has never really been addressed formally. What I will suggest instead is that the absence of zoology—as a category for historical analysis— in both the Mayr and Provine volume and in our historical consciousness is the result of its close identification with the achievements of the synthesis and with the fact that Ernst Mayr has written the historical account. In his mind, "zoology," which represents his area of expertise was virtually synonymous with the synthesis.

Given the space restrictions and the fact that the topic is enormous, what I hope to do is to first engage in a comparative history between the contributions of botany (which is better known) and zoology to the evolutionary synthesis and then to highlight some of the major features of the relationship of zoology—and zoologists— to the synthesis. I also hope to ask pertinent questions especially about the absence of substantive historical work on the subject that may lead to more detailed scholarly consideration in the future.

What was the Evolutionary Synthesis?

It might be appropriate to begin with the obvious first question. What exactly was the evolutionary synthesis? The answer to this question has eluded a veritable army of scientists, philosophers and historians of science (Mayr & Provine 1980, Mayr 1982, Mayr 1993, Burian 1988, Gayon 1990, Gayon 1992). Although some of the recent scholarship may have helped us understand some of the social or cultural aspects of the synthesis, it remains a controversial subject (Smocovitis 1992, 1994, 1996, Cain 1993, Ruse 1996, Junker & Engels 1999). All scholars agree that it was what William B. Provine (1980) has described as "an intellectual event of first-order magnitude."

First a brief historical background to the understanding of the synthesis. The story of the synthesis begins in the mid-nineteenth century. The fact that the diversity of life is the product of evolution—in Darwin's own terms descent with modification—was almost universally accepted by biologists soon after the publication of Darwin's *On the Origin of Species* in 1859. Although Darwin's specific explanation—descent with modification by the novel mechanism of natural selection was immediately adopted by colleagues like Joseph Hooker, Asa Gray, E.B. Poulton, August Weismann and of course his co-discoverer Alfred Russel Wallace, it was rejected by most biologists for a number of reasons including the fact that little direct evidence existed. Darwin knew this and spent the remainder of his life completing monograph-studies, many of which were botanical in nature—in support of phenomena like adaptation and natural selection. After 1870, after this work was published, natural selection appeared to gain in popularity only to suffer a demise again by the turn of the century when a number of alternative mechanisms were proposed. Only a handful of individuals were ardent selectionists, and these included Darwin's co-discoverer, Alfred Russel Wallace. Varied schools of thought arose in support of some of these alternative mechanisms and included belief in saltationism, orthogenesis (directed evolution including nomogenesis), mutation theory, and neo-Lamarckism. So popular were these alternatives to natural selection, that they led to a serious challenge to traditional Darwinian theory. Surveying this period, Julian Huxley in 1942 used the phrase the "Eclipse of Darwinism" to explain the demise of natural selection (Huxley 1942).

These divisions were only deepened and rendered more complex at the turn of the century by what Ernst Mayr and historian Garland Allen have repeatedly described as "a widening chasm" between naturalist-systematists or field workers, and the new breed of laboratory -oriented practitioner of experimental biology represented most by the new generation of geneticists (Mayr, 1982; Allen, 1979). These were such vastly different communities—cultures in fact—that, in addition, to using different scientific methods, they also spoke different scientific languages, had different scientific training, and held even to different standards of evidence or what counted as "good" science. Many of the younger geneticists saw the older systematics or natural history as unrigorous, poor or even bad sciences because they did not rely on laboratory experimentation or quantification. There were more than a few celebrated disagreements between biologists as a result of these divisions. How these disagreements shaped the course of evolutionary biology at the turn at the turn of the century was directly addressed by Provine in his 1971 book, *The Origins of Theoretical Population Genetics.*

Various attempts to reach a consensus about the actual or even the dominant mechanism of evolution failed in the 1920s. In the interval of time between approximately 1936-1950, however, the disagreements appeared to diminish, the number of alternative mechanisms appeared to diminish as well, and a seemingly new theory was synthesized that incorporated Darwinian selection theory with Mendelian genetics in a way that accounted for the diversity of life on earth. In the process natural selection emerged as the dominant mechanism of evolution, and the theoretical commitments to the continuity between microevolution and macroevolution (two terms that gained currency during the synthesis) were made.

The synthesis officially began with the establishment of the mathematical models of the theorists R. A. Fisher, J. B. S Haldane and Sewall Wright who both explored and mathematically demonstrated the efficacy of natural selection in a range of theoretical conditions (Provine 1971, Provine 1986). Their work was followed by the publication of Theodosius Dobzhansky's *Genetics and the Origin of Species* in 1937, which was the foundational volume that led to the birth of evolutionary genetics. Dobzhansky had also drawn on his Russian predecessors (like Sergei Chetverikov), who had pioneered populational approaches to evolution in the nineteen-teens and twenties, but who had been either exiled, dispersed or killed during the Stalinist period (Adams 1994). Dobzhansky's synthetic book was followed by a string of books that successively built on Dobzhansky's evolutionary framework or amended the framework in some way. In 1942 avian systematist Ernst Mayr wrote *Systematics and the Origin of Species. The Viewpoint of a Zoologist*; the counterpart to this volume, the viewpoint of a botanist was offered by Edgar Anderson, who did not complete a book-length manuscript. In 1942 Julian Huxley, wrote *The Modern Synthesis,* which officially announced the arrival of the new synthetic theory; in 1944, vertebrate paleontologist George Gaylord Simpson wrote *Tempo and Mode in Evolution*, and in 1950 George Ledyard Stebbins completed his enormous *Variation and Evolution in Plants.* Others were involved including Bernhard Rensch, who wrote *Neure Problem der Abstammunglehre* in 1947, C. D. Darlington and others. It should be noted here that with the exception of Stebbins and Darlington, the above scientists were zoologists in training. Dobzhansky's book had great international effect as well, and was instrumental in launching a European synthesis (Junker & Engels 1999).

Simultaneous to the publication of these synthetic volumes, there also took place an organizational synthesis that saw the first international society for the study of evolution established in the United States, the Society for the Study of Evolution. Britain was unable to win the bid since it was recovering from heavy war-related damages like the absence of paper (Smocovitis 1994). The society was launched beginning in March 1946 and led to the establishment of the journal *Evolution*. Many—in fact most— of the organizational leaders were zoologists, including individuals like Alfred Emerson and especially Ernst Mayr, who were both orchestrators and who served as organizational pivots. Of the first seven elected presidents of the SSE, only two were botanists—Stebbins and E. B. Babcock. The others included Simpson, J. T. Patterson, N.D. Newell, and Theodosius Dobzhansky. It therefore seems clear that zoology, and zoologists, led the way in efforts to organize evolutionary study in the United States.

The clear dominance of zoology—and zoologists—over botanists during the period of the evolutionary synthesis is easy to document by examination of simple numbers of participants and authors. But it is much harder to understand conceptual advances made by zoologists who contributed to the evolutionary synthesis. Here I will begin to explore this topic by first concentrating on the "rival" science of botany and its contributions, and then offering a comparative approach that highlights zoology.

Conceptual Contributions

Although much of the early work in genetics was the result of work on botanical study—Mendel himself was a botanist—the tide turned in favor of animal genetics with the discovery of that most perfect experimental organism—the dew-loving black stomached fly—*Drosophila melanogaster*. The success of *Drosophila melanogaster* as an experimental system in the hands of geneticist Thomas Hunt Morgan—and his school of fly-room geneticists in the first two decades of the twentieth century largely eclipsed comparable efforts to understand Mendelian genetics and later the genetic basis of evolutionary change in plant model organisms (Allen 1975, 1978, 1979, Kohler 1994). We all know Morgan and his organism, but few recall the pioneering work on the genus *Crepis*—a lowly weed in the Compositae family—through the efforts of Berkeley geneticist E. B. Babcock (Smocovitis 1997). One problem with plants as experimental model organisms was that their genetic systems were far more complex and difficult to understand than in animal systems. One recalls the widespread confusion precipitated by De Vries when he watched what he thought was the sudden appearance of new elementary species in *Oenothera lamarckiana*, the evening primrose. It took plant geneticists over twenty-some years to determine that *Oenothera* did not just "throw off such elementary species" but was in fact a permanent translocation heterozygote. Thus overall in genetics—we may say that although plants made notable contributions, animal systems like *Drosophila sp.* seemed to dominate conceptual advances in genetics that later fed into the synthesis.

For similar reasons, that is, the overwhelming complexity of plant genetic systems, evolution in plants tended to support a range of oftentimes contradictory theories. Unlike many zoologists who in fact did reject Neo-Lamarckism like Ernst Mayr, botanists continued to uphold neo-Lamarckian theories well into the 1930s and 1940s. One reason for this is the result of the fact that plants have open or indeterminate developmental systems—such a system made it difficult to separate phenotypic from genotypic variation rendering plant evolution susceptible to neo-Lamarckism.

Additional phenomena demonstrated widely in the plant world like frequent hybridization, polyploidy and apomixis—a method of asexual reproduction—and most importantly the interplay between all three made plants less tractable model study organisms. Added on to this was the phenomenon of cytoplasmic inheritance, and the greater plasticity of phenotypic responses in plants. Finding a coherent evolutionary theory for the plant world was thus far more difficult than that in the animal world.

All these biological complexities also led increasingly to serious differences of opinion between botanists about proper taxonomic methods. Many taxonomists preferred a strictly Linnaean taxonomic methodology while others entertained a dynamic, ecological view of species. By the 1930's many botanists were divided into the herbarium worker who preferred the Linnaean scheme and the more ecologically minded field experimentalist or naturalist. One of the pioneers of plant evolution the Swede Göte Turesson pointed these divisions out clearly in the late 1920's Turesson's own area of expertise—the study of plant adaptation to varied environments in the science called genecology—was in fact considered a discipline separate from botany! When Berkeley taxonomist Harvey Monroe Hall teamed up with the ecologist Frederic Clements to reform the practice of plant taxonomy into a more ecologically attuned study in their 1923 book, *The Phylogenetic Method in Taxonomy*, they ended up writing what amounted to a taxonomic manifesto. Both lost considerable status in the eyes of the staunch herbarium workers who continued to uphold the static Linnaean scheme. No such divisions existed in zoology since the middle of the nineteenth century when field-oriented collecting practices were introduced into zoology. By the twentieth century, a populational field-oriented mode of collecting and identifying specimens was routine practice. No doubt, the fact that animals could locomote—move from area to area rather than maintain a stationary existence— may have additionally contributed to a more dynamic view of species and in turn a more dynamic view of speciation.

Even simple collecting practices in systematics differed widely between zoologists and botanists. As Ernst Mayr has repeatedly pointed out, it was zoologists who collected specimens and arranged them in terms of series in order to appreciate the full range of variation in species. In zoology, it had been standard practice since the middle of the nineteenth-century to collect population samples or "series" as the museum workers named them. This tradition did not exist in botany. Duplicates in plants were very often samples from the same plant. The botanist who introduced the method of "mass collecting" to botany and who introduced a wholesale reappreciation of patterns of variation and devising methods to measure variation was Edgar Anderson. He had in turn appropriated the method from individuals like his close friends the zoologists Alfred Kinsey and Norman Fassett. It was in fact, the work of zoological systematists who had paved the way for one of the key aspects of the evolutionary synthesis—the switch from typological to populational thinking. The transition from typological or static essentialistic thinking about the natural world to a dynamic variational and populational understanding of the natural world was surely one of the vital components of the synthesis. Though botanists made notable contributions to areas like "biosystematics," in the 1940s, it was a zoologist, Julian Huxley, who first announced this dynamic, new evolutionary approach to taxonomy in his pivotal and influential book in 1940 titled *The New Systematics.*

The differences were only widened after the mid-1930s when zoologists like Dobzhansky and Mayr laid the groundwork for the biological species concept (BSC), thus recognizing the definition of species strictly in terms of sterility barriers and the existence of other isolating mechanisms. Though it was generally acknowledged by all zoologists, it should be noted that protozoologists like T. M. Sonneborn challenged its general applicability to all animals (Sonneborn, 1957) and maintained that it had limited use mostly to birds and mammals. Even though there was some notable disagreement between zoologists like Mayr and Sonnenborn, zoologists as a whole accepted the BSC. Botanists, however, argued vociferously between themselves and with zoologists about the applicability of the BSC to the frequently hybridizing species of plants.

The Invisible Subject

We can then highlight a few of the major features of the contributions that zoology made to the evolutionary synthesis:

1. Understanding the mechanism of Mendelian heredity.
2. Laying the foundation for the Biological Species Concept (BSC).
3. Transforming evolution and biology from a static or typological study to a dynamic populational area of study. Related to this was a move towards a view of collecting

practices and systematic study that stressed variational evolution and that led ultimately to the "new systematics."

There are of course numerous other contributions that we could discuss—such as Simpson's insights into the tempo and mode of evolution from his observations of vertebrate fossils, or perhaps Mayr's famous recognition of "founder events," and their importance in understanding speciation, but I think the above three suit the comparative purposes of this paper since they were not the result of botanical study.

Given that zoology—and zoologists are such vital subjects in the evolutionary synthesis, then why has zoology been left out of this history?

This is a good question: I suggest it has much to do with the fact that Mayr—both as the historian and zoologist who has been closest to the subject could not imagine that the topic of zoology and synthesis could be separated for historical analysis; they are one and the same. Following a similar logic, Mayr draws a line of demarcation around botany as a category for analysis; this is a conversation that only one outside the category of botany, but firmly inside the category of zoology might understand. Only from the perspective of a zoologist did the category botany exist in the 1940s; hence Mayr's repeated assertions that botany was very different from all the other biological disciplines and was somehow "delayed" in entering the synthesis (Mayr 1980). In this sense, I might suggest that the subject of zoology and the evolutionary synthesis has been rendered invisible by virtue of its own success; zoologists dominated the synthesis as both a scientific event and a historical event.

Additionally as well, Mayr's sense of the word "zoology" should be given close critical examination and its assumptions lain bare. There are at least two that deserve consideration. First, by zoology, Mayr generally means the zoology of birds and mammals, and not other animal systems like protozoa. Second, by zoology, Mayr generally means the zoological tradition that fed ultimately to the synthetic theory. This was the tradition in systematics that was dominated by his German predecessors like E. Streseman and later B. Rensch. The rival tradition that dominated German zoology after E. Haeckel that concentrated on morphology and phylogeny, what Mayr has characterized as the continental "idealist" morphological tradition, is not included in historical considerations. My overall sense is that it would be a most useful undertaking to explore the general subject of "zoology and the synthesis" in a full historical project. Any such attempt to do so must keep in mind definitional aspects of these two terms and the fact that much of the history of biology has been dominated by the leading historical player, Ernst Mayr.

References

ADAMS M. (ed.) 1994. *The Evolution of Theodosius Dobzhansky*. Princeton, Princeton University Press.

ALLEN G. 1975. *Life Science in the Twentieth Century*. Wiley, New York. Rep. ed. Cambridge University Press, Cambridge, 1978.

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

ALLEN G. 1979. Naturalists and experimentalists: the genotype and the phenotype. *Studies in the History of Biology* 3: 179-209.

BURIAN D. 1988. Challenges to the Evolutionary Synthesis. *Evolutionary Biology* 23: 247-288.

CAIN J.A. 1993. Common Problems and Cooperative Solutions. *Isis* 84: 1-25.

GAYON J. 1990. Critics and criticisms of the Modern Synthesis: The Viewpoint of a Philosopher. *Evolutionary Biology* 24: 1-49.

GAYON J. 1992. *Darwin et l'Après Darwin*. Éditions Kimé, Paris.

HALL F. & F. CLEMENTS 1923. *The Phylogenetic Method in Taxonomy*. Carnegie Institution of Washington no. 326.

HOSSFIELD U. 1999. Zoologie und Synthetische Theorie: Interview mit Wolf Herre. In Th. Junker & E.-M. Engels (eds), *Die Entstehung der Synthetischen Theorie. Beiträge zur Geschichte der Evolutionsbiologie in Deutschland 1930-1950*. Verlag für Wissenschaft und Bildung, Berlin, 1999, pp. 241-257.

JUNKER TH. & E.-M. ENGELS (eds) 1999. *Die Entstehung der Synthetischen Theorie. Beiträge zur Geschichte der Evolutionsbiologie in Deutschland 1930-1950*. Verlag für Wissenschaft und Bildung, Berlin.

HUXLEY J. (ed.) 1940. *The New Systematics*. Clarendon Press, Oxford.

HUXLEY J. 1942. *Evolution: The Modern Synthesis*. London, Allen and Unwin.

KOHLER R.E. 1994. *Lords of the Fly: Drosophila Genetics and the Experimental Life*. Chicago University Press, Chicago.

MAYR E. 1982. *The Growth of Biological Thought*. Belknap Press, Cambridge, Mass.

MAYR E. 1993. What was the evolutionary synthesis? *Trends in Ecology and Evolution* 8:31-34.

MAYR E. & W.B. PROVINE (eds) 1980. *The Evolutionary Synthesis. Perspectives on the Unification of Biology*. Harvard University Press, Cambridge, Mass. Reprinted with a new Preface by Ernst Mayr, 1998.

PROVINE W.B. 1971. *The Origins of Theoretical Population Genetics*. University of Chicago Press, Chicago.

PROVINE W.B. 1986. *Sewall Wright and Evolutionary Biology*. University of Chicago Press, Chicago.

RUSE M. 1996. *Monad to Man*. Harvard University Press, Cambridge, Mass.

SMOCOVITIS V.B. 1992. Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology. *Journal of the History of Biology* 25: 1-65.

SMOCOVITIS V.B. 1994. Organizing Evolution: Founding the Society for the Study of Evolution (1939-1950). *Journal of the History of Biology* 27: 241-309. .

SMOCOVITIS V.B. 1996. *Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology*. Princeton, Princeton University Press.

SMOCOVITIS V.B. 1997. G. Ledyard Stebbins, Jr. and the Evolutionary Synthesis (1924-1950). *American Journal of Botany* 84: 1625-1637.

SONNEBORN T.M. 1957. Breeding systems, Reproductive Methods, and Species Problems in Protozoa. In E. Mayr (ed.), *The Species Problem*. American Association for the Advancement of Science, Washington, pp. 155-324.