Geneticists and the Evolutionary Synthesis in Interwar Germany

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Summary

According to Ernst Mayr, most geneticists were not particularly interested in or well informed about macro-evolutionary processes and thus did not make major contributions to the evolutionary synthesis of the 1930s and 1940s. Although this characterization applies to many American geneticists of the period, it does not fit their German counterparts. German geneticists' active interest in evolutionary mechanisms can be clearly seen in the German debates of the 1920s and 1930s over the significance of cytoplasmic inheritance. While morphologists celebrated the evidence for cytoplasmic heredity as a basis for neo-Lamarckian mechanisms, those geneticists who actually studied cytoplasmic inheritance regarded it as a way of strengthening the case for natural selection. This German–American contrast suggests that our understanding of the evolutionary synthesis would benefit from an analysis of the institutional circumstances of the various contributing disciplines.

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1. Introduction

It is generally agreed that a major shift occurred in the life sciences around 1900. That shift entailed not only matters of method, namely the rapid spread of experimentation into new areas, but also matters of problem-definition. The younger generation of experimentalists was much less interested in the mechanisms of evolution than were their predecessors. The grand, speculative theoretical syntheses by Weismann, de Vries or Haeckel—encompassing the phenomena of inheritance, development and evolution—were gradually displaced by more narrowly defined specialized studies. Those calling themselves 'geneticists' or 'embryologists' increasingly left the question of evolutionary mechanism to systematists, ecologists, palaeontologists or those in other descriptive disciplines.¹

As Peter Bowler has recently demonstrated, debate over evolutionary mechanism from the 1880s to World War I was a noisy affair, with selectionists, mutationists, neo-Lamarckians and orthogenists all clamouring for attention.² As historians begin to devote more attention to twentieth-century evolutionary debate, it is becoming clear that such dissension carried on into the 1920s and 1930s. From the 1940s, however, a

¹ E.g. Garland Allen, Life Science in the Twentieth Century (New York, 1975).

² Peter Bowler, The Eclipse of Darwinism (Baltimore, 1983).

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rough consensus seems to have emerged which put heredity, development and evolution back together into a unified theoretical framework which has dominated the life sciences ever since.³ How did this 'evolutionary synthesis' arise?

In the course of studying the German genetics community between the wars, I have been impressed by the extent of their interest in evolutionary matters. This fact seemed at odds with Ernst Mayr's explanation of the synthesis in which during the interwar period geneticists, on the whole, are portrayed as being rather ignorant of evolutionary phenomena and so as playing a relatively minor role in the synthesis. Although much of the material I have looked at supports his interpretation the aim of this paper is to reformulate Mayr's thesis in accord with the evidence from German genetics. Once reformulated, Mayr's thesis has very far-reaching historiographical implications, for it indicates how much we need in future to develop the *institutional* history of twentieth century biological disciplines if we want to understand their *intellectual* history.

Let me begin by briefly outlining Mayr's thesis. Most geneticists, he argues, were not particularly interested in evolutionary questions,⁴ were poorly informed about the evidence for macro-evolutionary processes,⁵ or if they did address evolutionary issues, were sceptical about the sufficiency of natural selection as a creative mechanism.⁶ Furthermore, he rejects the importance often granted to the work of the 1920s and 1930s on population genetics by J. B. S. Haldane, R. A. Fisher, and Sewall Wright. Population genetics took Mendelian genetics as a starting point and merely demonstrated the powers of selection, drift, isolation and recombination at the populational level. However, the decisive step in the evolutionary synthesis was the demonstration that such micro-evolutionary selectionist models could be extrapolated to those macro-evolutionary phenomena (such as speciation) so familiar to naturalists. Outside genetics, palaeontologists⁷ and anatomists⁸ were especially vocal in their rejection of selection. Bridging this gap between laboratory-based geneticists and (for lack of a better term) 'descriptive morphologists' required exceptional people: either genetically-informed naturalists or systematists such as G. G. Simpson, Bernhard Rensch, F. B. Sumner, Julian Huxley, Erwin Stresemann and Mayr himself, or geneticists with a knowledge of systematics such as Dobzhansky.⁹

Mayr, of course, acknowledges isolated exceptions to his portrayal. Having studied zoology in Berlin in the 1920s, he is aware that geneticists such as Erwin Baur and Richard Goldschmidt were not only interested in evolutionary mechanisms but conducted genetic analyses of wild populations and (in Goldschmidt's case) advanced

³ E.g. Ernst Mayr and William Provine (editors), *The Evolutionary Synthesis* (Cambridge, Mass., 1980) [hereafter Mayr and Provine].

⁴ See various essays by Mayr in Mayr and Provine, especially 'Prologue: Some Thoughts on the History of the Evolutionary Synthesis', pp. 1-48; Provine, 'Introduction', in Mayr and Provine, pp. 51-58 (pp. 54, 57); Hampton L. Carson, 'Cytogenetics and the Neo-Darwinian Synthesis', in Mayr and Provine, pp. 86–95 (pp. 88, 91); Alexander Weinstein, 'Morgan and the Theory of Natural Selection', in Mayr and Provine, pp. 432-45 (p. 443).

⁵ See Mayr, 'Prologue...' (footnote 4), 8–9, 33; Mayr, 'The Role of Systematics in the Evolutionary Synthesis', in Mayr and Provine, pp. 123–36 (pp. 124, 131).

⁶ Mayr, 'Prologue' (footnote 4), 4, 7, 21–22, 12, 25, 29; Mayr, 'The Role of Systematics...' (footnote 5), 131– 33; Weinstein, (footnote 4), p. 439; Th. Dobzhansky, 'Morgan and his School in the 1930s', in Mayr and Provine, pp. 445–52 (pp. 447–50).

⁷ Mayr, 'Prologue' (footnote 4), 8, 13, 20–21, 28; Mayr, 'The Role of Systematics...' (footnote 5), 134. ⁸ Mayr to the author, 20.5.83.

⁹ Mayr, 'Prologue' (footnote 4), 7; Mayr, 'Role of Systematics' (footnote 5), 123, 133.

original theories of evolution.¹⁰ The problem with Mayr's hypothesis, as I will show in detail below, is that Baur and Goldschmidt were by no means unusual within the German genetics community. The Germans took it for granted in the 1920s that genetic analysis of wild populations was important; while Sumner struggled to get his work in this area published by the American journal *Genetics*,¹¹ German journals routinely published similar work by Timoféeff-Ressovsky, Baur and Goldschmidt.¹²

That Mayr's hypothesis works better for geneticists of T. H. Morgan's school than for the Germans derives from the fact that what went under the name of 'genetics' in the U.S.A. was a very different beast from its German counterpart. L. C. Dunn recalls being warned as a graduate student to avoid the problem of evolution because it was too speculative. At Columbia University, Dunn and his colleagues decided about 1936 to resurrect the Jessup Lectures on evolution which had lapsed in 1910. The lecturer whom they invited, Th. Dobzhansky, succeeded in awakening Dunn's interest in evolution^{12a} but he had found Morgan and his colleagues in Pasadena unenthusiastic.¹³ When Dobzhansky eventually came to the Department of Zoology at Columbia in 1941, there was no one teaching evolution. The Department first invited Ernst Mayr to give a seminar in the early 1950s, some 20 years after he had arrived in New York. When Mayr moved to Harvard in 1953, he discovered that no one there had been teaching evolution for 25 years.¹⁴ In the 1920s at Harvard, Stebbins had been told that evolution was all right for Sunday newspaper supplements, but real biology was biochemical.¹³ Morgan frankly admitted side-stepping the issue of evolution because in the early years of the century he felt that genetics was not yet advanced enough, and it would have been unfortunate for the new and precise discipline of genetics to become compromised through association with evolutionary speculation. Even in the early 1930s he was still cautious about a rapprochement.¹⁵

While American geneticists in the 1920s and 1930s put aside the problems of development and evolution in order to concentrate on what they saw as the relatively simple problems of transmission genetics (that is, the mechanisms of distribution of genes between generations and the localization of genes within chromosomes),

¹⁰ 'The Role of Systematics' (footnote 5), 128–9; 'Prologue' (footnote 4), 31. In the confines of a single paper, one cannot discuss all the major German geneticists who were seriously interested in evolution. I have omitted Goldschmidt here because his work is well known, and Valentin Haecker was not included since his writings on evolution do not concern cytoplasmic inheritance.

¹¹ W. Provine, 'F. B. Sumner and the Évolutionary Synthesis', Studies in History of Biology, 3 (1979), 211-40 (pp. 234-5).

¹² e.g. Erwin Baur, 'Die Bedeutung der Mutation für das Evolutions-problem', Zeitschrift für induktive Abstammungs- und Vererbungslehre [hereafter ZIAV], 37 (1925), 107-15; Goldschmidt, 'Untersuchungen zur Genetik der geographischen Variation', Archiv für mikroskopische Anatomie und Entwicklungs-Mechanik; 101 (1924), 92-337.

^{12a} 'The Reminiscences of L. C. Dunn', Columbia University Oral History Project, typescript, pp. 865-67.

¹³ 'The Reminiscences of Th. Dobzhansky', Columbia University Oral History Project, typescript, p. 345. ¹⁴ Conversation with Ernst Mayr, 30.5.84.

¹⁵ T. H. Morgan, 'The Rise of Genetics', Science, 76 (1932), 285–88 (p. 287). According to Dobzhansky, Morgan et al. liked to insist during the 1930s that genetics could be done without any reference to evolution (Dobzhansky, 'Morgan and his School...' (footnote 6), 449). This American–German contrast was, of course, not a static one. Before World War I geneticists in both countries seem to have been concerned with evolutionary mechanisms. And there is no doubt that American geneticists on the whole became more interested in evolution during the 1930s and 1940s (see Mayr, 'Prologue' (footnote 4), 30–32; Allen (footnote 1), 144). Bentley Glass recalls the considerable impact made upon geneticists by Dobzhansky's *Genetics and the Origin of Species* (1937); men such as J. T. Patterson and Wilson Stone switched from transmission geneticists, such as Hans Nachtsheim and Curt Stern, remained largely unconcerned with evolutionary mechanism. The national contrast was thus not an all-or-none phenomenon and may have been rather less distinct before and after the inter-war period.

geneticists in Germany tended to regard these problems as largely solved and thus of little interest. Instead, most of them addressed the genes' role in development or evolution. To an emigré like Goldschmidt the narrowness of genetics in his adopted homeland warranted mild ridicule. He admired Dobzhansky, Julian Huxley and Sewall Wright but was dismissive of 'dyed in the wool Drosophilists'.¹⁶ Congratulating Dobzhansky on his appointment at Columbia in 1940, Goldschmidt wrote:

I am...glad that a broadminded geneticist with a real scientific background (as opposed to the average gene shuffler) gets into a prominent position and can help to free genetics from the fetters of narrow-mindedness.¹⁷

The distinctiveness of the German tradition can be seen very sharply in the debate during the 1930s over cytoplasmic inheritance (CI).¹⁸ Of the various conceptions of CI discussed at that time, the most controversial was the 'Plasmon' theory advocated by F. von Wettstein, Correns, Kühn and Michaelis. According to their model, the Plasmon-unlike chloroplasts or mitochondria-acted in concert with chromosomal genes to codetermine all of an organism's traits. Furthermore, the cytoplasm was not merely a passive 'substrate' for chromosomal genes' activity but rather the site of a *aenetic* structure, the Plasmon, independent of chromosomal genes and directing their function. In advancing this model, the Plasmon theorists were rejecting the dominant view in genetics according to which genetic control over development resided entirely in chromosomal genes (the so-called 'nuclear monopoly'). Instead, the genetic structure of the cytoplasm was of a significance at least equal with, if not greater than, the genes in organizing development. The Plasmon theorists were dissatisfied with Morgan's chromosome theory of heredity because it had merely attributed phenotypes to atomistic nuclear particles without specifying how such particles could act upon the developing embryo in the temporally and spatially *coordinated* manner necessary to account for ontogeny. The Plasmon was thus designed to fill what Morgan admitted in 1932 was an 'unfortunate gap'¹⁹ between gene and phenotype.

But in the 1920s and 1930s the theoretical importance of the Plasmon theory went beyond the problem of development. For in Germany, as we shall see, the Plasmon theory was perceived as a solution to the puzzle of evolutionary mechanism, albeit in two diametrically opposed ways. For evolutionists hostile to selection, the Plasmon seemed to provide an alternative form of heredity which would be more compatible with neo-Lamarckian mechanisms than were Mendelian genes. But those geneticists actually developing the Plasmon theory were advocates of natural selection; for them the existence of the Plasmon provided an explanation of how complex adaptive traits could evolve gradually via selection.

Significantly, the literature on CI was almost exclusively German until after 1945. Where American geneticists responded at all to the evidence for CI, they were critical. By drawing the boundaries of their discipline so narrowly as to exclude development and evolution, American geneticists found little of significance in CI.

Because the Plasmon theory was advocated by disparate groups for very different ends, it will be useful at the outset to give an overview of the relations between these

¹⁶ Goldschmidt to L. C. Dunn, 27.5.40 (Dunn Papers); cf. ibid., 7.6.38.

¹⁷ Goldschmidt to Dobzhansky, 19.2.40 (Dobzhansky Papers).

¹⁸ I have discussed this debate at length in 'The Reception of Morgan's Chromosome Theory in Germany: Inter-war Debate over Cytoplasmic Inheritance', Medizinhistorisches Journal, 19 (1984), 3–32. See also Jan Sapp, Cytoplasmic Inheritance and the Struggle for Authority in the Field of Heredity, 1891–1981 (Ph.D. thesis, University of Montreal, 1984), chapter 3.

¹⁹ Morgan (footnote 15), 285.

groups and the concepts they supported as these are reflected in the structure of the paper. Section 2 introduces the Grundstock hypothesis: a speculative, usually neo-Lamarckian evolutionary theory in search of a cytoplasmic mechanism of heredity which would reduce evolutionists' dependence upon Mendelian genes. Section 3 then describes the arrival of the much sought-after mechanism: the Plasmon theory. But if the Plasmon was to make a neo-Lamarckian evolutionary theory credible, it had to be responsive to environmental direction. Although the Plasmon theorists themselves were, on the whole, uninterested in making the Plasmon subject to directed alteration by the environment, section 4 shows that another body of work (Victor Jollos' studies of 'Dauermodifikationen') could be appropriated to that end, even though Jollos himself objected. Finally, section 5 shows how the Plasmon theorists also drew upon Jollos' work but with a different aim in mind. They sought to extend the Plasmon theory so as to circumvent one of the standard objections to natural selection. Throughout the 1920s and 1930s the Plasmon theorists and Jollos found to their chagrin that their genetic work was much admired by anti-selectionist evolutionists. Having defined their discipline so broadly, German geneticists were more likely than their American counterparts to become the object of such unwanted attention.

2. The Grundstock hypothesis

'Grundstock' is the German term denoting the basic stock or holdings of a library or museum. The Grundstock hypothesis posited two forms of heredity and two corresponding mechanisms of evolution. Chromosomal genes were seen as the determinants of rather trivial characters involved only in intraspecific differences (for example, eye colour or bristle number in *Drosophila*).²⁰ Evolutionarily significant traits which distinguished higher taxa were determined by a basic structure, the Grundstock, thought to be located in the cytoplasm or throughout the cell as a whole. Since Mendelian genes were apparently stable in the face of environmental forces, they were believed to change via an internally generated process of mutation, thence becoming subject to selection. This was how micro-evolution was thought to occur. Macroevolution required gradual alteration of the Grundstock, usually directed by environmental forces.

In its many guises the Grundstock hypothesis was typically invoked in a rather speculative manner in order to fill two theoretical gaps: the causes of development and the mechanisms of evolution. As Jan Sapp has shown,²¹ the basic notion of the Grundstock dates from the late nineteenth century as embryologists observed that many of the earliest and most fundamental characteristics of the embryo (for example, its pattern of symmetry) were determined by the egg cytoplasm. The sperm's influence was only detectable later and appeared to affect less fundamental traits.²² Boveri's famous merogony experiments, conducted between 1890 and World War I, in which an enucleate sea urchin egg of one species was fertilized by sperm from another species, were designed to clarify just this issue: the relative contributions of nucleus and cytoplasm as bearers of heredity.²³ The subsequent advancement of a Mendelian

²⁰ The palaeontologist, Franz Weidenreich, referred disparagingly to such characters as *Kinkerlitzchen* (roughly, 'trifles', irrelevancies', 'itsy-bitsies') according to Mayr, 'Curt Stern', in Mayr and Provine, pp. 424–429 (p. 428).

²¹ Sapp (note 18), chapter 1.

²² E.g. Julius Schaxel, Ueber den Mechanismus der Vererbung (Jena, 1916); A. Penners, 'Ueber die Rolle von Kern und Plasma bei der Embryonalentwicklung', Die Naturwissenschaften, 10 (1922), 727-33, 761-5.

²³ Boveri, 'Ueber Zwei Fehlerquellen bei Merogonieversuchen und die Entwicklungsfähigkeit merogonischer, partiell-merogonischer Seeigel-bastarde', Archiv für Entwicklungs-Mechanik, 44 (1918), 417–71. chromosome theory by Morgan *et al.* failed to satisfy embryologists in several countries that nuclear heredity alone could explain development. Thus Grundstock hypotheses persisted after World War I. However, they were necessarily *a priori* until the late 1920s simply because the evidence for cytoplasmic heredity was confined to isolated instances in plants, and many experimental demonstrations were open to serious objections.

In German-speaking biological circles after World War I, however, Grundstock hypotheses were frequently advocated on evolutionary grounds: a Grundstock seemed necessary in order to compensate for the apparent inconsistency between Mendelian genes and macro-evolutionary processes. Even the geneticist Johannsen,²⁴ disappointed at how little genetics had contributed to our understanding of evolution, felt obliged to posit the existence of a Grundstock:

The great significance of the chromosomes as vehicles of recombination and linkage of genotypic elements is now established. But this does not rule out the presence of other cellular structures in the genotype....'Mendelising' elements usually affect abnormal or even pathological traits.... despite Mendelism we still lack a fundamental understanding of the core (*Zentrale*) of the organism's genotype. The more deeply embedded causation of the major differences between animal and plant classes, families and genera is actually hardly addressed by modern genetics. That only chromosomal make-up is involved here seems extremely doubtful. The significance of protoplasmic structures has yet to be explored.²⁵

A year later the Grundstock idea appeared to gain support from a speculative paper on CI given by the botanist Hans Winkler to the German Genetics Society.²⁶ Winkler noted that the standard arguments for the nuclear location of hereditary substance do not actually rule out an additional cytoplasmic location. The best evidence he could then find for CI came from species hybrids in plants. When two different species of the same genus were crossed, and the pollen transmits no cytoplasm, the offspring were almost always identical, whether species A contributed the pollen and B the egg, or vice versa. Occasionally, however, the results were non-reciprocal, suggesting that the egg cytoplasm might be a genetic determinant. Non-reciprocity was rare, Winkler admitted, but perhaps this was because each genus contained cytoplasm of a specific kind which determined the traits characteristic of that genus. Since most species of that genus would have the same cytoplasm, interspecific crosses within a given genus would usually be reciprocal. In postulating that not only genus differences but those between higher taxonomic categories might be rooted in cytoplasmic heredity, Winkler was fully aware of the resonance between his ideas and the Grundstock hypothesis. While saying very little about the evolutionary mechanisms which could alter cytoplasmic heredity, he did suggest that macro-evolution would proceed more slowly and gradually than micro-evolution if cytoplasmic heredity possessed a different structure from chromosomal genes. Whatever his own views on evolutionary mechanisms may have been, Winkler's review of the as yet sparse literature on CI undoubtedly gave heart to opponents of pure selectionism.

Although Johannsen rejected selection from a mutationist standpoint, most proponents of the Grundstock hypothesis regarded the Grundstock as subject to

²⁴ Though Danish, Johannsen was of German descent and published extensively in German.

²⁵ W. Johannsen, 'Hundert Jahre Vererbungsforschung', Verhandlungen der Gesellschaft Deutscher Naturforscher und Ärzte, 87 (1922), 70–104 (pp. 101–102).

²⁶ Winkler, 'Ueber die Rolle von Kern und Plasma bei der Vererbung', ZIAV, 33 (1924), 238-53.

directed alteration by the environment.²⁷ Boveri, for example, in keeping with his original assumption of cytoplasmic heredity, had advocated a version of neo-Lamarckism in addition to mutation and selection.²⁸ Bernhard Dürken also doubted that heredity was confined to the chromosomes. For one thing, this was too coarse and mechanistic a conception to do justice to the intricacies of inheritance and development, and it neglected what he saw as the unity of the hereditary substance. But Dürken's concerns were also evolutionary. While admitting that the evidence was still only tentative. Dürken proposed the cytoplasm as an additional carrier of heredity which would be much more responsive to environmental changes than were chromosomal genes. Neither selection nor the inheritance of acquired characteristics on its own sufficed to explain evolution.²⁹

Other critics of selection like Richard Woltereck were dissatisfied with mechanistic materialism and causal explanation in biology. Though now best known for his formulation of the concept of 'norm of reaction', Woltereck was a forceful advocate in the 1920s and 1930s of a Grundstock theory from a vitalist standpoint.³⁰ But because his work remained empirical and his arguments did not resort to mysterious unanalysable forces, his evolutionary ideas were acknowledged into the 1940s as among the most credible alternatives to selection.³¹ Rather than attribute heritable quantitative changes in his wild populations of the crustacean Cladocera to alterations of material units in the chromosomes. Woltereck drew attention to what he regarded as the undisputed existence of 'species plasma'. While 'accessory' (and usually pathological) traits Mendelized and were thus probably localized in the chromosomes, important 'constitutional' characters were a property of the plasma as a whole.³² Selection undoubtedly served as a sieve, and plasma-heredity could be altered by environmental induction, but a full explanation of evolution also required some form of orthogenesis.33

Another variation on the Grundstock theme was Ludwig Plate's 'Erbstock' hypothesis. Though he had been an early proponent of selection,³⁴ by the 1920s Plate had come to regard selection as a sieve rather than a creative force.³⁵ Pure selectionism was insufficient because:

(a) mutations (e.g. in Drosophila) usually seemed deleterious and to affect only superficial aspects of organs rather than their basic structures;

²⁸ F. Baltzer, *Theodor Boveri* (Berkeley and Los Angeles, 1967). Two of the most outspoken critics of Morgan's chromosome theory in Germany were the anatomists Rudolf Fick and Hermann Stieve who found support for Grundstock-like notions in the evidence for CI See Stieve, 'Neuzeitliche Ansichten über die Bedeutung der Chromosomen unter besonderer Berücksichtigung der Drosophila-Versuche' Ergebnisse der Anatomie und Entwicklungsgeschichte, 24 (1923), 491-587 (pp. 521, 533, 574-77) and Fick, 'Bemerkungen über einige Vererbungslehren', Die Naturwissenschaften, 13 (1925), 524-29 (p. 528).

²⁹ Dürken and H. Salfeld, Die Phylogenese (Berlin, 1921); Dürken, Allgemeine Abstammungslehre (Berlin, 1923), pp. 191-92; Dürken, Lehrbuch der Experimentalzoologie, Second edition (Berlin, 1928), pp. 563-606. ³⁰ E.g. Woltereck, 'Biologie als Grundwissenschaft vom Leben und Erleben', Der Biologe (1932/33),

352-55. ³¹ W. Ludwig, 'Die Selektionstheorie', in *Die Evolution der Organismen*, edited by G. Heberer (Jena, 1943), pp. 479-520 (p. 512).

 ³² Woltereck, 'Ueber Reaktionskonstanten und Artänderung', ZIAV, 33 (1924), 297–301.
³³ Woltereck, 'Beobachtungen und Versuche zum Fragenkomplex der Artbildung...', Biologisches Zentralblatt, 51 (1931), 231-53.

³⁴ G. Uschmann, Die Geschichte der Zoologie und der zoologischen Anstalten in Jena, 1779–1919 (Jena, 1959).

³⁵ Plate, 'Lamarckismus und Erbstockhypothese', ZIAV, 43 (1926), 88-113.

²⁷ On the perceived connection between CI and neo-Lamarckism, see also Sapp (footnote 18), chapters 4, 5.

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- (b) their undirected character made it difficult to explain the emergence of complex adaptive organs; and
- (c) since chromosomal genes mutated independently of one another, Mendelism could not explain the apparently coordinated and simultaneous changes in many traits which the fossil record presents.³⁶

If geneticists paid more attention to phylogenetic evidence, they would see that although the experimental evidence for inheritance of acquired characteristics was equivocal, it was impossible to account for macro-evolutionary phenomena without invoking it. One could not deny the Mendelian chromosome theory, but it was difficult to explain how inheritance of acquired characteristics could be reconciled with Mendelism. Therefore chromosomal genes had to be subordinate to another kind of heredity, the 'Erbstock', which determined the fundamental and characteristic organs of each species. Furthermore, Plate gave the Erbstock a self-contained, unitary character so that the phenotypes which it determined would not segregate. In this way the Erbstock would respond slowly and as a whole to use/disuse and to the shaping forces of the environment. Although Plate located the Erbstock in the nucleus (outside the chromosomes) rather than in the cytoplasm, he clearly felt that the key feature of his theory was its attribution of two mechanisms of evolution to two kinds of heredity. In support of his theory Plate cited Johannsen, Winkler and Woltereck; their theories of a cytoplasmic Grundstock he regarded as very similar to his own. The idea of a Grundstock of some kind, he concluded, was very much in the air.

The centrality of the Grundstock and CI to evolutionary debate was soon evident in the opening paper to the 5th International Congress of Genetics at Berlin in 1927: 'The Problem of Evolution and Modern Genetics' by Richard von Wettstein.³⁷ As not only a grand old man of German botany and systematics and a neo-Lamarckian, but also as a cofounder of both the Zeitschrift für induktive Abstammungs- und Vererbungslehre (the first journal devoted to genetics, founded 1908) and the German Genetics Society (1921), von Wettstein's perspective on the development of genetics was an influential one. He began by noting, in the face of rapidly expanding and increasingly specialized knowledge in genetics, how necessary it was to stand back occasionally and assess how such knowledge relates to the broader problems of biology, of which the mechanism of evolution was one of the most important. Of the two major approaches to evolution, the limitations of nineteenth-century morphology were by then well known, but its value was in describing the characteristic evolutionary processes of differentiation, adaptation, orthogenesis, etc. Genetics' contribution had been to clarify through experiment which of the hypothesized mechanisms of evolution were tenable. Unfortunately, von Wettstein noted, that contribution had so far been largely negative; neither selection nor neo-Lamarckism had found much support. The apparent contradiction between the findings of evolutionary theorists and genetics derived from one assumption central to genetics: the stability of the gene in the face of the environment. Consequently selection had seemed to many geneticists to be the only conceivable evolutionary mechanism. Citing virtually the same objections to selection as Plate had a year earlier, von Wettstein respectfully asked his audience to consider

³⁶ In the United States F. B. Sumner was simultaneously voicing the same dissatisfactions with selection; see Provine (footnote 11).

³⁷ R. von Wettstein, 'Das Problem der Evolution und die moderne Vererbungslehre', ZIAV, supplement vol. 1 (1928), 370-80.

whether the chromosome theory was the sole basis of heredity. His alternative was, in all but name, a Grundstock hypothesis. Acknowledging the weaknesses of inheritance of acquired characteristics, he recommended nevertheless more systematic exploration of the possibility of environmentally-directed heritable change, especially if cytoplasmic heredity behaved differently from chromosomal. Concluding his address, von Wettstein conceded the right of geneticists to define their conceptual territory as they saw fit, even if this meant ignoring the consequences of genetics for other branches of biology. Nonetheless he expressed the hope that geneticists would broaden the sope of their inquiries in future so that the mechanisms of evolution could be clarified.

It is difficult to say just how much influence R. von Wettstein had upon geneticists and selectionists in the 1930s.³⁸ What is obvious, however, is that the Grundstock and its proponents could not be ignored, at least in Germany. Ernst Mayr recalls having adhered to such a dualist position into the 1930s, ³⁹ and Dobzhansky acknowledged in 1937 that dualist views of heredity and evolution were still accepted by very well known biologists.⁴⁰ In Germany even pure selectionists were cautious. One of them was the geneticist Erwin Baur, occasionally designated as an early contributor to the evolutionary synthesis.⁴¹ In one respect Baur was rather 'American' in his conception of genetics. He rapidly endorsed the chromosome theory of Morgan et al, and his large school at the agricultural college in Berlin concentrated more on problems of transmission genetics than on the genetics of development.⁴² But Baur was much more concerned with evolutionary problems than were Morgan et al. A staunch anti-Lamarckian before World War I, in the mid-1920s Baur sought to defend natural selection (which he saw as everywhere under threat).⁴³ His argument was that continuous micromutations were much more prevalent in plant populations than was commonly thought, since they are usually recessive and alter the phenotype only imperceptibly. They thus constituted abundant raw material for selection.⁴⁴ Baur also had an answer to what he acknowledged as 'the gravest objection that can be made to the theory of selection today',⁴⁵ namely that micromutations seemed to have no selective value. Claiming that such mutations were generally selectively neutral, he argued that they would thus be able to persist in populations and combine with other

⁴⁰ Dobzhansky, Genetics and the Origin of Species (New York, 1937). See also W. Ludwig, 'Selektion und Stammesentwicklung', Die Naturwissenschaften, 28 (1940), 689–705 (p. 696) and F. Schwanitz, 'Genetik und Evolutionsforschung bei Pflanzen', in G. Heberer (editor) (footnote 31), 430–78.

⁴¹ E.g. G. Ledyard Stebbins, 'Botany and the Synthetic Theory of Evolution' in Mayr and Provine, pp. 139–52 (p. 140).
⁴² Erwin Baur, *Einführung in die experimentelle Vererbungslehre*. Third and fourth editions (Berlin, 1919)

⁴² Erwin Baur, *Einführung in die experimentelle Vererbungslehre*. Third and fourth editions (Berlin, 1919) [hereafter referred to as *Einführung*], pp. 160, 164, 167, 171; Baur, 'Die Faktorenkoppelung bie *Antirrhinum* im Lichte der Morganschen Theorie', *ZIAV*, 30 (1923), 289. See also the biography by E. Schiemann, 'Erwin Baur', *Berichte der Deutschen Botanischen Gesellschaft*, 52 (1935), 51–114 and the tributes from his coworkers in *Die Naturwissenschaften*, 22 (1934), issue of 27 April, no. 17/18.

⁴³ For Baur's early attacks on neo-Lamarckism see his review of Richard Semon's work in ZIAV, 6(1912), 244-47, or 'Die Frage nach der Vererbung erworbener Eigenschaften im Lichte der neuen experimentellen Forschung mit Pflanzen', Archiv für Sozial Hygiene, 8 (1913), 117-30. He defended selection in Baur (footnote 12), 115.

⁴⁴ Untersuchungen über das Wesen der Entstehung, und Vererbung der Rassenunterschiede bei A. majus', Bibliotheca Genetica, 4 (1924), at pp. 145–48; cf. Einführung, pp. 340–46, and (footnote 12).

⁴⁵ Baur, 'Evolution', Journal of the Royal Horticultural Society, 56 (1931), 176-82 (p. 181).

³⁸ That another grand old man, Richard Hertwig, should have put forward virtually the same argument a few months later suggests that von Wettstein had voiced a common view (Hertwig to Goldschmidt, 19.12.27. Goldschmidt Papers).

³⁹ Mayr, 'How I Became a Darwinian', in Mayr and Provine, pp. 413–23 (pp. 416–17). An exchange of letters with Dobzhansky in 1935 confirms this: see Dobzhansky to Mayr, 12.11.35. and Mayr's reply, 25.11.35 (Mayr Papers).

similar mutations; some of these combinations would then prove to be of selective value. In addition Baur presented important evidence that trait differences between various wild species of snapdragon (Antirrhinum) were almost exclusively due to Mendelian genes of the same kind as the micromutations observed in his laboratory plants. He thus explained species-formation in the genus Antirrhinum in terms of selection favouring different combinations of Mendelian alleles in geographically isolated populations.46

But as Ernst Mayr has remarked, even such a determined selectionist as Baur remained cautious about extrapolating his snapdragon model to all of nature.⁴⁷ Like other German selectionists (to be discussed below), he was not sure whether selection alone could account for the evolution of complex adaptive organs such as the eye.48 Although his own work suggested that species differences Mendelized, he hesitated to rule out extra-nuclear, non-Mendelian bearers of heredity.⁴⁹ Even Baur seemed at times open to Grundstock dualism: in 1919 he suspected that genus and higher systematic differences were of a different kind, and in 1930 he stated categorically that 'the problem of evolution cannot be solved for all organisms according to the same scheme'.50

During the 1930s, the Grundstock hypothesis may even have gained credibility within the German evolutionary debate. One observer felt that by 1940 almost no-one took a purely neo-Lamarckian position; most had conceded a partial role to selection.⁵¹ To understand why Germans sympathetic to selection, as well as those hostile, took seriously intermediary dualist positions, we must look at the conceptions of heredity being developed by German geneticists from the late 1920s. We will see how, by challenging what they called the chromosomal genes' 'monopoly', geneticists working on CI were altering the balance of power in the evolutionary debate. Dualism was becoming more plausible than ever.

The reception of the Plasmon theory in the 1930s 3.

During the late 1920s an important shift occurred in German thinking about CI. The older claims for CI had often been vulnerable to the objection that non-reciprocal hybrids could be explained by other mechanisms such as pre-determination: temporary effects due to the presence in the cytoplasm of substances of nuclear origin which would eventually disappear through dilution in subsequent generations. However, new work published between 1927 and 1929 demonstrated the persistence of non-reciprocity undiminished over several generations. In addition the new claims had wide theoretical implications. Alfred Kühn and Richard Goldschmidt, for example, found nonreciprocal hybrids in animals for the first time, and Correns, Fritz von Wettstein and Peter Michaelis argued that despite the rarity of non-reciprocity, the Plasmon might well be a universal phenomenon.⁵² As the evidence from these authors accumulated during the 1930s, the Grundstock hypothesis began to look less speculative than it had

⁴⁶ Baur, 'Artumgrenzung und Artbildung in der Gattung Antirrhinum Sektion Antirrhinastrum', ZIAV, 63 (1932), 256-302. cf. Einführung, seventh to eleventh editions (Berlin, 1930), pp. 399-400.

⁴⁷ Mayr, The Growth of Biological Thought (Cambridge, Mass., 1982), p. 787; Baur's reservations are expressed in his 'Untersuchungen...' (footnote 44), 148; 'Artumgrenzung...' (footnote 45), 301-02; and Einführung, 1930 edn, p. 398.

⁴⁸ Einführung, 1930 edn, p. 395.

 ⁴⁹ Baur, 'Untersuchungen ...' (footnote 44), p. 95.
⁵⁰ Einführung, 1919 edn, p. 345; 1930 edn, p. 400.

⁵¹ Ludwig (footnote 40), 689.

⁵² Harwood (footnote 18); Sapp (footnote 18), chapter 3.

during the 1920s. Accordingly, those advocates of pure selectionism who were familiar with the German literature regarded the new wave of CI research cautiously rather than dismissively.

At a meeting of the German Genetics Society in 1938, N. W. Timoféeff-Ressovsky reviewed the state of zoological thinking about evolution. Geneticists had shown that selection of Mendelian genes could account for micro-evolution, he argued, but although he was confident that this model would also hold true for macro-evolution, he acknowledged that this extrapolation was an empirical matter.⁵³ One phenomenon in need of clarification was the nature of CI as demonstrated in plant species hybrids; perhaps, he suggested, these differences would eventually prove to be determined by chromosomal genes? Evidently he was vaguely uneasy about how to accommodate CI into his synthesis of Mendelism and Darwinism.

Dobzhansky, perhaps because he was writing from the safety of Pasadena, was less tentative. The four pages devoted to non-Mendelian inheritance in his *Genetics and the Origin of Species*⁵⁴ began by attacking the evidence usually cited in favour of the Grundstock hypothesis. He then proceeded to the evidence for CI, concluding that most alleged instances of CI were probably only pre-determination. The remaining evidence for CI—such as that of von Wettstein and Michaelis—was, he admitted, stronger but was such an isolated phenomenon that CI could play only a very minor role in evolution.

That Dobzhansky and other selectionists found it necessary not only to reject Grundstock dualism but also to dismiss the much stronger genetic evidence for the Plasmon is an indication of the anti-selectionist evolutionary implications then being ascribed to CI. Significantly, however, this was *not* the way in which the Plasmon theorists themselves saw their work. All four of them in fact explicitly rejected the Grundstock hypothesis.⁵⁵ They pointed out that Plasmon differences were sometimes found between varieties but not between species. It was wrong, therefore, to ascribe intraspecific trait differences to chromosomal genes and trait differences between higher taxa to CI. Instead they argued that chromosomal genes and Plasmon played an equal genetic role in the determination of *all* traits, regardless of the taxonomic level for which those traits were characteristic. Similarly, all the Plasmon theorists were critical of evolutionary dualism; they rejected the inheritance of acquired characteristics,⁵⁶ and

⁵³ Timoféeff-Ressovsky, 'Genetik und Evolution', ZIAV, 76 (1939), 158–218. This 'undogmatic' willingness to concede at least the possibility of other evolutionary mechanisms was praised by Wilhelm Ludwig, one of the very few mathematical population geneticists then in Germany: see his 'Selektion' (footnote 40), 700 and 704; and his 'Selektionstheorie' (footnote 31), 513 and 517–18.

⁵⁴ The relevant pages of the German edition (Jena, 1939) are 47-50.

⁵⁵ F. von Wettstein, 'Morphologie und Physiologie des Formwechsels der Moose auf genetischer Grundlage II', Bibliotheca Genetica, 10 (1928), 1–216 (pp. 189–92); A. Kühn, 'Vererbung und Entwicklungsphysiologie', in Wissenschaftliche Woche zu Frankfurt, I: Erb-biologie, edited by W. Kolle (Leipzig, 1934), pp. 37–48 (p. 43); P. Michaelis, 'Die Bedeutung des Plasmons für die Pollenfertilität reziprok-verschiedenen Epilobium-bastarde', Berichte der Deutschen Botanischen Gesellschaft, 49 (1931), 96–104 (pp. 103–04); and C. Correns, 'Die ersten 20 Jahre Mendelscher Vererbungslehre' in Festschrift der Kaiser-Wilhelm Gesellschaft, edited by Carl Neuberg (Berlin, 1921), pp. 42–49 (p. 45). So close were the perceived connections between C.I. and the Grundstock hypothesis that von Wettstein was still misunderstood to have endorsed Grundstock as late as 1939; see G. Melchers, 'Genetik und Evolution', ZIAV, 76 (1939), 229–59 (p. 252).

⁵⁶ Correns (footnote 55), 48; von Wettstein, 'Die natürliche Formenmannigfaltigkeit' in Handbuch der Pflanzenzüchtung (Berlin, 1941), pp. 8–45; Kühn stressed the lack of experimental evidence for the inheritance of acquired characteristics in several editions of his celebrated textbook, Grundriss der allgemeinen Zoologie, for example the third edition (Leipzig, 1928), p. 258, and emphasized instead mutation and selection. Michaelis never explicitly rejected the inheritance of acquired characteristics but in 1933 believed it unlikely that Plasmon changes could be directed by environmental stimuli (see his 'Entwicklungsgeschichtlichgenetische Untersuchungen an Epilobium II...', ZIAV, 65 (1933), 1-71 and 353-411.

in the 1930s all regarded random mutation and selection as the only well established mechanism. Nevertheless, they were aware that one of the major problems facing the theory of selection was how it could account for the emergence of complex adaptive traits, and some of their empirical work (including that on the Plasmon) was designed to solve this puzzle.⁵⁷

Much of von Wettstein's work from the late 1920s was devoted to extending the explanatory power of selection theory.⁵⁸ He speculated that given a close 'partner' relation between genes and Plasmon, the disharmony brought about by gene mutation might be compensated by corresponding environmentally-induced (but not directed) changes in the Plasmon.⁵⁹ In this way small, otherwise deleterious, mutations need not be lost immediately through selection. A second strand in von Wettstein's research was the study of polyploidy. By placing different polyploid variants of a given species at different Alpine locations, he sought to clarify the selective value of polyploidy in certain environments. In 1943 he argued that polyploidy allowed the accumulation of recessive mutations (which would have been deleterious in a homozygous state) until combinations of selective value could occur through crossing.⁶⁰

Von Wettstein's (and to a lesser extent Kühn's) work thus helped to show how selection could overcome the difficulty that intermediate stages in the evolution of complex organs would be of no selective advantage. Another way round this problem might be directed variation. If mutation possessed some kind of inertia, pushing it progressively in one direction, the selective neutrality of intermediate stages would pose less of a problem; selection could take effect once the organ was far enough advanced. Even if chromosomal genes mutated randomly, perhaps the Plasmon mutated directionally. Once again, CI was at the centre of discussion.

4. The controversy over 'Dauermodifikationen'

If one had attended the 7th Annual Meeting of the German Genetics Society in Tübingen in 1929, it might at first have seemed as though Richard von Wettstein's appeal to geneticists two years earlier had begun to take effect. For the first session of the meeting was held jointly with the (German) Palaeontological Society and was apparently intended to seek a reconciliation between their members' different perspectives on evolutionary mechanism. Unfortunately this laudable attempt at

⁵⁸ Joseph Straub, an assistant of von Wettstein's between 1939 and 1941 at the Kaiser-Wilhelm Institute for Biology, recalls von Wettstein defending natural selection at conferences in which at least half of the participants were very sceptical of selection's sufficiency (interview, 3.5.83.).

⁵⁹ F. von Wettstein, 'Wie entstehen neue vererbbare Eigenschaften?', Züchtungskunde, 2 (1927), 241–59; von Wettstein (footnote 55), 202–6; von Wettstein, 'Die genetische und entwicklungsphysiologische Bedeutung des Cytoplasmas', ZIAV, 73 (1937), 349–66.

⁶⁰ Warum hat der diploide Zustand bei den Organismen den grösseren Selektionswert?, Die Naturwissenschaften, 31 (1943), 574-77. Again Dobzhansky had judged von Wettstein's earlier work on polyploidy important enough to cite it in the first edition of Genetics and the Origin of Species.

⁵⁷ This generalization applies least to Correns who died in 1933 and had, according to Otto Renner, little to say in print about evolution after 1904 (Renner, 'William Bateson und Carl Correns', *Sitzungsberichte der Heidelberger Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse* (1961), 159–8f (p. 171). Although evolution was not one of Alfred Kühn's principal research interests, he was impressed by the evolutionary work of Timoféeff and Rensch during the 1930s (interviews with H. Hartwig. 1.5.83, and W.-D. Eichler, 10.6.83., conversation with Viktor Schwartz, 28.7.83), and his broad knowledge of biological theory enabled him to recognize the evolutionary significance of a mutant discovered in his laboratory. Although certain micromutations altering the pattern of wing coloration in the flour moth seemed to have no obvious selective value, Kühn noticed that their viability was in fact altered and drew attention to such pleiotropy as support for selection theory ('Ueber den biologischen Wert von Mutationsrassen', Forschungen und Fortschritte, 10 (1934), 359–60). Dobzhansky regarded the evidence important enough to cite it in *Genetics and the Origin of Species* (New York, 1937).

transcending disciplinary boundaries seems to have failed badly.⁶¹ Nevertheless, the conference proceedings nicely illustrate one of Ernst Mayr's points about the evolutionary synthesis: that it required individuals who could bridge the wide gap between genetics and (loosely speaking) morphology, as Kuhnian research traditions committed to different methods and problems. Furthermore the conference demonstrates how differently various sectors of the biological community perceived the evolutionary implications of Muller's report in 1927 of X-ray induced mutation.⁶² As we shall see, one consequence of Muller's work was that a key question in Germany evolutionary debate in the 1930s became whether or not mutation was directed.

In the opening paper the neo-Lamarckian palaeontologist Franz Weidenreich sought compromise.⁶³ Morphologists, he said, could not overlook the evidence for the gene's relative stability, but on the other hand they need not accept the evolutionary conclusions (i.e. selection) which geneticists tended to draw from such evidence. First of all, the mutations which geneticists commonly studied (e.g. in Drosophila) were rare, generally concerned evolutionarily trivial traits and were thus unlikely to be as important in evolution as geneticists thought. Moreover, Muller had just shown that genes were after all responsive to the environment; it was now important to know whether such mutation was directed. The failure until then to direct genes' mutation after relatively short exposures (e.g. 50 generations) to environmental stimuli told us nothing about what might occur after evolutionarily significant exposures. Besides, there were indications that semi-heritable, directed and adaptive changes situated in the cytoplasm (so called 'Dauermodifikationen') arose after exposure to environmental stimuli and might, with longer exposures, become as stable as chromosomal gene mutations. This phenomenon would be important for geneticists to explore because the coordinate and simultaneous changes which palaeontologists commonly observed throughout the whole organism during evolutionary sequences were very difficult to explain on the basis of independent random mutations in genes affecting different traits.64

Weidenreich's rather cautious attempt at reconciliation brought only a brusque and condescending rejection from the Finnish geneticist, Harry Federley.⁶⁵ The inheritance of acquired characteristics, he replied, had been totally demolished by genetic research. Kammerer's experiments before World War I were impressive and had offered the best evidence at that time, but had subsequently declined in quality and credibility. If genes were as malleable as neo-Lamarckians would have us believe, he argued, all of Mendelism would have to be scrapped.⁶⁶ The attempt to side-step this problem by speculating as to the existence of a Grundstock had no foundation since chromosomal genes affected the most *basic* traits central to macro-evolution. No, insisted Federley, the key to evolutionary mechanism lay not with palaeontology's current speculative theories but with genetics' future experiments. With a sentence

⁶² Muller, 'The Problem of Genic Modification', ZIAV, supplement vol. 1 (1928), 234-60.

⁶³ Weidenreich, 'Vererbungsexperiment und vergleichende Morphologie', ZIAV, 54 (1930), 8-19.

⁶⁴ Most features of Weidenreich's argument were soon echoed by Woltereck in 'Beobachtungen' (footnote 33).

⁶⁵ Federley, 'Weshalb lehnt die Genetik die Annahme einer Vererbung erworbener Eigenschaften ab?', ZIAV, 54 (1930), 20–43.

⁶⁶ Having rejected the generality of CI (see footnote 18), Morgan, too, saw Mendelism and neo-Lamarckism as incompatible, see his 'The Rise of Genetics', *Science*, 76 (1932), 261–67 (p. 263).

⁶¹ This was the judgment of Woltereck in 'Beobachtungen' (footnote 33), 231 and of Victor Jollos in 'Die experimentelle Auslösung von Mutanten und ihre Bedeutung für das Evolutionsproblem', *Die Naturwissenschaften*, 19 (1931), 171–77.

reminiscent of Muller or, more recently, of the sociobiologists, Federley defined the problem of evolution as the question of genes' malleability:

... genes or the genotype represent the essential and the constant element while the organism, the individual or the phenotype is merely something accidental, and as the consequence of an accidental combination of genes, has no significance for evolution. 67

With such a definition he shoved aside as irrelevant the older descriptive morphological analyses of evolution which necessarily dealt only with phenotypes. It was understandable, wrote Federley, why palaeontology had had to resort to the inheritance of acquired characteristics out of dissatisfaction with geneticists' failure so far to account for the emergence of complex adaptive traits. But palaeontology would have to face up to hard genetic facts and accept that geneticists' agnosticism on the question of evolutionary mechanism was the only defensible position.

In the ensuing discussion various contributors tried to argue that the findings and methods of the two disciplines were more compatible than Federley had indicated, and Weidenreich again drew attention to the possibility of extra-chromosomal inheritance as a way of resolving apparent contradictions,⁶⁸ but Federley remained unmoved. After replying to various specific points, he concluded that discussion with neo-Lamarckians was pointless since they did not seem to understand genetics.⁶⁹ It is interesting, however, that Federley, both in his lecture and reply, avoided the subject of Dauermodifikationen and did not challenge Weidenreich's claim that the randomness of mutation was not yet proven. As we will see, Federley's views were not widely shared within the German genetics community.⁷⁰ The Plasmon theorists and others were much less estranged from their colleagues in morphology.

The Dauermodifikationen (DMs) to which Weidenreich had referred were associated most strongly in inter-war Germany with the work of Victor Jollos.⁷¹ By exposing populations of *Paramecium* over several generations to ever-increasing nonlethal levels of arsenic, Jollos could increase their resistance to arsenic to several times the normal level. After replacing the organisms in arsenic-free medium, their resistance persisted (*dauer* translates as 'lasting') over hundreds or even thousands of cell divisions before finally declining to the original level of sensitivity. If DMs were simply phenotypic changes (*Modifikationen*) due to some gene product which was eventually diluted out by cell division, they should have disappeared within 10 cell divisions or so, not 1000. Whatever the biochemical basis of DMs was, it must have replicated over many cell divisions. Such effects of intermediate stability could be induced in other protozoa by various environmental treatments⁷² as well as in *Drosophila*. Furthermore, by crossing the DM strains with wild-type strains, Jollos could show that DM-phenotypes were transferred not with the nucleus but with the cytoplasm. Jollos

⁶⁷ Federley (footnote 65), 21.

68 Weidenreich, 'Diskussion', ZIAV, 54 (1930), 43-50 (p. 47).

69 Ibid., 50.

⁷¹ See R. A. Brink, 'Victor Jollos, 1887–1941', Science, 94 (1941), 270–72.

⁷² Jollos, 'Untersuchungen über Variabilität und Vererbung bei Arcellen', Archiv für Protistenkunde, 49 (1924), 307-74.

 $^{^{70}}$ Curt Stern was perhaps sympathetic to Federley's position, having himself had an unproductive exchange with Weidenreich over the nature of mutation the same year (in *Natur und Museum*, 59 (1929) and 60 (1930)).

had thus produced a progressing sequence of adaptive, semi-heritable alterations which appeared to arise not by selection but by direct environmental action.⁷³

To observers like Weidenreich (as well as to Bernhard Rensch and Ernst Mayr) DMs appeared to offer experimental evidence for gradual change via a neo-Lamarckian mechanism whose cytoplasmic basis meant that it was still perfectly consistent with rare and random chromosomal gene mutations. Was this how orthogenetic sequences arose?74

In view of the fact that Grundstock advocates during the 1920s and 1930s had so often emphasized the moulding of cytoplasmic heredity by environmental forces, it is hardly surprising that Jollos was often seen by contemporaries as a neo-Lamarckian.⁷⁵ Nothing could have been further from the truth. In numerous papers Jollos had stressed that inheritance of acquired characteristics found no support from his work.⁷⁶ He sought instead to play down the evolutionary implications of his DM data, emphasizing that DMs were invariably unstable (thus of little evolutionary significance), that their phenotypes returned to normal at the same rate regardless of how long they had been exposed to the environmental agent (thus discouraging Weidenreich and others from hoping that longer exposure might finally make DMs stable),⁷⁷ and that (apart from resistance to arsenic) DMs were rarely adaptive (thus blocking the appropriation of DMs to support evolution by use-inheritance).⁷⁸

Unlike so many of his admirers, Jollos was a selectionist. As early as 1921 he was at pains to defend what he called 'the much abused doctrine of evolution by chance' (Zufallslehre) at a time when 'the most superficial attacks upon Darwinism enjoyed the widest distribution and uncritical acceptance'.⁷⁹ Neo-Lamarckism had been clearly refuted, he argued, and natural selection looked increasingly tenable. Unlike Federley, Jollos took seriously the morphological evidence from palaeontology which suggested some kind of directed mutation, and he sought to bridge the gap between morphology and genetics by producing experimental evidence for a mechanism, consistent with selection, which would avoid inheritance of acquired characteristics. DMs in protozoa did not seem to solve the problem, so he looked elsewhere. Sensitive to the objection that studies of X-ray-induced mutations relied upon doses far too large to occur in nature, Jollos chose instead to induce mutations in Drosophila through exposure to

⁷³ The fullest account of Jollos' experiments is to be found in his 'Grundbegriffe der Vererbungslehre: insbesonders Mutation, Dauermodifikation, Modifikation', Handbuch der Vererbungswissenschaft, vol. ID (1939).

⁷⁴ See Mayr (footnote 39), 414. In the early 1930s, Rensch even managed to persuade Timoféeff to let him look for temperature-induced DMs in Drosophila at the Department of Genetics in the Kaiser-Wilhelm Institute for Brain Research in Berlin. Though the experiments failed, Rensch recalls that the role of DMs in evolution was very topical at that time (Rensch, 'Historical Development of the Present Synthetic Neo-Darwinism in Germany' in Mayr and Provine, pp. 284-303 (p. 295)). W. Ludwig also found this argument plausible, see Ludwig to Hans Nachtsheim, 18.10.47 (Nachtsheim Papers).

⁵ See Jollos, 'Studien zum Evolutionsproblem ...', Biologisches Zentralblatt, 59 (1935), 390-436 (p. 423) and Alex Faberge to Hans Grüneberg, 23.8.46 (Grüneberg Papers). Though he refrained from calling Jollos a neo-Lamarckian, Muller was obviously annoyed that 'the widely advertised claims of Jollos' were 'being eagerly seized upon' by anti-Darwinians (Muller, 'Lenin's Doctrines in Relation to Genetics', (1934), reprinted in Loren Graham, Science and Philosophy in the Soviet Union (London, 1973), p. 459).

⁷⁶ For example, Jollos, 'Vererbung', *Neue Rundschau*, Dec. 1933, pp. 796–819 (p. 819); Jollos (footnote 75), 423-24, 430; 'Die experimentelle Auslösung v. Mutanten...', Die Naturwissenschaften, 19 (1931), 171-77 (pp. 171, 176), among others.

(pp. 1/1, 1/0, among others. ⁷⁷ Jollos, 'Genetik und Evolutionsproblem', Zoologischer Anzeiger, Supplement, 5 (1931), 252–95 (pp. 267–69, 275). ⁷⁸ Jollos (footnote 75), 416.

⁷⁹ Jollos, Selektionslehre und Artbildung (Jena, 1922), preface.

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high temperatures which actually occurred in *Drosophila*'s natural habitat. He found a series of stable mutations which affected the phenotype in a directional and progressive way, weakly altered forms giving rise to more strongly altered ones. He was careful to conclude, however, *not* that the mutation process itself was adaptively directed by the environment but only that the phenotypic consequences of such mutations *appeared* directional. Whether such mutants survived or not would depend on selection.⁸⁰

Jollos' earlier work on DMs in protozoa was regarded as both correct and important by that handful of Americans familiar with it, such as H. S. Jennings, Tracy Sonneborn or L. C. Dunn.⁸¹ And a variety of eminent biologists had considerable respect for Jollos' abilities.⁸² But the rise of National Socialism effectively destroyed any impact which his work might have made upon the evolutionary synthesis. In 1934 Jollos arrived as a refugee in the United States where DMs had never been taken very seriously by most geneticists,⁸³ and his experiments on *Drosophila* soon came under attack.⁸⁴ Unable to find a permanent academic job, Jollos was forced to support his family through lecture tours, short-term employment and eventually through charitable donations from his friends at the University of Wisconsin. Under these conditions he was hardly able to carry out the carefully controlled experiments with which he might have answered his critics, and his work was not taken up by others. Jollos' health rapidly deteriorated, and he died in 1941 at the age of 54, leaving his family in poverty.⁸⁵ In Germany, however, DMs remained at the centre of evolutionary discussion.

5. The Plasmon theorists and Dauermodifikationen

Although both concerned quasi-genetic structures in the cytoplasm, the Plasmon theory and the work on DMs had developed independently with different aims and methods. Plasmon theorists had analysed pre-existing stable heritable differences in higher animals and plants while Jollos had induced semi-stable phenotypic changes in protozoa. How, exactly, were these two phenomena related? Were they just two facets of the same phenomenon, DMs illustrating the induction mechanism whereby Plasmon differences had evolved? Grundstock theorists evidently thought so. Jollos himself was very sceptical, not only of Grundstock dualism but even of the Plasmon theory; eventually, he argued, Plasmon-determined phenotypes would decline like DMs. The cytoplasm, in his view, had no independent genetic significance; it was simply a substrate for chromosomal gene action.⁸⁶

Despite Jollos' dismissal of their work, the Plasmon theorists could not ignore DMs since they offered a model which might prove useful in explaining how the Plasmon had evolved. But DMs were potentially a dangerous attraction. To regard them as fundamentally related to the Plasmon was to invite Jollos' charge that Plasmon effects were unstable and therefore of no evolutionary significance. The Plasmon theorists'

⁸⁰ See Jollos (footnote 77) and 'Die experimentelle Auslösung v. Mutanten...' (footnote 76).

⁸² R. Hertwig to Goldschmidt, 11.12.33 (Goldschmidt Papers); unpublished obituary of Jollos by Goldschmidt (carton 3, Goldschmidt Papers); testimonials from E. Guyénot, T. H. Goodspeed and F. A. E. Crew (folder 2004, as footnote 81).

⁸³ This was Sonneborn's view in the letter to Hanson cited in footnote 81.

⁸⁴ E.g. H. Plough and P. Ives, 'Induction of Mutants by High Temperature in Drosophila', Genetics, 20 (1935), 42–69.

⁸⁵ See folders 2004 and 2005 (footnote 81).

⁸⁶ Jollos (footnote 72), 372-73; Jollos (footnote 77); Jollos (footnote 75).

⁸¹ Dunn (footnote 12 a), 406; Sonneborn to F. B. Hanson, 11.2.40. and Hanson's memo of an interview with H. S. Jennings dated 27.6.40 (folder 2005, box 163, R.G. 1.1, sub-ser. 200D, International Education Board Collection).

response to DMs, therefore, displays a variety of strategies designed to contain this unwelcome threat while exploiting DMs' explanatory value.

Von Wettstein sharply separated DMs from Plasmons. DMs he regarded merely as an instance of predetermination. For von Wettstein the genetic independence of the Plasmon was of paramount importance, and he was critical of fellow Plasmon theorists whenever they suggested that certain Plasmon effects wore off—even if only partially under the influence of foreign nuclei.⁸⁷

Alfred Kühn's stance was less severe. Although he consistently favoured 'Darwinism' (i.e. mutation and selection) over the inheritance of acquired characteristics and had no time for the Grundstock hypothesis, Kühn long remained uncertain whether mutation and selection alone would suffice to explain macro-evolution:⁸⁸

How can one imagine [the hydroids'] evolution? Thank goodness that a Lamarckian explanation is excluded. But how can such a sophisticated mechanical and chemical construction arise via random mutations in the cellular machinery?⁸⁹

Even if selection (along with mutation, recombination, isolation) was basically correct, there might well be ancillary mechanisms:

On no account is it permissible to become rigidly dogmatic as if the chromosome theory were the whole story and everything had to be 'in principle' explainable on that basis....As old Weismann used to say, 'There you see it: the fittest species survives'. But to conceive how that can work in concrete cases is another thing altogether.⁹⁰

Even in the last editions of his texts he cautiously voiced the possibility—while emphasizing that it was not yet proven—that DMs, if exposed to environmental stimuli long enough, could eventually become stable.⁹¹ This mechanism would aid the survival of intermediate stages of complex adaptive traits.

While von Wettstein strictly separated DMs from CI and Kühn emphasized their similarities, Peter Michaelis sought to account for the emergence of both DMs and stable Plasmon mutations in terms of a unitary model relying only upon selection.⁹² He began with the observation that certain changes in Plasmon-determined phenotypes in *Epilobium* can either disappear in the following generation (mere transient phenotypic changes) or persist over several generations before declining (like DMs) or persist indefinitely (like mutations). In order to account for all three phenomena with a single model, Michaelis seems to have borrowed an idea from Erwin Baur, the man who had brought him to the Kaiser-Wilhelm Institute for Breeding Research in 1932. Before World War I Baur had hypothesized that maternally-inherited variegation in plants was due to the differential replication of chloroplasts (or their white variants) plus random distribution to the daughter cells, thus giving rise to green, white or light green

⁸⁷ Von Wettstein, 'Die genetische und entwicklungsphysiologische ...' (footnote 59), 361–62. Though no friend of the Plasmon theory, Joachim Hämmerling acknowledged that von Wettstein's cytoplasmic phenomena were stable and thus probably different in kind from DMs (Hämmerling, 'Dauermodifikationen', Handbuch der Vererbungswissenschaft, vol. IE (1929), 1–65.

⁸⁸ See his Grundriss der allgemeinen Zoologie, sixth edition (Leipzig, 1939), or his Grundriss der Vererbungslehre, second edition (Heidelberg, 1950).

⁸⁹ Kühn to F. Baltzer, 1.1.55 (Kühn Papers).

⁹⁰ Kühn to H. O. Wagner, 28.12.47 (Kühn Papers).

⁹¹Kühn, Grundriss der allgemeinen Zoologie, fourteenth edition (Stuttgart, 1961), p. 281.

⁹² For an introduction to Michaelis' work on CI, see my paper cited in footnote 18.

(mixed) offspring.⁹³ In 1935 Michaelis conceptualized the Plasmon as an aggregate of mutable genetic units whose replication rates were influenced by environmental factors.⁹⁴ As an aggregate the Plasmon would consist of a variety of mutant units whose replication rates would be differentially influenced by an environmental change such that the daughter cells' Plasmon would be of a slightly different composition than the parents'. In 1938, Michaelis explicitly noted the similarities between natural selection shifting gene frequencies within a population's gene pool and environmental factors affecting the replication rates of genetic variants within a Plasmon population.⁹⁵ The advantage of such a model, though speculative, was that the rapid and apparently directional shift of cytoplasmically-determined phenotypes which made DMs so attractive to neo-Lamarckians, could instead be explained by random rare mutations of Plasmon units which then became subject to intra- and inter-cellular selection. This would produce over time a series of continuously graded variants, resembling the orthogenetic sequences which palaeontologists so often emphasized.⁹⁶

The model could also explain why a given phenotypic change could behave like a phenocopy, a DM or a mutation. The differing degrees of stability displayed by these three categories would be due to the speed with which the original Plasmon composition was re-established following return of the plant to the original environment. For phenocopies the shift-back in replication rates of 'normal' and mutant Plasmon units would regenerate the original mix within a generation. DMs would arise where it took many generations. Stable Plasmon mutants would occur where one type of Plasmon constituent had replicated so slowly in the altered environment as to be lost altogether from the cell.⁹⁷

Despite Jollos' criticism of the Plasmon theory and the differences of opinion among von Wettstein, Kühn and Michaelis over the conceptual relation between DMs and the Plasmon, all four of them shared a rejection of the evolutionary dualism central to the Grundstock hypothesis as well as the inheritance of acquired characters upon which it so often relied. All four of them took seriously the responsibility of geneticists to explore possible genetic mechanisms which would account for evolutionary phenomena within a broadly selectionist framework. Their work on polyploidy, pleiotropy and directed mutation sought to demonstrate how selection could explain the evolution of complex adaptive traits.

6. The evolutionary synthesis reconsidered

The foregoing account of German evolutionary debate between the world wars sustains Ernst Mayr's explanation for the evolutionary synthesis in several respects. Between pure selectionists at one pole and neo-Lamarckians at the other there was a broad intermediate category occupied by those such as the Grundstock dualists who explained micro-evolution by selection and macro-evolution by the inheritance of acquired characteristics and other mechanisms. As Mayr has pointed out, claims for the existence of 'soft' inheritance such as CI played a major role in defending this

⁹³ See A. Barthelmess, Vererbungswissenschaft (Freiburg/Munich, 1952), pp. 287-88.

⁹⁴ Michaelis, 'Entwicklungsgeschichtliche Untersuchungen an Epilobium III...', Planta, 23 (1935), 486-500.

⁹⁵ Michaelis, 'Ueber die Konstanz des Plasmons', ZIAV, 74 (1938), 435-59.

⁹⁶ Michaelis, 'Prinzipielles und Problematisches zur Plasmavererbung', lecture to the German Botanical Society in Berlin, 24.11.44., published in *Biologisches Zentralblatt*, 68 (1949), 173–95.

⁹⁷ Michaelis, 'Ueber parallele Modifikation, Dauermodifikation, und erbliche Abänderung des Plasmons', Zeitschrift für Naturforschung, 3b (1948), 196–202, and his 'Cytoplasmic Inheritance in Epilobium and its Theoretical Significance', Advances in Genetics, 6 (1954), 287–398.

middle ground.⁹⁸ Moreover, the Tübingen conference of 1929 illustrates just how ignorant and uninterested in evolution some geneticists, such as Federley, then were.

On the other hand, Mayr's thesis requires qualification and reformulation in several respects. The more we learn about genetics outside the Anglo-Saxon world, the more difficult it is to generalize about the contribution to the synthesis of 'geneticists' ner se. For example, it is misleading to portray the biological community of the 1920s and 1930s as consisting of evolutionarily-naive geneticists defending Mendelism and selection against evolutionarily sophisticated naturalists who advocated soft inheritance and non-selectionist mechanisms.⁹⁹ As we have seen, those German geneticists actually working on CI largely accepted selection, rejecting both the Grundstock hypothesis and the inheritance of acquired characteristics. A belief in soft inheritance, therefore, did not simply 'retard' the evolutionary synthesis. Furthermore, relatively few in the German genetics community were as simplistic about evolution as Federley and the Morgan school or as unconcerned with the gap between micro- and macro-evolution as were Fisher and Haldane. Rather, German geneticists, like the architects of the synthesis themselves, were more broadly educated and interested than their American brethren. Alfred Kühn's range of biological knowledge and interests was legendary,¹⁰⁰ and Correns and Michaelis possessed extensive knowledge of systematics and other areas relevant to evolution.¹⁰¹ One of Jollos' colleagues at the University of Wisconsin emphasized the 'unusually broad and profound' range of Jollos' biological interests and the 'extraordinary extent of his scientific' knowledge.¹⁰²

Fritz von Wettstein well illustrates this breadth. When Richard von Wettstein died in 1932, he had only begun to work on the fourth edition of his *Handbook of Systematic Botany*. That his son, Fritz, should have elected to complete this time-consuming task is characteristic of the outlook of the inter-war generation of German geneticists. According to a close friend and colleague, the younger von Wettstein took on this responsibility not merely out of filial piety but because he was genuinely interested in the subject matter.¹⁰³ As Otto Renner wrote of him:

... probably no experimental botanist could have done this but von Wettstein who had been steeped in systematics since his youth and for whom the greatest biological problem had always been the variety of form in nature, since this problem contained all others....[In Berlin] the universality of von Wettstein's interests flourished and he could pursue genetics as the science of genesis in the widest sense.¹⁰⁴

¹⁰¹ On Correns, see the obituaries by Renner (footnote 57) and F. von Wettstein, 'C. E. Correns zum Gedächtnis', ZIAV, 76 (1939), 1–10. Although Michaelis devoted virtually his entire career to CI in *Epilobium*, his knowledge of systematics was large (interview with W. Stubbe, 4.5.83.) and his interest in evolution considerable (interview with H. Ross, 2.5.83).

¹⁰² Brink (footnote 71).

¹⁰³ Kühn, 'F. von Wettstein zum Gedächtnis', Jahrbuch der Akademie der Wissenschaften zu Göttingen, (1947), 1–6.
¹⁰⁴ Renner, 'F. von Wettstein', Jahrbuch der Bayerischen Akademie der Wissenschaften (1944/48), 261–65

¹⁰⁴ Renner, 'F. von Wettstein', Jahrbuch der Bayerischen Akademie der Wissenschaften (1944/48), 261–65 (pp. 263–64). Within a few years after arriving at the Kaiser-Wilhelm Institute for Biology in Berlin, von Wettstein organized within the Prussian Academy of Sciences a 'Working-Party on Evolution' whose perspective was altogether more modern than those of the biological projects previously sponsored by the Academy and whose participants included Timoféeff-Ressovsky, even though Timoféeff was not a member of the Academy (see: C. Grau, W. Schlicker and L. Zeil, editors, *Die Berliner Akademie der Wissenschaften in der Zeit des Imperialismus: vol.* III (1933–1945) (East Berlin, 1979), pp. 312–13.

⁹⁸ Mayr, 'Prologue' (footnote 4), 4-6.

⁹⁹ E.g. Mayr (footnote 47), 793.

¹⁰⁰ Harwood, 'The Reaction Against Specialization in 20th Century Biology: a Study of Alfred Kühn', forthcoming in *Freiburger Universitätsblätter*, 1985.

Thus when von Wettstein took up the question of evolution at a joint meeting of the German Zoological and Botanical Societies at Vienna in 1938, his conception of the problem was much broader and more conciliatory than Harry Federley's had been a decade earlier.¹⁰⁵ The massive evidence from comparative morphology, palaeontology and biogeography, he said, all pointed towards Darwinism, but the ultimate proof of mechanism required direct experimental evidence from genetics. Gently but firmly reminding his audience that there was no evidence for the heritability of phenotypic changes. the key question was whether random mutation (whether in chromosomes, plastids or Plasmon) as well as recombination-acted upon by isolation, selection and drift—could provide a sufficient mechanism. Though more experimental evidence was necessary, it appeared likely that complex adaptive traits could emerge via selection due to pleiotropy, neutral mutations and ploidy. In conclusion von Wettstein called for cooperation between practitioners of the comparative and the experimental methods. Mutual respect and appreciation of each others' problems and methods would create the basis for an eventual solution to the problem of evolution, from which all areas of biology could only benefit.¹⁰⁶

What, then, is the historiographical significance of the German case? The synthesis, according to Mayr, required the existence of biologists who were 'willing' and who 'took the trouble' to learn about specialities other than their own.¹⁰⁷ This language suggests that the synthesizers were exceptional individuals. No doubt they were persons of exceptional ability, energy and vision. But it seems to me that this can be only part of the story. The case of the German geneticists suggests that the breadth of knowledge and interests necessary (though not sufficient) for contributing to the evolutionary synthesis did not vary randomly among individuals but was especially common in particular contexts. Though common among German geneticists, such breadth seems not to have been characteristic of the Morgan school.

That breadth versus narrowness of focus vary from one *institution* to another is implicit in Mayr's remark that Julian Huxley and E. B. Ford were the products of a 'school' at Oxford.¹⁰⁸ The importance of institutions is also obvious in the excellent work of Mark Adams on Soviet population genetics during the period.¹⁰⁹ We know that most Soviet 'geneticists' had extensive knowledge of natural populations¹¹⁰ and resented being told by Severtsov to stay away from evolutionary problems.¹¹¹ The

¹⁰⁷ Mayr, 'Prologue' (footnote 4), 40-41.

¹⁰⁸ Mayr, 'Prologue' (footnote 4), 11, 37, 39.

¹⁰⁹ Two recent attempts to trace the cognitive development of American genetics to its institutional structure are: Barbara Kimmelman, 'The American Breeders' Association: Genetics and Eugenics in an Agricultural Context, 1903–1913', *Social Studies of Science*, 13 (1983), 163–204; and Jan Sapp, 'The Struggle for Authority in the Field of Heredity, 1900–1932: New Perspectives on The Rise of Genetics', *Journal of the History of Biology*, 16 (1983), 311–42.

¹¹⁰ Muller was surprised at the extent of Timoféeff's knowledge of natural populations (Adams, 'S. Chetverikov, the Kol'tsov Institute, and the Evolutionary Synthesis', in Mayr and Provine, pp. 242–78 (p. 269).

¹¹¹ Th. Dobzhansky, 'The Birth of the Genetic Theory of Evolution in the Soviet Union in the 1920s', in Mayr and Provine, pp. 229–42 (p. 240).

¹⁰⁵ F. von Wettstein, 'Botanik, Paläobotanik, Vererbungsforschung, und Abstammungslehre', *Palaeobiologica*, 7 (1939), 154-68.

¹⁰⁶ Significantly, many other German geneticists of the period also appealed for cooperation between genetics and the older descriptive specialties in order to solve the problem of evolutionary mechanism. See Kühn, 'Genwirkung und Artveränderung', *Der Biologe*, 3 (1934), 217–27; Ludwig (footnote 31), and (footnote 40); or Correns (footnote 55).

distinction between experimentalists and naturalists, so familiar to us from twentiethcentury Anglo-Saxon biology, was far weaker in the Societ Union.¹¹² In his Institute for Experimental Biology Kol'tsov sought to unite (rather than to replace) the older morphological tradition with the newer experimental one and to avoid narrow and analytic approaches to biological problems in favour of synthetic ones. A premium was placed upon broad-based training, then specialization, followed by collaboration among specialists within research teams. Filipchenko and Vavilov were also broadly educated and interested in evolution.¹¹³ Clearly, that Soviet breadth, so consequential for the evolutionary synthesis, was the product of institutions which *integrated* genetics with older descriptive traditions and did not allow geneticists to specialize in the Morganian manner, pushing aside the big complicated problems in order to focus on easier ones.

If we want to understand, therefore, why some biologists were better equipped than others to contribute to the synthesis, we must devote more attention in future to the institutions in which they were trained and in which they taught and researched. What institutional differences can explain the apparent breadth of German geneticists compared to their American counterparts? Part of the answer (as I will argue in detail elsewhere) lies in the fact that the structure of American universities fostered specialization while the German university system hindered it. In the U.S., rapid expansion of higher education and the agricultural experimental stations in the late nineteenth century created a wide range of institutions in which geneticists could seek employment. In the universities the department system permitted specialists in genetics, morphology, embryology, etc. to occupy (potentially) secure and independent positions alongside one another. The power of university presidents prevented individual professors from blocking new developments out of self-interest, and the dependence of the universities upon public approval (whether in attracting students or in keeping state legislators happy) induced a readiness to innovate in response to the educational market. American geneticists could thus free themselves relatively early from dependence upon traditional botanical or zoological institutions. With that autonomy came the freedom to define the subject-matter of genetics as narrowly as one wished.

In Germany, by contrast, the late nineteenth century saw a marked slow-down in the creation of new chairs and institutes, and in the post-1918 economic crisis total spending on the universities remained below pre-World War I levels for over a decade. Until 1945, in consequence, there was only one chair (and very few other tenured posts) devoted to genetics in the twenty-six German universities. Those interested in genetics, therefore, had to find jobs in institutes of botany or zoology or in the Kaiser-Wilhelm Institute for Biology which was created in 1914 to compensate for the universities' failure to develop the new experimental biology.¹¹⁴ The structure of the university institute, however, placed a premium upon breadth of knowledge since professors preferred to teach *general* botany or zoology. Junior staff were assigned to teach specialist courses such as genetics but, given their dependence upon the professor for access to laboratory space and facilities as well as their lack of tenure, they were under considerable pressure to obtain chairs and their own institutes. And to be regarded as

¹¹² Dobzhansky (footnote 111); M. Adams, 'The Founding of Population Genetics: Contributions of the Chetverikov School, 1924–1934', *Journal of the History of Biology*, 1 (1968), 23–39.

¹¹³ See Adams (footnote 110), Dobzhansky (footnote 111) and Adams, 'Severtsov and Schmalhausen: Russian Morphology and the Evolutionary Synthesis', in Mayr and Provine, pp. 193–225.

¹¹⁴ See Natasha Jacobs' paper presented at this meeting, unfortunately not available for this issue.

'appointable' to a chair, they had to display the requisite breadth. Thus very few German practitioners of the new genetics could afford to ignore the classic biological problems of ontogeny and phylogeny and to pursue genetics in the specialized manner so common in the U. S. The only way out of this impasse, given the structure of the university system, was the creation of institutes of genetics, independent of botany and zoology. This did not occur, partly because of the economic climate, but also because new institutes would have competed with established ones for students and finance. And in Germany, unlike America, professors had the power to block the formulation of new institutes. Thus except for a few Kaiser-Wilhelm institutes, genetics in Germany remained institutionally and intellectually subordinate to botany and zoology until after World War II.¹¹⁵

Finally, some will want to ask how historically significant were the German geneticists of the inter-war generation. Obviously they have not been adjudged important enough to join the pantheon of neo-Darwinist heroes alongside their Soviet and Anglo-Saxon colleagues. On the other hand, until recently only very few of them were known to historians of biology. And the challenge facing synthesizers in the German-speaking world may have been greater. For although the Plasmon theorists saw no contradiction between CI and Mendelism, CI was nonetheless widely perceived as a way of marginalizing the evolutionary significance of chromosomal genes and thus of selection. The analysis presented in this paper suggests that in countries where the evolution will prove to have been relatively uncommon. Perhaps the task of constructing a unified theory of evolution was simpler in such countries because biologists could ignore the complications posed by CI, a luxury denied to their German contemporaries.

Furthermore, consensus among modern evolutionists is wavering at the moment; Goldschmidt's *The Material Basis of Evolution* has just been reprinted after forty years and is being brought back into the evolutionary debate. It is, therefore, a nerveracking time in which to have to judge the value of past traditions of evolutionary thought, and I find it hard to see how historians of the synthesis will be able to make such judgments, short of becoming evolutionists themselves. Should we not instead be asking a more tractable question, namely: to what extent have the institutional settings of various biological specialities this century constrained or facilitated particular theoretical developments?

Acknowledgments

For taking the time to answer my questions I am indebted to Professors I. Anton-Lamprecht, W.-D. Eichler, B. Glass, H. Hartwig, H. Kalmus, H. Kuckuck, E. Mayr, G. Melchers, H. Ross, V. Schwartz, J. Straub, H. Stubbe and W. Stubbe. For providing access to unpublished material I wish to thank: Drs. E. Pratje and G. Michaelis, Prof. H. Querner (Alfred Kühn Papers, Institut für Geschichte der Medizin, Universität Heidelberg), Stephen Catlett and Beth Carroll-Horrocks at the American Philosophical Society Library (L. C. Dunn Papers, Th. Dobzhansky Papers),

¹¹⁵ German psychology and biochemistry between the wars were also broader in theoretical scope than their American counterparts. There, too, the explanation seems to lie in different patterns of institutional provision in the two countries. The analyses of both Mitchell Ash ('Academic Politics in the History of Science: Experimental Psychology in Germany, 1879–1941', *Central European History*, 13 (1980), 255–86) and Robert Kohler (*From Medical Chemistry to Biochemistry: the Making of a Biomedical Discipline* (Cambridge, 1982)) have proved very useful in understanding German and American genetics.

Columbia University Oral History Project, Rockefeller Archive Center (International Education Board Collection), Archiv und Bibliothek zur Geschichte der Max-Planck-Gesellschaft (H. Nachtsheim Papers), Bancroft Library, University of California/Berkeley (Richard Goldschmidt Papers), Staatsbibliothek Preussischer Kulturbesitz (Ernst Mayr Papers), and Contemporary Scientific Archives Centre, Wellcome Institute for the History of Medicine (Hans Grüneberg papers).

For financial support of this research I thank the University of Manchester, the Royal Society, and the Volkswagen-Stiftung. Lastly I am grateful to Robert Olby for valuable criticisms of a previous draft, and to Andrea Charters of Leeds University for the typing of the paper.