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OUTLINES OF POPULATION THEORY*

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Efforts to establish and justify a theory of populations require no apology, the need being obvious. Nevertheless, it must be noted that such efforts are particularly necessary at present, since the population school is undoubtedly dominant in modern biology. Despite the fact that there is every reason for development of a theory in this area, the process itself is far from simple, in view of the inexhaustibility of the subject. It is therefore a practical impossibility to consider all aspects of population theory in a single book. The inevitability of this situation forces an author to limit himself to examination of the most general properties of populations, those that can be studied from the standpoint of different disciplines.

Recognizing this, the authors of the book here reviewed point out that they have attempted to emphasize "the importance and necessity of broad study of populations as elementary units of the evolutionary process" (p.6). The selection of this basis for creation of a theory of populations is quite logical, since, firstly, most biological disciplines have a bearing on evolutionary theory and, secondly, such a foundation should permit examination of the subject itself from the most general standpoints. However, in addition to "taxonomic" biology, for which the concept of "species" and the problem of the origin of species are central, there is a "nontaxonomic" biology, which has no less (if not more) right to investigate life at the population level. The underestimation of this fact can be sensed in the "Introduction," where the authors write: "Life... is represented by discrete individuals ..., which, on the whole, form a system of discrete aggregates, or taxons" (p.7). Why only taxons? Why not trophic units, levels, and chains, as well as populations?

In speaking of "nontaxonomic" biology, we have in mind primarily ecology, whose theoretical concepts (ecological niches, food chains, and population pyramids) directly indicate a nontaxonomic approach to biological subjects. It is sufficient to recall that the concept of ecological niches postulates the possibility that populations of a given species can exist in different niches and, conversely, populations of different species can exist in the same niche. In other words, ecology systematizes its objects in accordance with the position they occupy in food chains, i.e., in a fashion totally different from the procedure in taxonomy. The concept of "species" enters ecology in connection with the synthesis of "taxonomic" and "nontaxonomic" biology. The central problem in ecology is therefore not that of the origin of species but that of the development of food chains and the changes they have undergone with time.

This brief discussion of the relationship of ecology to other areas of biology is necessary to show that a theory of populations cannot be developed separately from ecology, i.e., without giving consideration to populations as elements of biocenoses (links in the trophic chain). The need for such an approach is instinctively recognized by the authors, since their first chapter begins with a discussion of the biosphere, biogeocenoses, biocenoses, and populations. However, subsequent chapters ignore the fact that a population is not only an elementary evolutionary unit but also a biocenotic element, thus making the first chapter completely superfluous. It must be considered merely an obeisance to current trends in the development of biology.

Thus, creation of a contemporary population theory is meaningless unless the energy-producing role of populations in natural ecosystems is taken into account. This is due primarily to man's practical

* Nauka, Moscow (1973).

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requirements, since the human population is the only real object of the exploitation of natural recources.

It is undoubtedly to the authors' credit that they distinguish phenetics as a separate biological discipline. It seems odd that, after having been in the foreground for so long, this notion only came to fruition now. However, while giving the initiators of this approach their due, it is difficult to agree with the specific implementation.

The starting point in the authors' arguments is the concept of the "phenotype" proposed by Johannsen. Proceeding from this concept and ignoring the fact that Johannsen did not consider the "phenotype" and "genotype" to correspond, the authors define the concepts of "phene," phenetics, and the content of phenetics.

Johannsen arrived at the concept of the "phenotype" by studying the action of selection in pure strains. He established that pure strains are the material for selection but that the results of the process may not be permanent. This enabled him to draw several very important conclusions: 1) The variety of expressions of given traits in "populations" may be to a significant extent independent of hereditary properties; 2) the action of selective factors can have permanent results only when the genetic diversity in a "population" is greater than that in pure strains. From this Johannsen quite logically concluded that there are two relatively independent systems in the organism: the phenotype and the genotype. The former can provide material for selection quite independently, while the latter can reinforce the results of selection; the properties of these systems are manifested at different times (the results of selection can be reinforced only after the "selective" factors have operated), which in turn means that they cannot be equated with one another. It would therefore have been logical to have attempted to define the "phene" on the basis of the characteristics of the phenotype itself, i.e., of the systems that provide material for selection.

Darwin noted in discussing the action of selective factors that the selection process favors better-adapted organisms. In other words, selection can "distinguish" greater or lesser degrees of adaptation, i.e., make a quantitative evaluation of given traits (their elementary variations) or sets of traits. On this basis, the concept of the "phene" can be defined as a greater or lesser degree of adaptation, i.e., the degree of susceptibility to selective factors. We can naturally somewhat modernize the entire definition by replacing the phrase "better adapted" with the notion of increasing "probability of realizing the reproductive function over a succession of generations," which leaves the sense of the definition unchanged. All degrees of variation below the threshold for the action of selective factors can exist without keeping us from postulating that the phene is an indivisible (with respect to the action of selective factors) unit of elementary variation.

Here it is pertinent to note another strongly pronounced tendency shown by the authors throughout the book. Essentially, they are inclined to give rather "rigid" definitions, i.e., virtually every definition is as limited as possible. Introduction of such restrictions is theoretically justified, but the authors seem to be attempting to absolutize them. This might account for the fact that they often avoid defining the criterion used as the basis for asserting that an object is indivisible, a criticism wholly applicable to their definition of the "phene." Without stating the criterion used to show the phene to be indivisible, the authors merely give rather unconvincing examples by way of illustration. Thus, in regarding the triangular shape of the cells in a dragon fly wing as a phene (p. 138), they fail to take into consideration the fact that selection might have been not for cell shape itself but for the sum of the cell sides, i.e., the triangular shape might not be indivisible under the action of selective factors.

The reasons for this absolutization lie in the authors' methodological viewpoint, which is unambiguously expressed in the "Introduction" and on p. 178: "... one of the most important general properties of life on our planet is the discreteness of its expressions at different levels. Use of the concept of the 'phene' in various morphophysiological investigations introduces the principle of discreteness into them." While using this approach, the authors fail to note its affinity with one already outmoded in biology. The only difference lies in the fact that this prior methodology was applied to the evolutionary process, while the authors in question have brought it to bear on biological "subjects." If the principle is considered to be universal, it is difficult to understand why the evolutionary process is represented as being exclusively a continuous process when the book also holds it to lead to discrete manifestations on "different levels." This is easily comprehended if one recalls that any biological object, being a closed system (discrete) on the basis of some one criterion, can be open (nondiscrete) on the basis of many other criteria. The book under discussion gives good examples of this (p. 181).

While insisting on the absolute discreteness of the phene and objecting to the "diffuseness" of morphophysiology (p. 178), the authors lose sight of the important fact that it is precisely this "diffuseness," which has permitted detection of the transition phases in the evolutionary process, that has saved evolutionary theory from a one-sided representation of evolution (as an exclusively discrete process), one that might have arisen as a result of the use of genetic concepts. One example is de Vries' theory. Attempts to introduce the "discreteness principle" into morphophysiology (phenetics) have had sad consequences.

Even though they consider their most important task to be the achievement of great clarity in their definitions, the authors have not always been successful in doing so. Thus, they note on p. 181 that: "The lack of fundamental differences in the course of the microevolutionary and macroevolutionary processes enables us to regard them as two aspects of a single evolutionary process." It is impossible to make out from this statement whether we are to consider micro- and macroevolution to be two aspects of the evolutionary process or whether we are to see no fundamental differences between them.

A similar non sequitur is found on p. 134, where the authors assert that the genotype is the "unit of selection," although there are many other places where it is stated that the genotype is coselected, i.e., that the actual selection unit is the phenotype rather than the genotype. The latter assertion does not contradict the commonly held view.

On p. 180 the authors criticize "numerical taxonomy" because it constructs "a systematics of animals and plants that takes no account of their evolutionary origin and relationships." However, it is an established view in centers of numerical taxonomy that the tasks of taxonomy and systematics are not identical, i.e., they are each "indivisible" on the basis of some criteria. Thus, "taxonomy is the theory and practice of the classification of organisms," while "systematics is the science of the diversity of organisms" and entails all the consequences flowing therefrom, i.e., takes into account "evolutionary origin and relationships" [see Mayr, Principles of Zoological Taxonomy, Mir, Moscow (1971), p. 16]. Actually, the definition of a "taxon" proposed by the authors (p. 213) therefore differs materially from that found in Mayr (p. 19).

The authors consequently should have formulated their approach to taxonomy and systematics more clearly, since other opinions have previously been advanced in this regard. Without doing so, they have no moral justification for reducing taxonomy to systematics.

In concluding this brief review of Outlines of Population Theory, it must be noted that, in addition to the above shortcomings (we have not dealt with purely technical errors), the book contains much that is well done and of interest. The most successful part of the book is the formulation of two new problems. On the other hand, the posing of any new problem requires that it be examined very critically, since it begins its official life at this point and the course of its subsequent development cannot but be a matter of concern.

The chapter on population genetics is written out of an extensive knowledge of the subject. This is particularly gratifying, since this topic has been very inadequately covered in the Soviet literature. Especially welcome is the judicious evaluation of the achievements of genetics offered in the authors' discussion of problems relating to the actions of selective factors and the capabilities of classical genetic analysis, although the achievements and possible extension of genetics are overestimated in other chapters.

It would be unfair to fail to note that other sections contain very interesting hypotheses and data, many of which appeared in an earlier book (Timofeev-Resovskii et al., A Brief Outline of the Theory of Evolution [in Russian], Nauka, Moscow, 1969).

Although this attempt at the creation of a theory of populations is far from completely successful (and the authors do not pretend it to be so), the book rather clearly delineates the form it will take. Special mention should be made of the undoubted usefulness of this work as a possible text of the type needed for a number of courses (zoogeography, Darwinism, population genetics, etc.).