Metaphysical Foundations of the Evolutionary Synthesis: A Historiographical Note

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At a symposium on speciation in 1939, Ernst Mayr appealed for dialogue among biologists interested in evolution:

> Evolution is a very complicated and many-sided process. Every single branch of biology contributes its share of new ideas and new evidence, but no single discipline can hope to find all the answers or is justified to make sweeping generalizations that are based only on the evidence of its particular restricted field. This is true for cytology and genetics, for ecology and biogeography, for paleontology and taxonomy. All these branches must cooperate.[1]

Mayr was hardly alone: other evolutionary theorists – Julian Huxley and George Gaylord Simpson among them – were voicing similar cells at that time.[2] That cross-disciplinary cooperation had become

1. Ernst Mayr, "Speciation Phenomena in Birds," *Amer. Nat., 74* (1940), 249.

2. For example, Huxley (1942): "The consideration of evolution thus demands data from [many] branches of biology. . . . All of them are necessary, but none of them alone is sufficient" (cited by Steven Waisbren, "The Importance of Morphology in the Evolutionary Synthesis as Demonstrated by the Contributions of the Oxford Group: Goodrich, Huxley, and de Beer," *J. Hist. Biol., 21* [1988], 320–321). Or Simpson (1937): "there is no natural barrier between genetic and paleontological research and . . . both must eventually unite in any final synthesis of modes of evolution" (cited by Léo F. Laporte, "George G. Simpson, Paleontology, and the Expansion of Biology," in *The Expansion of American Biology*, ed. Keith Benson, Jane Maienschein, and Ronald Rainger [New Brunswick, N.J., and London: Rutgers University Press, 1991], p. 90). On the emphasis upon cooperation among members of the "New York Circle," see Joseph Allen Cain, "Common Problems and Cooperative Solutions: Organizational Activity in Evolutionary Studies, 1936–1947", *Isis, 84* [1993], 1–25. Cain argues convincingly that the "New York Circle's" emphasis upon cooperation, while promoting the modern synthesis during the 1940s, is attributable to their institutional circumstances. His argument complements the one advanced here since I focus, not upon the promotion of the synthesis during the 1940s, but upon the intellectual predispositions which arguably forstered its construction during the 1920s and 1930s.

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so urgent by the 1930s is understandable in view of the accelerated specialization in the biological sciences since the late nineteenth century. Many practitioners of the new experimental biology were increasingly turning their backs upon the findings and theories of the older field- and museum-oriented "naturalists."[3] While this attitude seems to have been especially marked in the United States, above all in T. H. Morgan's school of genetics, the same trend can be found in Europe.[4] Conversely, many paleontologists and anatomists were ill informed about developments in genetics.[5] As a result, historians of the "modern synthesis" (as Huxley then called it) are agreed that dialogue across speciality boundaries was crucial in bridging the intellectual (and institutional) gap between geneticists, on the one hand, and naturalists, on the other.[6]

That field and experimental biology should have diverged is unsurprising, given the attractions of specialization. Reading or working outside a relatively manageable field,then as now, has rarely been perceived as a recipe for a successful career. But if that is so, how was the evolutionary synthesis possible at all? Mayr has suggested that the "architects" of the synthesis were exceptional individuals with a wide range of knowledge and interests – either genetically informed naturalists such as Simpson, Bernhard Rensch, Huxley, and Mayr himself, or geneticists with extensive knowledge of systematics, such as Theodosius Dobzhansky. Presumably every society has it share of unusual individuals who may be blessed with boundless energy, extraordinary talent, or an indifference to worldly reward. And perhaps that is sufficient to explain the architects' breadth: it was simply the product of biographical (or chromosomal) accident, producing a rare individual who is to be found in all times and places.

On the other hand, there may have been *systematic* causes fostering intellectual breadth among biologists, such that the evolutionary synthesis was more likely to occur at some times

3. See Garland E. Allen, *Life Sciences in the Twentieth Century* (New York: John Wiley, 1975); *J. Hist. Biol., 14:1* (1981); Ronald Rainger, Keith Benson, and Jane Maienschein, eds., *The American Development of Biology* (Philadelphia: University of Pennsylvania Press, 1988).

4. See Jonathan Harwood, *Styles of Scientific Thought: The German Genetics Community, 1900–1933* (Chicago: University of Chicago Press, 1993), chap. 1.

5. Laporte, "Simpson, Paleontology, and Expansion" (above, n. 2), esp. pp. 92–94. On Germany see sect. 9 of Ernst Mayr and William Provine, eds., *The Evolutionary Synthesis* (Cambridge, Mass.: Harvard University Press, 1980); W. Reif, "The Search for a Macroevolutionary Theory in German Paleontology," *J. Hist. Biol., 19* (1986), 79–130; and Harwood, *Styles*, chap. 3.

6. Mayr and Provine, *Evolutionary Synthesis*.

and places than at others. This possibility is implicit in Mayr's remark that Julian Huxley and E. B. Ford were the products of a "school" at Oxford.[7] And a few years ago I argued that at least one source of that breadth, so characteristic of geneticists in Germany (though less common in the United States), lay in the structure of the institutions in which geneticists were educated and employed.[8] In contrast with the United States, where a favorable job market allowed geneticists to specialize with impunity, young German geneticists were well advised to acquire a knowledge of general botany or zoology so as to be plausible candidates for chairs in those subjects. A similar institutional milieu may help to explain why so many of the figures who made important contributions to the evolutionary synthesis were born and educated in Russia: As Mark Adams has shown, the premium placed upon broad-based training in the biological sciences meant that most Russian geneticists had a more extensive knowledge of natural populations than their American or British counterparts.[9]

Although such institutional explanations are important, it is quite clear – at least in the German case – that they are not sufficient to explain the emphasis so often placed upon breadth of knowledge and intellectual synthesis. Many German biologists of the interwar period had become favorably disposed toward breadth during their secondary schooling (if not earlier), *before* encountering career pressures in the university or the job market. The key to this attitude, as Fritz Ringer has shown, was the ideology of *Bildung* (cultivation), which was transmitted by the classical secondary schools and endorsed by most sections of the educated middle class in Germany before World War II.[10] As an educational ideal, *Bildung* emphasized not simply the nurture of intellect, but the development of the whole person. A well-proportioned person was someone whose sensibilities and achievements were not narrowly focused, but who was instead aesthetically and morally

7. Ernst Mayr, "Prologue," in Mayr and Provine, *Evolutionary Synthesis*, pp. 1–48, esp. 11, 37, 39.

8. Jonathan Harwood, "National Styles in Science: Genetics in Germany and the United States between the World Wars," *Isis, 78* (1987), 390–414; a revised version of this paper appears as chap. 4 of Harwood, *Styles*.

9. Mark B. Adams, "The Founding of Population Genetics: Contributions of the Chetverikoff School, 1924–1934," *J. Hist. Biol., 1* (1968), 23–39; idem, "Sergei Chetverikov, the Kol'tsov Institute, and the Evolutionary Synthesis," in Mayr and Provine, *Evolutionary Synthesis*, pp. 242–278, esp. 269; Theodosius Dobzhansky, "The Birth of the Genetic Theory of Evolution in the Soviet Union in the 1920s," in ibid., pp. 229–242, esp. 240.

10. Fritz K. Ringer, *Decline of the German Mandarins: The German Academic Community, 1890–1933* (Cambridge, Mass.: Harvard University Press, 1969).

aware as well as learned. Once the entire range of one's capacities was perfected, one acquired balanced judgment and perspective, making it possible to grasp all sides of a problem and thus to apprehend the whole truth. But most important for the purposes of this paper is the fact that from the end of the nineteenth century into the 1930s, those scholars most enamored with *Bildung* called repeatedly for intellectual "syntheses" that would counter the growing fragmentation of scholarship. In their search for a unified *Weltbild* (world-picture), they developed a variety of holistic concepts in their scholarly work (e.g. *Gemeinschaft* within sociology, *Gestalt* within psychology, to cite only the best known). Although Ringer's analysis focuses upon the social sciences and humanities, I have recently argued that similar concerns can be found among German geneticists at that time, as well as in various other sectors of the interwar German scientific community.[11]

How might this German tradition be relevant for our understanding of the evolutionary synthesis? It seems very likely that theoretical problems of a particular kind are more likely to attract individuals who happen to be committed to a particular set of metaphysical assumptions.[12] Gerald Holton and Paul Forman, for example, have demonstrated that ontological predispositions have played a role in problem- and/or theory-choice in physics.[13] And many of those who joined the search during the 1930s and 1950s for the "master molecule" that would provide the "key to life" held reductionist views.[14] If calls for synthesis in interwar Germany

11. See, for example, T. J. Horder and Paul Weindling, "Hans Spemann and the Organiser," in *A History of Embryology*, ed. T. J. Horder, J. Witkowski, and C. C. Wylie (Cambridge: Cambridge University Press, 1985), pp. 183–242; John Heilbron, *Dilemmas of an Upright Man: Max Planck as Spokesman for German Science* (Berkeley: University of California Press, 1986); Mitchell Ash, "Academic Politics in the History of Science: Experimental Psychology in Germany, 1879–1941," *Central Eur. Hist., 13* (1980), 255–286.

12. Whether those of a particular metaphysical persuasion are more likely to *solve* the problems to which they are attracted is, of course, a separate matter altogether. Dozens of quasi-vitalists have taken up various biological problems in this century without notable success.

13. Gerald Holton, "The Roots of Complementarity," in Holton, *Thematic Origins of Scientific Thought: Kepler to Einstein* (Cambridge, Mass.: Harvard University Press, 1973), pp. 115–161; idem, "Subelectrons, Presuppositions, and the Millikan-Ehrenhaft Dispute," in Holton, *The Scientific Imagination* (Cambridge: Cambridge University Press, 1978), pp. 25–83; and Paul Forman, "Weimar Culture, Causality, and Quantum Theory, 1918–1927: Adaptation by German Physicists and Mathematicians to a Hostile Intellectual Environment," *Hist. Stud. Phys. Sci., 3* (1971), 1–115.

14. See John Fuerst, "The Role of Reductionism in the Development of Molecular Biology: Peripheral or Central?" *Soc. Stud. Sci., 12* (1982), 241–278.

were often bound up with some kind of holistic metaphysics, it bears asking whether similar assumptions might have prompted Dobzhansky, Mayr, Simpson, et al. to adopt a synthetic framework in tackling the problems of evolutionary theory. An answer to that question could enlarge our understanding of why the evolutionary synthesis occurred when and where it did. It is clear, for example, that the metaphysical assumptions taken for granted within scientific communities vary, not only over time, but also from one cultural context (or country) to another. If so, it follows that certain kinds of theoretical problem are more likely to be formulated (and perhaps solved) by scientists from one context than from another. If we assume that reductionist assumptions have been more widespread in this century among American than among European scientists (especially before 1945), this might help to explain, not only the United States' strength in fields like genetics and molecular biology, but also the comparative weakness – into the 1960s, at any rate – of its developmental biology (see my conclusion below). Above all, it might help to account for the evident predominance of Europeans among the architects of the evolutionary synthesis.

Needless to say, none of these larger comparative problems can be dealt with here. Nor do I claim to have established what the architects' metaphysical assumptions actually were. My aim in this paper is a more modest one: to persuade historians of the synthesis that the issue is important and the available evidence is promising. I begin by demonstrating how the theoretical syntheses sought by two German zoologists of the interwar period, Alfred Kühn and Richard Woltereck, were constructed upon an anti-reductionist metaphysics. The following section considers whether the architects of the evolutionary synthesis might have endorsed a similar metaphysics. In the conclusion I explore how study of the evolutionary synthesis from this perspective might shed light on a more general question: the heuristic function performed by metaphysical assumptions in the biological sciences.

THE QUEST FOR SYNTHESIS: GERMAN BIOLOGISTS BETWEEN THE WORLD WARS

With Hans Spemann and Karl von Frisch, Alfred Kühn (1885–1968) was generally regarded as one of Germany's leading zoologists during the interwar period.[15] A student of August

15. This account of Kühn's life and work is condensed from chap. 7 of Harwood, *Styles* (above, n. 4).

Weismann, he was called to the chair of zoology of at Göttingen in 1920 and moved to the Kaiser Wilhelm Institute for Biology in 1937. Although his research from the mid-1920s focused upon developmental genetics, Kühn's interests ranged far more widely. The first twenty years of his career were devoted to a variety of cytological and physiological problems, including cell division in amoebae and color perception in bees – the latter work culminating in an influential little book on spatial orientation in animals[16] and the founding (with Karl von Frisch) of the *Zeitschrift für vergleichende Physiologie* in 1924. Among the books that Kühn authored was an introduction to genetics, but this never acquired the significance of his introductory zoology textbook which remained the major text of its kind in West Germany well into the postwar era.[17] His broad mastery of zoology was widely acclaimed by his colleagues.[18] Of his textbook on embryology, Jane Oppenheimer wrote:

> he is unique in having at his command an exhaustive knowledge of the development of a wide variety of organisms that is unequalled in scope by that of any other investigator who currently concerns himself with developmental problems. . . . To his familiarity with morphogenetic phenomena he adds an equally profound understanding not only of the heredity of organisms, but also of their characters of life and habit, and he can therefore evaluate their developmental traits in terms of their broadest possible biological significance.[19]

What prompted Kühn to range so widely were worries about the consequences of specialization. During the nineteenth century, he felt, the scientific polymath began to be replaced by discipline-

16. Alfred Kühn, *Die Orientierung der Tiere im Raum* (Jena: G. Fischer, 1919). In his Nobel Prize acceptance speech: Konrad Lorenz attributed the concept of "taxes" to Kühn (Richard Burkhardt, "On the Emergence of Ethology as a Scientific Discipline," *Conspect. Hist., 1* [1981], 62–81), and Kühn's analysis of different modes of spatial orientation was said to have borne fruit in the ethological work of Otto Koehler and his students (Alfred Kühn, "Alfred Kühn," *Nova Acta Leop., 21* [1959], 274–280).

17. Alfred Kühn, *Grundriss der Vererbungslehre* (Heidelberg: Quelle und Meyer, 1934; 4th ed. 1965) and *Grundriss der allgemeinen Zoologie* (Leipzig: Georg Thieme, 1922; 17th ed. 1968).

18. See, e.g., H. Autrum, "A. Kühn zum 80. Geburtstag," *Naturwiss., 52* (1965), 173; Richard Goldschmidt to Kühn, August 8 and April 15, 1955; Richard Harder to Kühn, March 23, 1953; and H. Stubbe to Kühn, April 22, 1955, all in Alfred Kühn Papers, University of Heidelberg.

19. Jane Oppenheimer, [review of Alfred Kühn, *Vorlesungen über Entwicklungsphysiologie*], *Quart. Rev. Biol., 31* (1956), 32.

based specialists who lacked any grasp of the interrelation among disciplines.[20] The trend toward specialization accelerated in the twentieth century, but since it was sometimes fruitful – and in any event impossible to reverse – Kühn saw teamwork as one way to counteract its fragmenting effects. Creating a community of related specialists under one roof was, as he saw it, the organizational genius of the Kaiser Wilhelm Institute for Biology. And his keenness to collaborate with others at Göttingen, such as the physicist Robert Pohl or the biochemist Adolf Butenandt, made Kühn particularly attractive to Warren Weaver at the Rockefeller Foundation.[21] Despite the value of teamwork, however, the prospect of a single mind achieving intellectual synthesis remained Kühn's ideal. On the death of the Swiss zoologist Jean Strohl, his close friend since their days as students in Weismann's institute, Kühn reflected:

> Strohl is irreplaceable and not just for us, his friends. For our times produce ever more specialists. Not only is the broad humanistic overview of all areas of knowledge disappearing, but even in our own field one finds a narrowing not only in the empirical scope of work but in the perception of problems. This phenomenon has to occur with the growing complexity of work in each area and sometimes yields depth of understanding, but it has to be compensated by others who place individual results in an overall problem-structure as well as in their historical context.[22]

Kühn's wide-ranging interests were not confined to the biological sciences. As a student he had read not only the classics of nineteenth-century biology, but also Gottfried Keller, Hermann Hesse, and the cultural historian Jacob Burckhardt. In later years his reading encompassed contemporary psychology, a variety of historians and philosophers, and – needless to say – Goethe and Schiller.[23] These works provided him with more than just a pleasant intellectual diversion reserved for evenings and vacations. When Reinhard Dohrn invited him to contribute an essay on the work

20. I infer this from notes that Kühn took, based on his reading of various works in the sciences and humanities over the period 1916–1944, and recorded in a notebook (henceforth "Kühn notebook"), kindly lent to me by Prof. Albrecht Egelhaaf, University of Cologne. See the entries on pp. 105–106, 111, 153–154.

21. Memo from W. E. Tisdale, dated September 18, 1934, Rockefeller Foundation papers, RG 1.1, ser 717D, box 13, folder 123.

22. Kühn to H. Fischer, November 18, 1942, Kühn Papers, Heidelberg; cf. Kühn to R. Dohrn, October 13, 1942, Naples Zoological Station Archive.

23. Kühn notebook.

of Anton Dohrn to a special issue of the Naples Zoological Station's journal, Kühn spent the better part of 1941 and 1942 reading late nineteenth-century evolutionary and morphological literature in order to place Dohrn's work in intellectual context.[24] In the process, the "essay" grew into a 200-page historical work: *Anton Dohrn und die Zoologie seiner Zeit*. In addition to the humanities, Kühn was interested in architecture, Italian Renaissance art, and expressionism.[25] An involvement with art, he believed, lent scholarly insight.[26]

Underlying the breadth of knowledge to which Kühn aspired was a particular form of nonvitalist holism: Human beings could only understand those living phenomena which were amenable to physical-chemical explanation, and there were no issues that were in principle unresearchable.[27] Kühn combined this materialist position with selected elements of the Romantic tradition in biology. While Goethe's scientific work won his admiration, many *Naturphilosophen* did not. Kühn was attracted to the holism of the Romantics and their search for intellectual synthesis, but he condemned those guilty of unbridled speculation and the overenthusiastic search for analogies in nature. Goethe represented the best of the Romantic tradition, not only because of his remarkable polymathy, but also because he embodied Kühn's methodological ideal: the combination of ambitious theorizing and disciplined observation. Some of Goethe's theories, of course, turned out to be wrong, occasionally because he failed to round them empirically. But in Kühn's judgment, a holistic perspective helped Goethe to anticipate the central problems of what would later be called perceptual physiology, ecology, and above all, embryology.[28]

Although evolutionary theory did not loom large among Kühn's interests, his quest for synthesis was shared by the evolutionist Richard Woltereck (1877–1944):

24. Kühn to Reinhard Dohrn, January 23, 1941; April 4, 1941; August 9, 1942, Naples Zoological Station Archive.

25. See the documents and recollections by Kühn's former colleagues in G. Grasse, ed., *Alfred Kühn zum Gedächtnis (5. Biologisches Jahresheft)* (Iserlohn: Verband Deutscher Biologen, 1972), pp. 50, 220, 246; interview with Albrecht Egelhaaf, May 3, 1983.

26. Kühn notebook, p. 174.

27. Kühn notebook, pp. 60–61, 162–163, 186–187.

28. Alfred Kühn, "Biologie der Romantik", in *Romantik: Ein Zyklus Tübinger Vorlesungen* (Tübingen/Stuttgart: Rainer Wunderlich/Hermann Leins, 1948), pp. 215–234; idem, "Goethe und die Naturforschung," *Nachr. Ges. Wiss. Göttingen* (1932–1933), 47–69. While it was hardly universal within the German genetics community during the 1920s and 1930s, there are strong indications that others shared Kühn's brand of materialist holism (see Harwood, *Styles* [above, n. 4], chap. 7).

> Experimental genetics on the one hand and paleontology, ecology, and biogeography on the other have such different views of evolution at the moment that the very timely discussion that took part last year [at a joint meeting of the German genetics and paleontological societies in 1929] ended with a breakdown in communication [*non possumus*]. Nevertheless, some geneticists and some ecologists are convinced that the problems of speciation and evolution can only be solved through cooperation between these two fields.[29]

Despite the familiar ring of this appeal for dialogue between field and experimental biologists, Woltereck's own proposal for an evolutionary synthesis made little room for Mendelism or natural selection. Nevertheless, a brief outline of his work will better equip us to identify the metaphysical assumptions of his neo-Darwinian counterparts.

Like Kühn a student of Weismann's, Woltereck received his doctorate in 1898 and moved to the University of Leipzig, where he spent the next few years studying the embryological development of lower marine organisms in order to shed light upon their phylogeny. The publications emerging from this work – along with the popularity of his lectures on histology and vertebrate and invertebrate zoology – won him the title of associate professor (*ausserordentlicher Professor*) in 1905. His appointment the following year as director of a hydrobiological research institute in Austria (Biologische Station Lunz) marked a turning point in Woltereck's research. Although his embryological studies of marine organisms had attracted favorable attention, he was discouraged with the results: his descriptive and comparative methods allowed him to hypothesize about phylogeny, but not to illuminate the questions of evolutionary mechanism. At Lunz, therefore, he outlined an ambitious new program of experiments aimed at general hydrobiological problems, but above all at those concerned with heredity, variation, adaptation, and evolution.[30] Discovering that tiny

29. Richard Woltereck, "Beobachtung und Versuche zum Fragenkomplex der Artbildung: 1. Wie entsteht eine endemische Rasse oder Art?" *Biol. Zentralbl.*, *51* (1931), 231–232. For his attempt to foster dialogue between geneticists and paleontologists, see idem, "Einige Tatsachen und ein Vorschlag zum Streit um die sogenannte Mikro- und Makro-phylogenese," *Zool. Anz.*, *142* (1943), 105–121. For a sketch of Woltereck's life and work, see Gottfried Zirnstein, "Aus dem Leben und Wirken des Leipziger Zoologen R. Woltereck (1877–1944)," *Naturwiss., Tech., Medizin*, *24* (1987), 113–120.

30. Richard Woltereck, "Mitteilungen aus der Biologischen Station in Lunz," *Biol. Zentralbl.*, *26* (1906), 463–480.

freshwater crustaceans were well suited for such work, he began a long series of studies of the water flea *Daphnia*. In 1908 he founded the *Internationale Revue der gesamten Hydrobiologie und Hydrographie*. Although not the first in its field, it was distinctive by virtue of its broad scope and it provides an early indication of the synthetic concerns that are so characteristic of his subsequent work. Besides aiming to foster a "synthesis of the results of pure and applied studies" and to encourage communication between limnology and marine biology, he and his coeditors "[felt] the need for a synthesis of our biological and geographic-geological knowledge of bodies of water."[31]

Because of its relevance for evolutionary theory, the new Mendelism immediately attracted Woltereck's attention, and from about 1900 he gave lectures annually on evolution and inheritance.[32] Like many students of heredity in the years before World War I, he was absorbed by the contemporary debate over evolutionary mechanism waged by selectionists, neo-Lamarckians, and deVriesian mutation theorists, and his experiments on *Daphnia* were designed to contribute to this debate. His research strategy was to establish whether a continuously distributed trait (head-length) could be genetically altered, either by continued selection or by prolonged exposure to extreme environmental conditions. And if such a change could be brought about, did it occur in a single jump or via a series of intermediate stages? Repeated attempts to bring about heritable shifts in head-length via selection failed, thus confirming Wilhelm Johannsen's similar findings. Very rarely, saltatory variants arose in *Daphnia* populations, but they bore no adaptive relation to the environment in which they had been selected – from which Woltereck concluded that deVriesian mutations could not be a major mechanism of evolution. Natural selection, he believed, was clearly the mechanism by which such unadapted variants were eliminated, and accounting for the fact that one rarely found genetically mixed populations in any given lake, but it appeared not to be a creative force.

Woltereck's most promising *Daphnia* experiments were the attempts to induce small shifts in head-length through prolonged cultivation in extreme nutritional conditions. After a few generations of treatment, only phenotypic changes could be induced, but

31. Prospectus for the *International Revue*, cited in F. Ruttner, "Richard Woltereck," *Arch. Hydrobiol., 41* (1947), 602.

32. Richard Woltereck, *Variation und Artbildung: Analytische und experimentelle Untersuchung an pelagischen Daphniden und anderen Cladoceren: Teil I – Morphologische, Entwicklungs-geschichtliche und physiologische Variationsanalyse* (Bern: Franke, 1919), p. 8.

after five to seven generations in the extreme medium the forms with enlarged heads took longer to return to the original head size. After forty generations in extreme medium, the long-headed *Daphnia* remained long-headed after reproducing once in normal medium, but by the second generation in normal medium they had returned to normal head-size. (These experiments provided the earliest example of the phenomenon known as "dauermodifications" [persistent phenotypic modifications], which was to excite considerable discussion in German evolutionary circles during the 1930s.[33]) Although his results failed to identify which of the contending mechanisms was a major factor in evolution, Woltereck's work was soon cited as evidence against neo-Lamarckism.[34] Some of the *Daphnia* studies by Woltereck and his students appeared in book form in 1919;[35] five of the book's six chapters were devoted to the systematics, physiology, morphology, embryology, and ecology of variation in *Daphnia*, and reviewers were struck by its "extraordinarily comprehensive" scope.[36]

Apart from his ambitious synthetic aims, Woltereck's approach to science before World War I was unexceptional. After the war, however, a radical shift is evident in his conception of biology.[37] Rejecting his previous belief in the sufficiency of a mechanist, materialist, and causal perspective in biology, his writings from the early 1920s are rich in affirmations of "holism" as well as rejections of "materialism." This can be seen in a series of articles on philosophy, politics, and educational reform that Woltereck wrote for *Vivos Voco*, an intellectual monthly that he founded with Hermann Hesse in 1919 as a forum for the German youth movement.[38] His holism is also apparent in a popular-scientific monthly that he and his students established in 1925, *Die Erde* [The Earth].[39] As the

33. Jonathan Harwood, "Genetics and the Evolutionary Synthesis in Germany," *Ann. Sci., 42* (1985), 279–301; Jan Sapp, *Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics* (Oxford: Oxford University Press, 1987), pp. 60–65.

34. Wilhelm Johannsen, *Elemente der exakten Erblichkeitslehre*, 2nd ed. (Jena: G. Fischer, 1913), pp. 438–439.

35. Woltereck, *Variation und Artbildung* (above, n. 32).

36. See, e.g., the review by K. Gruber in *Z. indukt. Abstam. Vererb., 29* (1922), 83–87, at 83.

37. For an account of Woltereck's life and work that pays particular attention to this shift, see Jonathan Harwood, "Biological Theory and Weimar Culture: A Study of Richard Woltereck (1877–1944)" (in preparation).

38. *Vivos Voco* appeared in five volumes between 1919 and 1926, published by a cooperative that Woltereck had set up with students and younger staff at the University of Leipzig.

39. *Die Erde: Illustrierte Monatsrundschau* (Braunschweig: Vieweg, 1925–1926).

editorial in the first issue explained, the journal sought to foster cooperation among university staff, students, and schoolteachers who shared the desire to fashion a "multifaceted overview" of the advances in scientific knowledge. Unlike other similar journals, *Die Erde* would not simply present a "mosaic" of diverse articles from every imaginable speciality, but rather would emphasize

> what have recently been described as the *holistic features* of the animate and inanimate world.
>
> The editors and contributors wish to enable their readers to conceive nature about us, above all the earth, as *a whole*, in spite of the countless individual phenomena and issues that preoccupy the scientist daily, thus narrowing his horizon such that he no longer notices the problems and advances of others, and no one sees the whole.
>
> This journal aims to foster *understanding*; it will demonstrate and emphasize the connections between specialities, and above all it will encourage *recognition of the whole amidst the individual details* [das Ganzheitliche im Einzelheitlichen erkennt].[40]

The first issue of the journal opened with an article by Woltereck on "biology as the study of wholes."[41] In the nineteenth century, he argued, biologists had been primarily concerned with the discovery of new facts about the structure and function of organisms. It was essential that this activity continue and fortunate that many biologists were content to conduct this kind of work, but such specialized factual research could not yield "understanding" of living systems as totalities, any more than a detailed analysis of every orchestral instrument or each bar in a symphony could convey a musical grasp of the whole piece. For an organism was more than the sum of its parts, and identifying the causes of each of its constituent processes would not yield a causal understanding of the whole organism.

The most systematic discussion of Woltereck's philosophy of biology was published seven years later: *Grundzüge einer allgemeinen Biologie* proposed a total reconstruction of the methodological foundations of biology.[42] The analytical method in biology,

40. Die Leipziger Werkgemeinschaft, "Zur Einführung," *Erde, 3* (1925), 1 (emphasis in original).

41. Richard Woltereck, "Biologie als Ganzheitsforschung," *Erde, 3* (1925), 3–10.

42. Richard Woltereck, *Grundzüge einer allgemeinen Biologie: Die*

based upon exclusively causal and materialist assumptions, had been very productive, Woltereck emphasized, and would remain necessary. But several features of organisms could not be understood using this method. One of these was their holistic or *Gestalt* character, evident in the power of regeneration as well as in the capacity to develop a complete organism out of a primitive egg.[43] Another limitation derived from the fact that the living world has a nonmaterial as well as a material aspect; conventional analysis could probe the latter, but not the former.[44]

The revised theory of evolution that Woltereck constructed upon such holist and antimaterialist foundations during the 1920s was a "dualist" one.[45] That is, he believed that micro- and macroevolution proceeded by different mechanisms, acting upon two different forms of heredity. Although he acknowledged that both selection and neo-Lamarckism could account for certain features of evolution, he argued that a form of orthogenesis was the principal mechanism of macroevolution. However non-Darwinian Woltereck's synthesis, the analytical rigor of his work, along with the fact that some of his findings on *Daphnia* were indeed awkward to explain in terms of selection, meant that during the 1930s his views were taken seriously by geneticists. And although they disagreed with him profoundly, both Ernst Mayr and Bernhard Rensch cited Woltereck in their own contributions to the modern synthesis.[46]

METAPHYSICAL ASSUMPTIONS OF THE NEO-DARWINIANS

Although Alfred Kühn's and Richard Woltereck's views on heredity, evolutionary mechanism, and materialism were altogether

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Organismen als Gefüge/Getriebe, als Normen und als erlebende Subjekte (Stuttgart: F. Enke, 1932).

43. Ibid., pp. 80, 550–553, 559.

44. See, e.g., ibid., pp. xii–xvi, 67–68, 71, 76, 511–513. Chap. 17 is entitled "The Limits of Materialist and Causal Analysis: The Second Approach to Researching Life."

45. Harwood, "Genetics" (above, n. 33).

46. Ernst Mayr, *Systematics and the Origin of Species* (New York: Columbia University Press, 1942), pp. 213–215; Bernhard Rensch, *Neuere Probleme der Abstammungslehre* (Stuttgart: F. Enke, 1947), pp. 55, 306, 371. The mathematical population geneticist Wilhelm Ludwig paid tribute to Woltereck as a worthy opponent: Ludwig, "Die Selektionstheorie," in *Die Evolution der Organismen*, ed. G. Heberer (Jena: G. Fischer, 1943), pp. 479–520. Ernst Caspari recalled Woltereck as a "very important vitalist" during the 1930s (interview, September 23, 1981).

different, what they shared was a search for intellectual synthesis, reflected in the wide range of their knowledge and interests, both inside and outside the natural sciences. Can they be said to have endorsed a common metaphysics? Characterizing scientists' ontological assumptions is extraordinarily difficult, since few of them declare their views as explicitly as Woltereck, but their epistemological predilections are often more visible. Rather than describing Kühn, Woltereck, and many other German biologists of this period as "holists," therefore – a categorization that is difficult to substantiate in many cases, and is, in any event, open to a variety of misunderstandings – I would emphasize merely the *antireductionist* features of their work. With that in mind, we can ask to what extent the architects of the evolutionary synthesis might have endorsed a similar metaphysics. Although the available secondary literature has barely begun to address the metaphysical issue,[47] it reveals a number of similarities between the architects and their German contemporaries. Almost all of the architects, for example, displayed a wide range of intellectual and "cultural" interests outside the sciences.[48] Of course, caution must be exercised here; wide-ranging knowledge coupled with synthetic preoccupations *need* not have been rooted in some kind of antireductionism. A search for synthesis is in principle also consistent with a reduc-

47. A notable exception is Betty Smocovitis's recent claim that "only within a positivist theory of knowledge . . . was the unification of biology . . . [seen to be] desirable" (V. B. Smocovitis, "Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology," *J. Hist. Biol.*, *25* [1992], 4). Just how her interpretation of the architects' epistemological assumptions is related to the one I have outlined here is difficult to establish. If by "positivism" she means "opposed to nonnaturalistic explanations of evolution" (as on pp. 20–21), then yes: the architects were undoubtedly so opposed – but little is gained by calling them "positivists." The more usual meaning of positivism in philosophy of science is the view that non-observable concepts are to be avoided and that empirical laws are preferable to (speculative) theories. On this score, it is not clear that *any* of the architects would qualify as positivists. And as Smocovitis herself points out, the architects were wary of the Vienna Circle's reductionism (pp. 6–7, 59). On the other hand, her remark that the architects sought to "strike just the right balance between mechanistic materialism and some form of emergentism" (note 81; cf. note 27) is much closer to my interpretation.

48. G. Ledyard Stebbins may be an exception to this generalization; see Vassiliki Betty Smocovitis, "Botany and the Evolutionary Synthesis: The Life and Work of G. Ledyard Stebbins Jr.," Ph.D. diss., Cornell University, 1988. Although Richard Goldschmidt's own evolutionary synthesis was not of the Darwinian variety, the wide range of his interests (within science as without), his admiration for Goethe, and his insistence upon the importance in science of an "artistic" perspective place him firmly within the German tradition of *Bildung*; see Harwood, *Styles* (above n. 4), chap. 7.

tionist epistemology.[49] Thus one cannot simply infer the architects' metaphysical assumptions from their breadth of knowledge and interests alone. But the similarities also extend in some cases to epistemological premises (which is emphatically *not* to claim that the architects' metaphysical views were *identical* to Kühn's or Woltereck's).

Consider George Gaylord Simpson. A voracious reader who "wanted to know *everything*", he was interested in linguistics, medieval architecture, music, painting, sculpture, and ethnography.[50] Simpson's metaphysics is more difficult to pin down; although his essays from the 1960s on the relations between biology and the physical sciences emphasize hierarchies of complexity, within biological systems as well as throughout nature, his views during the 1930s and 1940s have yet to be characterized.[51]

The broad sweep of Julian Huxley's interests is well documented, and the fact that he published works on politics, philosophy, and poetry makes it rather easier to identify his metaphysical predilections.[52] The basic intention of his scholarly concerns was unmistakably synthetic: "to unite the physical, the mental, the moral, and the spiritual in one gospel of evolutionary progress."[53] And although students of Huxley's thought emphasize that he did not adhere consistently to a single philosophy throughout his life, there is general agreement that he adopted an antireductionist position during the interwar period.[54] In the living world the aggregation of units – e.g. from protozoa to metazoa to communities – led to the formation of new entities of higher order, which possessed

49. German-speaking advocates of logical positivism were evidently a case in point; see Gerald Holton, "Ernst Mach and the Fortunes of Positivism in America," *Isis, 83* (1992), 27–60, esp. 38 and 46.

50. The phrase is Simpson's, quoted in Léo Laporte, "The World into Which Darwin Led Simpson," *J. Hist. Biol., 23* (1990), 500; cf. George Gaylord Simpson, *Concession to the Improbable: An Unconventional Autobiography* (New Haven: Yale University Press, 1978), and Léo Laporte, ed., *Simple Curiosity: Letters from George Gaylord Simpson to His Family, 1921–1970* (Berkeley: University of California Press, 1987). On the breadth of Simpson's scientific knowledge and interests, see Laporte, "Simpson, Paleontology, and Expansion" (above, n. 2).

51. Personal Communications from Léo Laporte and Marc Swetlitz.

52. See P. G. Werskey, "Haldane and Huxley: The First Appraisals", *J. Hist. Biol., 4* (1971), 171–183; J. R. Baker, "Julian Sorell Huxley", *Biog. Mem. F.R.S., 22* (1976), 207–238; and F. B. Churchill, "The Modern Evolutionary Synthesis and the Biogenetic Law," in Mayr and Provine, *Evolutionary Synthesis* (above, n. 5), pp. 112–122.

53. John C. Greene, "The Interaction of Science and World View in Sir Julian Huxley's Evolutionary Biology," *J. Hist. Biol., 23* (1990), 40.

54. Personal communications from Colin Divall, Vassiliki Betty Smocovitis, and Marc Swetlitz.

their own unity. Attempts to explain all of the properties of higher levels in terms of those of lower ones were guilty of "nothing-buttery." Evolution, too, displayed the same emergent properties; the characteristics of later forms were entirely unpredictable on the basis of full knowledge of preexisting ones. In ontological terms, Huxley was a monist in the sense that he believed the universe to consist of a "world-stuff" that bore the properties of both matter and mind.[55]

The mathematical population geneticist Sewall Wright is not usually described as an "architect" of the synthesis, and, unlike Woltereck et al., he constructed his theory of evolution from a relatively limited body of knowledge (viz., genetics and animal breeding), making no attempt to draw together related phenomena from field biology. On the other hand, the scope of Wright's work *within* genetics – embracing both physiology and evolution – was unusually broad for an American geneticist in the 1920s.[56] Furthermore, the emphasis upon different processes occurring at different levels within an evolving species conferred certain antireductionist features upon Wright's shifting-balance theory. Given the nonadditive phenotypic effects of genes, selection generally acted upon gene-systems rather than upon individual genes. Similarly, the processes that facilitated selection at the local populational level (inbreeding and random genetic drift) did not apply at the species level. Lastly, the philosophy of mind that occupied Wright throughout his life was antireductionist in its refusal to attribute the properties of mind to those of matter.[57]

55. The fullest discussion of these issues so far is Colin Divall, *Capitalising on 'Science': Philosophical Ambiguity in Julian Huxley's Politics, 1920–1950,* Ph.D. diss., University of Manchester, 1985. See also *idem,* "From a Victorian to a Modern: Julian Huxley and the English Intellectual Climate," *in* Julian Huxley: Biologist and Statesman of Science, C. K. Waters and Albert van Helden, eds. (Houston: Rice University Press, 1993).

56. This is one of the reasons why he was much admired by geneticists in Germany; see Harwood, *Styles* (above, n. 4), chap. 5.

57. I am indebted to Jonathan Hodge for helping me to understand Wright's views; see Hodge, "Biology and Philosophy (Including Ideology): A Study of Fisher and Wright," in *Founders of Evolutionary Genetics*, S. Sarkar, ed. (Dordrecht: Kluwer, 1992), pp. 231–293. See also Sewall Wright, "Biology and the Philosophy of Science," *Monist, 48* (1964), 265–290; and William Provine, *Sewall Wright and Evolutionary Biology* (Chicago: University of Chicago Press, 1986). In this otherwise excellent book, Provine asserts that Wright's philosophy had no effect upon his science while declining to discuss the fact that antireductionist features appear to be common to both Wright's evolutionary theory and his philosophy of nature.

Although J. B. S. Haldane had little to say about speciation, the range of his interests, both inside and outside of the sciences, is well known. Moreover, Sarhotra

As a scientist Theodosius Dobzhansky is said to have preferred grand projects and big generalizations to narrow specialization, and the broad range of his interests extended to art, music, history, literature, and philosophy.[58] Although his philosophical premises have not yet been studied in detail, it is evident that by the late 1930s Dobzhansky, too, was thinking in terms of levels of biological organization.[59] Zhores Medvedev's remark that not only Dobzhansky but also Sergei Chetverikov and N. V. Timofeev-Ressovsky were "scholars of enormous breadth and erudition" suggests that a study of the philosophical foundations of their work might be illuminating.[60]

But if Germany was the country during the interwar period where holistic philosophies associated with the ideology of *Bildung* were especially common within the academic community, we might expect similar ideas to have been endorsed by the German architects. This is precisely what one finds in Bernhard Rensch's autobiography. During the 1920s he was interested in expressionist painting, philosophy, and the history of Near and Far Eastern cultures, and he sought to develop "as all-embracing a world-picture as possible."[61] Finally, having started this paper with Ernst Mayr, I come full circle. Several years ago I gave a paper on Alfred Kühn, arguing that the impressive breadth of his biological knowledge, as indeed of his historical and artistic interests, reflected both a general commitment to intellectual synthesis and an assumption that the universe was an integrated whole.[62] After the talk, Mayr came up to tell me, not only that he agreed with my analysis, but that everything I had said about Kühn also applied to him.

Sarkar finds a persistent strand of antireductionism in Haldane's philosophical views; see Sarkar, "Science Confronts Philosophy: The Case of J. B. S. Haldane" (paper read at Haldane Centenary meeting, London, April 10–11, 1992).

58. William Provine, "Origins of the 'genetics of natural populations' series," in *Dobzhansky's Genetics of Natural Populations (numbers 1–43)*, ed. R. C. Lewontin, J. A. Moore, W. B. Provine, and Bruce Wallace (New York: Columbia University Press, 1981), pp. 1–76; Francisco Ayala, "Theodosius Dobzhansky," *Biog. Mem. Nat. Acad. Sci.*, *55* (1985), 163–214.

59. John Beatty, personal communication.

60. Zhores Medvedev, "N. W. Timofeeff-Ressovsky (1900–1981)," *Genetics*, *100* (1982), 5.

61. Bernhard Rensch, *Lebensweg eines Biologen in einem turbulenten Jahrhundert* (Stuttgart: G. Fischer, 1979), p. 53.

62. Jonathan Harwood, "The Reaction against Specialization in 20th-Century Biology: A Study of Alfred Kühn," *Freiburger Universitätsbl. 87/88* (1985), 193–203.

CONCLUSION

Should it prove to be the case that antireductionist views were widely held among architects of the evolutionary synthesis, it would not necessarily follow that antireductionist assumptions were, in fact, important for that intellectual achievement. To demonstrate that would require a careful analysis of the reasoning used by both those evolutionary biologists who contributed to the synthesis and those who did not. Obviously antireductionism was hardly a *guarantor* of successful work in evolutionary theory; various antireductionists (e.g. Woltereck and Richard Goldschmidt) developed synthetic theories of evolution that bore little relation to Darwinism. Conversely, an antireductionist perspective was probably not even *essential* for making a contribution to the modern synthesis. This would be to portray the construction of the synthesis as an overly homogeneous process, ignoring the diversity of intellectual tributaries that fed into that stream. Several historians of the synthesis, for example, have noted the importance of Erwin Baur's work on the Mendelian basis of species differences in natural populations (1930), but Baur was anything but an antireductionist.[63]

Nevertheless, it seems altogether plausible that some kinds of theoretical problem are more readily approached from a particular metaphysical starting point. The enormous expansion of chemical and physical approaches within the biological sciences in this century indicates widespread confidence that many of an organism's properties – notably the structure and function of inheritance – are best explained in reductionist terms. Some historians of biology have advanced more far-reaching claims. In a series of papers on nineteenth- and early twentieth-century biology, Nils Roll-Hansen has argued that "reductionism . . . has in general been the most fruitful approach to experimental biological research."[64] Central to the Morgan school's chromosome theory, he argues, was a reductionist conception of the gene.[65] Neither

63. On Baur's work in evolutionary genetics see Mayr and Provine, *Evolutionary Synthesis* (above, n. 5); on his metaphysical inclinations see Harwood, *Styles* (above, n. 4), chap. 7. A similar point could be made about molecular biology. However fruitful a reductionist perspective has been in that field, Barbara McClintock's achievements appear to have been rooted in a rather different metaphysics; see Evelyn Fox Keller, *A Feeling for the Organism: The Life and Work of Barbara McClintock* (San Francisco: W. H. Freeman, 1983).

64. Nils Roll-Hansen, *Reductionism in Biological Research: Three Historical Case Studies* (Oslo: Institute for Studies in Research and Higher Education, 1979), p. 1.

65. Nils Roll-Hansen, "Drosophila Genetics: A Reductionist Research Program," *J. Hist. Biol., 11* (1978), 159–210.

the holistic objections advanced by the geneticists William Bateson and Wilhelm Johannsen, nor those of E. S. Russell and J. H. Woodger, led to a successful alternative conception of heredity.[66] Nevertheless, Roll-Hansen concedes that antireductionist research programs have been fruitful during certain historical periods and that it "is still *possible* that holism may be closer to the truth on certain basic issues in biology."[67]

One such basic issue might be the problem of development. It is probably no accident that Woodger was a practicing embryologist for many years, and that the major criticism that both Bateson and Russell leveled at the chromosome theory was its apparent inability to account for the process of development. Thirty years ago Jane Oppenheimer posed the question, Why have so many of the greatest embryologists been German? Her answer: "[they were] in a sense in love with the embryo, and thus able to fathom some of its secrets by processes of understanding that transcend the usual . . . procedures of scientific thinking. And why? Because they could see the embryo whole. . . . They were the flower of the . . . romantic movement which could enable them to comprehend the wholeness of the embryo as part of the wholeness of nature."[68]

The importance that Oppenheimer ascribes to German embryologists' holism has since been echoed by Johannes Holtfreter, who knew personally many of the major figures in embryology during the interwar period.[69] The best known of these was, of course, Hans Spemann, who received a Nobel Prize in 1935. Viktor Hamburger, Holtfreter's fellow student in Spemann's laboratory at Freiburg during the 1920s, has also emphasized the importance of Spemann's holistic inclinations in shaping his choice of experimental methods.[70] Similarly, in the dispute between Wilhelm Roux and Hans Driesch over the causes of differentiation, Spemann clearly sided with the latter.[71] Thus the holistic perspective so common

66. Nils Roll-Hansen, "E. S. Russell and J. H. Woodger: The Failure of Two Twentieth-Century Opponents of Mechanistic Biology," *J. Hist. Biol., 17* (1984), 399–428.

67. Roll-Hansen, *Reductionism* (above, n. 64), p. 10.

68. Oppenheimer, review of Kühn's *Vorlesungen* (above, n. 19), p. 33.

69. A "holistic spirit . . . animated all the pioneers in our field" (Johannes Holtfreter, "Address in Honor of Viktor Hamburger," *Devel. Biol. Supp. 2* [1968], xii).

70. Viktor Hamburger, "Evolutionary Theory in Germany: A Comment," in Mayr and Provine, *Evolutionary Synthesis* (above, n. 5), pp. 303–308. For a brief account of the artistic and philosophical interests of other members of Spemann's school, see Viktor Hamburger, "Hilde Mangold, Co-Discoverer of the Organizer," *J. Hist. Biol., 17* (1984), 1–11.

71. Horder and Weindling, "Spemann and the Organiser," (above, n. 11), p. 210.

among German embryologists of that generation might explain why they were attracted to development phenomena in the first place, and why thereafter they made particular methodological and theoretical choices.

If a holistic metaphysics was fruitful in interwar embryology, it is certainly worth considering whether antireductionist assumptions might have predisposed the architects, not only to become knowledgeable in many areas of biology, but also to search for an evolutionary-theoretical framework that could integrate evidence from each of those areas.

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