INTRODUCTION

MARJORIE GRENE

At the suggestion of Professor Wolf Lepenies of the University of Berlin, and under the sponsorship of the Werner Reimers Stiftung, a conference was held on August 27 and 28, 1981, at the Foundation's headquarters in Bad Homburg in West Germany, on the topic of twentieth-century evolutionary theory. Our leading concern might be formulated in terms of the question: How complete and how stable is, and has been, the evolutionary synthesis, or "neo-Darwinism"? A small meeting, with fourteen invited participants (of whom thirteen were present), the conference made no claim to be in any way exhaustive either of the historical or the philosophical issues involved in our subject matter. As the meeting was conceived, the primary focus was to be historical; but both the interests of the participants and the nature of the history we were concerned with made it inevitable that we carry our discussion forward to contemporary issues.

The essays that have resulted from our discussions speak to a number of very different aspects of our general question, let alone its answer(s). And to a thoroughly historicist philosopher of science, such as the organizer of the meeting and editor of this volume, this is as it should be. Let me fill in this general boast a little before taking up a few aspects of the particular questions we dealt with. I shall not, even then, affront the reader by summarizing each essay in turn; I trust that they are readable in themselves.

First, on the question of philosophy of science in general, let me make a confession of faith. By now, I believe, what used to be called the "received view" in philosophy of science may be decently buried and, indeed, forgotten. It was a view that divorced its analysis of science entirely from science as history, science as human activity, science as search. By now, thanks to historians of science, and to some philosophers and reflective scientists, we may reflect, more constructively, I believe, on science as a nexus of activities, of "practices,"

to use A. C. MacIntyre's term. Practices are characteristically located in certain segments of certain societies, making certain kinds of epistemic claims in accordance with the patterns of thought of their various disciplines or subdisciplines at a given time and stage of development, and authorized by the standards of the society that permits and sustains them (MacIntyre, 1981; cf. Brown, 1977).[1] This is not to say that philosophy of science is thereby reduced to the sociology of science. Philosophers are interested not just in putting one darned thing before or after another, nor in making "pure" causal connections whether in psychoanalytical, Marxist, or other historiographic fashions. We are interested in the nature of epistemic claims; but we recognize that these are always embedded in a history from which they take their shape and, to some extent, their content (Grene, 1976, 1978b; cf., e.g., Kitcher, 1982).

Moreover, history is always partial and fragmentary, characterized, like everything alive, by what Merleau-Ponty called "patterned mixed-upness" (Merleau-Ponty, 1968, p. 176). There is no end to its complexity, and no way, on principle, to be sure what is and is not illuminating. That statement may be partly an excuse for the very assorted content of this volume – and of our discussions at Bad Homburg – but it is also, in my view, a reflection of scientific-historical-philosophical reality.

If, further, an unresolved, and possibly irresoluble, plurality of perspectives is appropriate to metascientific questions in general, whether they are (primarily) historical or (primarily) philosophical, so much the more emphatically does this hold for our present subject matter, the recent history of evolutionary theory. Darwinism has been correctly described as a hypertheory, or supertheory that serves to tie together a variety of scientific disciplines within biology (Tuomi, 1981; Wassermann, 1981). Ethology, paleontology, taxonomy (of the evolutionary variety), and even, remotely, biochemistry depend at various but crucial points on its organizing power. But perhaps because of that very comprehensive and regulative status, Darwinian theory has been, since the beginning, the subject of unending debates, reinterpretations, and revisions. In the discussion that is here partly recorded, we concentrated on two major themes or clusters of themes: questions about the history of the modern evolutionary synthesis and questions of contemporary history centering on the problem of the role and limits of adaptation as an explanatory concept.

[1] For a statement of the standard, and, as I believe, mistaken, view that it is science that should contain and legislate for the self-understanding of society, see, e.g., Simon, 1982.

In fact, these questions too are closely interconnected; they are both touched on, directly or indirectly, in all four parts of this collection.

Historians of science often distinguish between internal and external causes of scientific change. The question may be raised, however, whether these are different in kind or only in degree. If science is viewed as a network of practices, dependent on the standards, concepts, and procedures of each subdiscipline, but authorized by and, to this extent at least, dependent on standards and beliefs of the wider society of which each discipline forms a part, there is no sharp separation, in principle, between broader social concerns and those of a given scientific practice. Granted, it is essential to the existence of any science that it observe its *own* ethical principles: truthfulness, accuracy, the demand for repeatable experiments, special criteria of experimental design, and so on. It is essential to the practice of any science, for example, that respect for truth take priority over ambition, vanity, or greed. But motives other than truth-seeking do, of course, play their part and so do the larger interests of the society as well as of the individual. Bernard Norton's essay about Fisher's interest in eugenics seems to illustrate a purely external relation of personal interest to scientific inquiry. What Fisher accomplished in evolutionary theory appears to have no connection with his early interest in eugenics, whatever we may think of it from our present perspective. And Wolf Reif refers to Beurlen's Nazi affiliation as having no effect on his scientific work. Perhaps. But Rupert Riedl mentions in passing a widely acknowledged case of the interaction of social and scientific beliefs: the relation of the Victorian middle class to Darwinism. Admittedly, social Darwinism cannot be fathered on Darwin himself nor yet on the theory of natural selection as a theory of organic evolution. Nevertheless, the recurrence of organic and social Darwinism as a team in the nineteenth century, in the early twentieth (with Sumner and company), and more recently in some of the offshoots of sociobiology, if not in the fountainhead itself, attest to the probable existence of some essential connection between the two. And more generally, it seems to me, a good case can be made for the existence of something about the Victorian state of mind that makes "utility," whether in Bentham's social thought or in the adaptationist bent of selection theory, seem self-explanatory.[2] Adaptations, like utility generally, are means and explain what they explain not in themselves but in relation to ends. But is the end of survival really adequate for human as well as organic history? Whatever the answer, the point

[2] See, e.g., the suggestions made by Philip Sloan (1981), about the broader influences on Darwin's thought.

here is just: There is something teasing about the way in which both utilitarianism and selection theory (in the strictest, or perhaps most reductive form) appeal to thinkers of a certain cast of mind. In any case, the question here is, rather, whether there is any such intrinsic connection or hint of an intrinsic connection in Fisher's case between his social theory and his genetical theory of natural selection. I don't know.

Another seemingly external factor in the history of science, however, surely does count as "internal" as well, and serves to show how difficult such a distinction may be to make, that is, the matter of national styles. Science is allegedly, and up to a point even is, international. Yet Darwinism has had notoriously different destinies in different European countries (Glick, 1972) and, as this collection partly shows, has continued to do so in this century. Despite Haeckel's popularization of nineteenth-century Darwinian theory, the synthesis took root only very partially in the twentieth-century German-speaking world. Rensch is, I believe it is fair to say, the only major German contributor who remained in Germany, and indeed his contribution to this volume illustrates scientific development in its genuinely international form. The story Wolf Reif tells is different: Notwithstanding Heberer's anthology of essays by subscribers to the synthesis, in German-speaking countries evolutionary thought, and the style of biological argument, retained, on the whole, its heavily morphological commitment. The largely English-language "modern synthesis," on the other hand, entailed at least in some of its bearers a positively antimorphological component: Witness, for instance, the remark of Mayr quoted by Riedl, and see also my comparison of the arguments of Simpson and Schindewolf (Grene, 1974).

Granted, the situation here is complicated and has grown in complexity in recent years with the growth of cladism, which derives from the intensely Germanic phylogenetic taxonomy of W. Hennig (1950). Cladism itself boasts of its anti-Darwinian bent and, from the point of view of orthodox evolutionists, appears to be something of an alien excrescence. Still, it is an increasingly vocal and increasingly prestigious self-proclaimed school; it may well contribute to a new "new synthesis" that will eventually overcome the less than global perspective of the present – or recent – orthodoxy. Indeed, even within the orthodoxy of the synthesis, Mayr has suggested a way to use fruitfully the approaches of all three contemporary taxonomic schools (Mayr, 1981, 1982*a*). For the relatively simple point I want to make here, however, that is by the way. What needs to be noticed, as against the overabstract conception of science as above and beyond any culture that carries it, is the presence in any given case of scientific

thought of what Fleck calls a "thought-style" expressive of a "thought-complex" – and such styles or complexes, in turn, are carried and shaped by local, even linguistic, traditions (Fleck, 1981). As both Reif's narrative and Riedl's presentation of his own position make plain, there is a motif in German-language evolutionary thought that derives not only from a stress on morphology as such, but, acknowledged or not, from the heritage of Goethe and the *Urpflanze*. Similarly, as I have found in talking with followers of sociobiology, there is a lingering commitment to Newton's "hard, solid impenetrable particles" as well as to Newtonian linear causality in some versions of present Darwinian thinking. Some of Gould's adjurations to evolutionists to recall the importance of the constraints that limit the plasticity of natural selection at any given juncture in evolutionary history, or his references to the "science of form," represent, in part, efforts to overcome this parochial character (Gould, 1980*a*,*b*,*c*; Gould and Vrba, 1982). But the diversity, and even contradiction, certainly has existed and still exists, as Riedl's essay in this volume amply testifies.

Moreover, the difference is not only one of style in any superficial sense. It represents, in my view, a puzzling difference of substance as well, and the two, indeed, are intrinsically connected. Ernst Mayr has established as canonical the distinction between typological and population thinking in biology (Mayr, 1982*a*). The Continental, specifically the German-language, strain à la Beurlen–Schindewolf and Remane–Riedl clearly remains on the typological side. On the other hand, the development of the view that "species are individuals" has lately characterized population thinking to the point of denying the need ever to notice *any* similarities whatever among living things. Taxa are to be taken purely as lineage taxa, and that, said Ghiselin and Hull, is that (Ghiselin, 1974; Hull, 1976, 1980*b*). Yet, carried to its logical conclusion, this view seems to undercut the very starting point of any biological science, including the theory of evolution. How does one tell which "individuals" (in the everyday sense) are parts of which larger "species – individuals" except by noticing some kind of likeness among some and not others? David Hull has faced this issue by admitting that here, as in other areas, theory just does have to go against common sense – and so much the worse for common sense.[3] Yet what Riedl calls our "hereditary common sense" about natural kinds does seem, at some level, to underlie the practice of even the most theoretical biology. Doesn't one need some judgment of what something is *like* in order to notice either homologies or analogies? (cf., e.g., Pantin, 1954; Grene, 1976; Wiggins, 1980). Perhaps

[3] Personal communication; cf. Hull, 1980*b*.

judgments of "this such" are only everyday starting points, to be left behind, like physicists' everyday judgments, in the more sophisticated statements of a developed evolutionary science. But, then, how could Mayr have been so persuasive in the debate over numerical taxonomy by insisting on the importance of the weighting of taxonomic traits by the experienced taxonomist? (quoted by Riedl, this volume; cf. Mayr, 1981, 1982*a*; Pantin, 1954, 1968). Again, there seems to be some minimal, almost foundational, contribution here that some arguments drawn from a rigorous selection theory want us not only to overlook but to abandon. As against this extreme conclusion, Stephen Jay Gould's adjuration to "restore the organism to biology" seems reasonable (Gould, 1980*c*). Yet the morphological tradition generates its own puzzles. When I read Riedl's essay, or Hennig's original (1950) treatise on *Phylogenetic Systematics*, I find myself entering a different world, where what might have been modest methodological suggestions are somehow assimilated to an alien metaphysic. That I know this "other" scientific style fairly well and have even tried (vainly) to introduce it to the English-speaking world, by no means lessens that sense of strangeness (Grene, 1974, chs. 16–19).

Of course this is an oversimplification. As I have already pointed out, the cladistic school, who boast direct descent from Hennig, are English speakers (Hennig, 1966, introduction), and there are certainly non-English speakers attached to the synthesis, as not only the case of Rensch, but the essays of Peters and Hoffman attest. Reif's contribution is especially interesting in this connection, because it records the power of the morphological tradition without itself exemplifying its peculiar tenets. And further back in history there are also all sorts of interactions (see, e.g., Smith, 1982). Nevertheless, it seems undeniable that some kind of linguistic-cultural-scientific difference of style exists and needs to be reckoned with in any adequate account of the conceptual structure of recent evolutionary theory. The French case, it should be added, is different again; until recently, at least, it has represented a more finalistic than morphological resistance to Darwinism (Gavaudan, 1967; Boesiger, 1980; Limoges, 1980). But since we had no French participant in our discussion, only the German–English problem could be raised here.

In more obviously "internal" respects also, the recent history of evolutionary theory again presents pertinent conceptual complexities that show up with a new clarity in the light of controversies now current. Some of these are discussed explicitly in Part Four of this collection. As I have already remarked, we had intended to focus on the question of the role and limits of adaptation as an explanatory

concept. Although this has been a recurrent question in evolutionary theory, it is the recent discussion of "adaptationism" that has brought it once more to center stage. Clearly – and Darwin himself was well aware of this – the theory of natural selection is a theory of organic change with respect to adaptation and only adaptation. It is a theory of the mechanisms by which organisms have become fit, that is, likely to leave offspring, in the environments in which they find themselves, environments which, indirectly, by the opportunities for new life-styles they offer, help to bring them about. But can "adaptation" do all the work? What other concepts belong to the core of modern evolutionary theory? The history of biology, Ernst Mayr writes, is not so much the history of theories (let alone of "facts") as it is of concepts (Mayr, 1982*a*,*b*). But concepts – and perhaps, especially, evolutionary concepts – have a way of expanding by cannibalizing other concepts that ought also to have a role in the whole explanatory framework. "Adaptation" seems to be particularly susceptible of such abuse. For example: the theory of natural selection is a two-step theory; there is random variation – plenty of it – and inheritance of those available characters that happen to prove slightly better adapted in given circumstances than the available alternatives. So undirected variation, basically a kind of randomness, not *only* selection, is an essential ingredient in the process. Moreover, biologists must recognize, if they think about it, the constraints imposed by past development – constraints of form, behavior, and physiology – within which variation and selection must take place. Differences in "tempo and mode" of evolution, too, may complicate the story. As the evolutionary synthesis developed, however, the conceptual plurality of the first – and founding – versions receded; and as Gould puts it, the synthesis hardened. Earlier versions, as the arguments of Provine and Gould demonstrate, had been less thoroughly "adaptationist," more tolerant of factors other than "means-to-survival" in the evolutionary story. In response to the hardening of the synthesis, the question of just how much work adaptation does or ought to do becomes a pressing one, especially in the light of proliferating challenges, both esoteric and exoteric, to the Darwinian tradition. Gould and Provine speak to this question from an historical perspective, and Burian and Peters address themselves more directly to the conceptual issue. The essays of Hoffman and Maynard Smith also bear indirectly on this problem, and, in fact, all three biologists directly dealing with current issues (Hoffman, Peters, Maynard Smith) defend the central adaptationist program. Kimler's essay, however, alongside Turner's, helps to complicate the picture. Turner, a student of P. M. Sheppard (Sheppard, 1958) would like to find mimetic theory leading directly into

the synthesis in its strictest form (Turner, 1981) but acknowledges a recurring schism in evolutionary thought. Kimler presents convincingly a more complicated picture, arguing that an ecological perspective was important in this field and at the same time that ecological thinking, though part and parcel of Darwin's biological thought-style, played no major role in the development of the synthesis. Thus, rather than a single line of thought leading to the synthesis, we find a complex network of interacting interests and influences in which at some points, though not always or necessarily, the selectionist emphasis, or overemphasis, on adaptation assumes a dominant part. And it is this complexity that is spilling over in the many-sided debates about evolutionary explanation that are conspicuous today.

We touch on only a few aspects of this complex debate in our collection. It may be worthwhile, however, in conclusion, to separate schematically some of the issues that have arisen in the recent literature. Questions about the adequacy of the synthesis are often taken, on principle, as challenges to Darwinism. Of the many lines of debate now current, however, it seems to me, only two, or perhaps better three, constitute such fundamental challenges: (1) neutral mutation theory, (2) cladism, and (3) a protest from the perspective of ontogenesis and sometimes also of morphology. The first is not touched on here at all, although it certainly should not be ignored in any comprehensive account of recent theory. That mutations are random even the most fervent selectionist admits: indeed, it is necessary to the structure of a neo-Darwinian, non-Lamarckian account that this be so (see Rensch's essay, for example). But that alleles wholly unconnected with fitness should persist for long periods and in great numbers is a thesis that selectionists find difficult to accept. Yet despite selectionist arguments to the contrary, the view persists (Kimura, 1976; King and Jukes, 1969). [Darwin, it should be noted, in the *Descent of Man*, seems to anticipate even this degree of pluralism. In that late work, he attributes a good deal of evolutionary change to "chemistry"! (Darwin, 1871).] Second, cladism is not only anti-Darwinian. Although it began, with Hennig, as phylogenetic taxonomy in opposition to idealistic morphology, it has by now turned, in its "pattern cladistic" form, against evolution itself, a paradox Maynard Smith refers to in passing (Beatty, 1982; cf. Hull, 1980*a*). In addition, perhaps one ought to mention a kind of morphogenetic challenge to Darwinism reminiscent of some aspects of Riedl's argument (Wiley and Brooks, 1982; Løvtrup, 1981).

On the whole, however, I find most objections raised largely from within a modified or enriched selectionist approach. This is the case,

for example, with Gould and Lewontin (1979), Gould (1980*a*,*b*,*c*, 1982, and this volume), Gould and Vrba (1982), Sober and Lewontin (1982). Here, again, however, various lines of argument should be distinguished. Gould and Lewontin's classic paper was subtitled "A Critique of Adaptationism." What is really under attack in that provocative piece is not apparent on its surface; I shall return to that question in a moment. As a whole, however, the "revolt against adaptationism" needs to be distinguished from two other current themes: (1) the controversy about the separability of macro- and microevolution; and (2) the controversy about the units of selection (to which, however, as we shall see, the "adaptationism" argument does bear a close relation). Both these questions are dealt with by Maynard Smith, who is, indeed, one of the most eminent and ingenious defenders of the neo-Darwinian orthodoxy (Maynard Smith in Scudder and Reveal, 1981; cf. Stebbins and Ayala, 1981). Hoffman, as a paleontologist, is also concerned with the former problem and professes skepticism of the new heresy. The vehicle for the separation is the theory of punctuated equilibrium (Eldredge and Gould, 1972; Gould and Eldredge, 1977), which offers a new perspective for reading the fossil record and thereby challenges the gradualist bias of Darwin himself as well as of modern Darwinism. As its originator(s) conceived it, this model was to allow paleontologists to accept the fossil record at face value, rather than having to apologize for the gaps "discovered" in it by a gradualist approach. This seemed to some paleobiologists a vindication of their discipline; to genetically based evolutionists, however, it undercuts precisely one of the great triumphs of the synthesis: its assimilation of macroevolution to its more manageable microevolutionary – that is, population-genetical – base. Yet there is nothing fundamentally antiselectionist about this theory, and it is not, in itself, an attack on but rather a modification of the synthesis (Gould, 1982; cf. Stebbins and Ayala, 1981; Levinton and Simon, 1980).

Even more clearly, the units of selection controversy should be seen as a dispute within the Darwinian tradition. Again, the theory of natural selection is a theory of how adaptations arise. But adaptations of *what*? What is it that is selected? Every least part of every organism – notably every gene? Every trait of every organism? Each organism as a whole? Demes? Populations? Species? G. C. Williams' influential book (1966) arguing against the unpopular and indeed unlikely notion of group selection put the reductionist, gene-oriented answer very well. Still, even in the heyday of the genetically dominated version of the synthesis ("natural selection *is* differential gene frequencies," etc.; see Burian, this book, Chapter 11; and cf. Grene, 1974, chs. 8 and 13), Waddington had warned biologists to remember that al-

though it is genes that differentially survive, it is phenotypes that are selected (Waddington, 1953, 1967, 1969). Since Lewontin's authoritative paper on "The Units of Selection" (Lewontin, 1970; cf. Wright, 1967), and with the work of Wade (1978) and others, however, a more flexible conception of the units of selection has been put forward – most definitively in my view in Sober and Lewontin (Sober and Lewontin, 1982; cf. Brandon, 1982; Richardson, 1982; Lewontin, 1982). Not that this means a global acceptance of group selection and allied concepts. In this volume, Maynard Smith argues against Stanley's concept of species selection for use in any but a very few cases (Stanley, 1975, 1979); and Gould, who had accepted the term, has now renounced its general use (Gould, 1982). Clearly, other things being equal, if a given species speciates faster than another, selection at the species level favors its "daughter species" over those of its competitors. This *is* species selection. But if a species is selected because "it" runs faster, that is just shorthand for the fact that its members (in Hullian terms, its parts!) run faster. In such a case, it is the individual phenotype, not the whole species, that the process of natural selection affects. But neither is it the gene. (Genes don't run, any more than species do.) And the possibility of occasional selection of some larger units remains open. The conceptual changes needed to effect this change in modeling are much more intricate and subtle than I have indicated (see Sober, 1980; Wade, 1978; Wilson, 1980; Wimsatt, 1980, 1981). The point here is simply, first, that these are alterations *in*, not against, what is basically Darwinian evolutionary thought, and second, that this controversy, like the others I have mentioned, should be distinguished from the critique of adaptationism – although, as I shall now proceed to say, it, unlike the others, is closely connected with that critique at least in its "San Marco" version (Gould and Lewontin, 1979).

With those distinctions made, we may look briefly at the direct attack on adaptationism. As I understand it, the "Spandrels of San Marco" was directed chiefly against two kinds of excess or exaggeration in evolutionary theory: a misplaced atomism and an irresponsible teleologism. Both these distortions of Darwinism – let us call them cryptoatomism and pseudoteleology – are especially conspicuous in the arguments of sociobiologists, and it seems reasonable to conjecture that the explosive expansion of that new "discipline" had some connection with the genesis of the "Spandrels" paper.[4] What is important here is to recognize the multidimensionality of biological, and indeed of evolutionary, explanation: that is what is ignored in

[4] For a more explicit reference, see Lewontin, 1979; this ought, I believe, to have been a definitive refutation of sociobiological principles.