REVIEWS

CHARLES DARWIN, THE YEARS OF CONTROVERSY: THE "ORIGIN OF SPECIES" AND ITS CRITICS 1859-82. Peter J. Vorzimmer. University of London Press, 1970. Pp. 300+xv.

Peter Vorzimmer is surely mistaken about at least one thing. In April of 1970 it was not the case that no manuscript other than his provided "a detailed analysis of Darwin's theory which treats it at the same time in its proper historical and scientific setting". In fact, Michael Ghiselin's *The Triumph of the Darwinian Method* was published in 1969, and there is no question that the two books are comparable in scope and scholarship. Comparison of the two books is made altogether unavoidable by their starkly antithetical conclusions.

Vorzimmer carefully delineates the position taken by Darwin in the first edition of the *Origin* and then develops the thesis that the lack of an adequate theory of heredity forced Darwin, in successive editions of the *Origin*, and in the *Descent of Man*, into a bewildering maze of contradictions ending in drastic concessions to Lamarckism. In constructing this argument, Vorzimmer concentrates upon Darwin's response to criticism in the interval from 1859 until his death in 1882, with particular emphasis upon the problems of variation (its nature and its causes) and inheritance.

The contrast with Ghiselin's approach could not be more complete. Paying somewhat less attention to Darwin's critics, but surely drawing from a much greater range of Darwin's biological publications, Ghiselin finds a substantial methodological and doctrinal continuity ranging from the early theories of the formation of coral reefs and variability in barnacles to the *Power of Movement in Plants*, in 1880. For Ghiselin, Darwin is among the most effective exponents of the hypothetical-deductive method:

> The entire corpus of Darwinian writings constitutes a unitary system of interconnected ideas. It strives, with astonishing success, to encompass all organic phenomena within the structure of one comprehensive theory. (p. 12)

Morse Peckham's "Variorum" edition of the *Origin of Species*, a composite of all six editions which were published between 1859 and 1872, provides the basis for considering the changing structure of the theory of natural selection. Vorzimmer finds the same mechanism in the first Sketch of the theory in 1842, in a longer essay of 1844, and in the first edition of the *Origin*. Its structure is as follows (premisses identified by Roman numerals; theorems by capital letters):

I. All organisms possess a natural tendency to a geometric rate of reproductive increase.

II. The elements which constitute their nutritive sustenance will not match this rate of increase.

A. There is a struggle for existence among living organisms (from I and II).

III. Inheritable variation appears in all organic forms; some of it advantageous in the struggle for existence.

B. Those organisms which possess advantageous variations survive the struggle for existence (from A and III).

C. Permanent and adaptive changes in the form of organisms will result (from B and I). (pp. 6-7)

The key to Vorzimmer's account is Premiss III and its relation to Theorem C. What is the nature and extent of the " variation " that can be attributed to causes other than natural selection? In particular, can this variation be sharply distinguished from the " permanent and adaptive " changes which are ingredient in the larger process of speciation? The problem must be considered in the context of the evidence available at that time. Lamarckism identified the causes of variation and those of speciation.

Darwin recognised five different causes of variation from his earliest writing on the species question: the direct effect of the conditions of life; indirect effect of conditions; habit, use, and disuse; correlation of growth; compensation or balance. Lamarck's *sentiment intérieur*, an intrinsic drive to organic improvement, was always explicitly rejected by Darwin. But Vorzimmer claims that Darwin failed to notice the extent to which his attribution of an increasing role to the causes of variation (particularly to habit, use, and disuse; and to the correlation of growth) tended to merge the issues of variation and speciation in a fashion which was increasingly close to the letter, if not the spirit, of Lamarck.

Clearly, Darwin never recanted the basic thesis that natural selection is an important cause of evolutionary change; the debate centers around the qualifiers " only " or even " the most important ".

Just as clearly, Darwin did state in the *Descent of Man* that he had " perhaps attributed too much to the action of natural selection ", an excess he traced to his imperfect escape from the doctrine of special purposeful creation and its corrolary: that every detail of structure is of " some special, though unrecognised service ". In 1871 he no longer thought of all details of structure as adaptive.

A few methodological remarks are in order here. Consider

1. All of the stable and heritable characteristics of organisms are adaptive.

and

2. Not all of the stable and heritable characteristics of organisms are adaptive.

An elementary logic textbook would agree with Vorzimmer in identifying 1 and 2 as flatly contradictory. There is at least one interpretation, however, under which they are no longer so starkly opposed. If both are regarded as " general research directives " rather than " factual assertions " (the Kantian distinction of the regulative and constitutive uses of a proposition) then both are consistent with the rule: every feature of every organism must be analysed to discover its adaptive value (admitting that this value may be zero).

A great deal depends on this shift in the semantic interpretation of theoretical statements of science. Consistently and completely implemented, the interpretation of theoretical statements as having a regulative rather than a factual meaning is equivalent to " instrumentalism ", the view that science

does not tell us what the world is really like but only how to conduct research more or less successfully.

But neither Darwin nor any neo-Darwinian need insist upon a straightforward factual interpretation of either 1 or 2. Those who give the matter careful thought (cf. T. Dobzhansky's "What is an Adaptive Trait?" *American Naturalist*. XC (1956), pp. 337ff.) are most likely to confine themselves to the observation that factual evidence is not adequate for the support of 1 and that the investigation of any particular trait should be open to the possibility that it is not adaptive. At the same time, Dobzhansky offered detailed cautionary remarks concerning the dangers of deciding that any particular trait is inadaptive: these included the possibilities that it is controlled by a pleiotropic gene selected because of some one of its other phenotypic effects, or that the putatively "neutral" trait is positively adaptive at some stage in the life cycle not under investigation. The net effect of these cautions was to make a proposition such as "X is an adaptive trait" almost impossible to falsify, and correspondingly less factual in its import.

A reasonable realist must admit that such propositions as 1 and 2 have a significant scientific function as "general research directives". To this extent, they escape the over simple confines of the logical square of contradiction. This implies that neither Vorzimmer nor Ghiselin is correct: Darwin does not fall into self-contradiction, but neither does his work fit into a unitary hypothetical-deductive pattern.

A second approach might concede to Vorzimmer that Darwin gave an increasing amount of weight to such factors as the heritability of the direct effects of the environment, and of habit, use and disuse; the secondary effects of the developmental laws of correlation and compensation; and even a tendency of variant organisms themselves to have offspring likely to vary again in the same direction.

Obviously, Darwin was not as well situated as a contemporary neo-Darwinian to insist that there was no systematic correlation between the causes of organic variation and the adaptive needs of the organism. Not even Weismann established that thesis as clearly and decisively as it is stated in the Central Dogma: information is never transferred from protein to nucleic acid. But there is one clear text from the Introduction to the *Origin*, which Darwin did not hedge or modify in six editions, which is compatible with the concessions he made in *Variations in Plants and Animals* and in the *Descent of Man*, and which surely provides a powerful paradigm for every Darwinian from Weismann to Crick and Monod:

> Naturalists continually refer to external conditions, such as climate, food, etc., as the only possible cause of variation. In one limited sense, as we shall hereafter see, this may be true; but it is preposterous to attribute to mere external conditions, the structure, for instance of the woodpecker, with its feet, tail, beak, and tongue, so admirably adapted to catch insects under the bark of trees. In the case of the mistletoe, which draws its nourishment from certain trees, which has seeds that must be transported by certain birds, and which has flowers with separate sexes absolutely requiring the agency of certain insects to bring pollen from one flower to the other, it is equally preposterous to account for the structure of this parasite, with its relations to several distinct organic

> beings, by the effects of external conditions, or of habit, or of the volition of the plant itself. (lines 23-25)

The problem of adaptation, after all, is very nearly one with the problem of coadaptation, and it is the solution of the latter which Darwin set as the condition of the adequacy of any evolutionary theory.

Vorzimmer neither contests nor notices that condition. Nor does he clearly formulate the thesis that his argument requires: that Darwin came to admit a systematic correlation of the causes of variation and the adaptive needs of organisms. In fact, that thesis is false. In consequence, although his book contains valuable information concerning the interaction of Darwin and his critics, his central conclusions about the import of Darwin's concessions to Lamarckism are not established.

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COEFFICIENTS OF NATURAL SELECTION. L. M. Cook. Hutchinson University Library 1971. Pp. 207. £1·25.

Though population genetics is some 50 years old, the mathematical theory is only slowly becoming sufficiently sophisticated to deal with natural selection in wild populations in the true sense of the word " wild ". This has mostly been because we have been unable to deal with the environment in its full complexity, in which the physical environment of the species varies in time and space and its biological environment (those other species which compete with it or prey upon it) has a population genetics of its own. This book attempts to present fairly simply (but with a quite misleading title) " the theory of natural selection as used in ecological genetics ". The algebra takes up only a small part of each section which is then devoted to a discussion of its relevance to the real world.

In the main, the author succeeds in his intentions and makes available in one cover topics such as gene-frequency dependent selection, selection in several environments and so on, the theory of which is only to be found in the original papers. There are, however, too many misprints in the algebra.

The main gap in existing theory concerns natural selection at the level of metric characters. It may be that it will be impossible to construct an adequate theory—one in which predictions of reasonable accuracy can be made—but the necessary condition which must hold before the observed interrelationship between a metric character and fitness can be used in any predictive way is not generally realised and is certainly not given by the author in the relevant chapter. This is that variation in fitness between genotypes at the loci affecting the measurement are completely determined by the phenotype for the measurement—in other words that these loci form a closed system affecting fitness solely through the measurement being made. It is very doubtful whether this condition is ever satisfied in real life.

Although population density and number as factors in natural selection are thoroughly discussed, the author does not attempt to deal with genetic drift, probably the right decision in a book of this size. There is little treatment of plants (Allard's work on partially-selfing species like Avena finds no reference in the chapter on " polymorphism in non-panmictic conditions ")