Letters

Population Biology

In their flippant reply to Amadon's criticism (*1*) of their article on "Patterns and populations" (*2*), Ehrlich and Holm have shown themselves adept at gamesmanship without, however, deigning to encounter the issue. It is often sound strategy to deflect criticism by charging the critic with emotionality. However, in view of the peremptory manner in which Ehrlich and Holm have presented some rather startling notions, it seems desirable to scrutinize their contentions in greater detail.

The particular framework in which Ehrlich and Holm attempt to develop their ideas on population biology appears to be strongly influenced by the operationalism introduced into physics by Bridgman (*3*). This notion, which is a kind of ultimate development of logical empiricism, has apparently proved of some use in physics in bridging the gap between "paper-and-pencil" theoretical work and laboratory manipulation. However, as Bridgman himself observed (*4*), operationalism is scarcely more than a point of view, not a developed philosophy. Furthermore, not all physicists are in sympathy with the operationalist attitude [for example, Lindsay (*5*)].

At any rate, Ehrlich and Holm seem to be suggesting that the new field of population biology be organized along strictly operationalist lines. One can certainly sympathize with them in their distress at the prevalent misuse of systematic and ecological concepts. Most biologists would not go along with them, however, in summarily dismissing concepts such as "competition," "community," and "species" as having "low information content and little or no operational meaning." In answer, it may be pointed out (i) that words at the level of abstraction of "community" are not necessarily intended to convey specific, detailed information and (ii) that, at least in the opinion of many investigators, the term *species* does have a clear and well-defined operational meaning. As shown in the discussions at a AAAS symposium by Mayr and others (*6*), systematists are not unaware of the difficulties encountered in application of the species concept to certain critical cases.

The species concept seems to be one of the main targets for operationalist criticism, and Ehrlich and Holm go to considerable lengths to suggest a parallel (unjustified, in my opinion) between the species and the Newtonian concept of absolute time. Here, however, as in several other places, they are setting up a straw man by imputing to present-day systematics philosophical concepts (in particular, Platonism) that have been discarded by virtually all leading systematists. As Simpson (*7*) has pointed out, it is in the taxonomic procedures of the operationalists themselves that we find typologically oriented practices!

The operationalist argument against the biological species concept may seem convincing to those who assume an engineering point of view in attacking biological problems. But when the principles of numerical taxonomy [as enumerated by Sneath and Sokal (*8*), for example] are examined critically, most practicing systematists will have numerous reservations about the possibilities of the method. The great advantage of numerical taxonomy (better called computer taxonomy) is that it does achieve the desirable goals of increased objectivity and repeatability. Unfortunately, the delimitation of "phenons" with great mathematical precision is achieved at the price of a high degree of arbitrariness. Phenons may be "rigged" at the proper percentage level to make them approximate natural taxonomic groups, but then, it must be asked, what has been gained in return for all the time and expense of data programming and computer analysis. There would appear to be a real use for computer taxonomy in classifying intractable groups such as the bacteria and in comparing higher categories (genera and above), but I fail to see that it is the panacea for all systematic problems.

The most striking defect in computer taxonomic studies thus far is the priority they give description over experiment. On the basis of Ehrlich's analysis of 13 male butterflies, we are informed that the species concept is of doubtful applicability in animals! Edwards (*9*), who has given this proposition the appraisal it deserves, suggests (facetiously, no doubt) that Ehrlich is attempting to lead students from biology back into museumology. It is extraordinary, in fact, how little regard computer taxonomists seem to have for genetic evidence. They generously permit the use of genetic relationships as characters, but would, for example, presumably allow the degree of chromosome pairing in an interspecific hybrid the same weight as a trivial morphological feature (for example, degree of hairiness). Since virtually no attempt has been made in these computer studies to account for the environmentally affected component of variation, this disregard for genetic evidence seems the more incomprehensible. One would think that Turesson, Clausen, Stebbins, Dobzhansky, and other evolutionists had labored in vain! In my opinion, this Adansonian insistence on equal weighting of all characters (contrary to the experience of most competent systematists) is clung to more out of expedience—that is, for ease of programming data for the digital computer—than from any consideration of sound theoretical basis.

The fact is that Ehrlich and Holm are the most radical contemporary representatives of what we may call the reactionary party in systematics. As pointed out by Gilmour (*10*), who presents a more balanced exposition of this school of thought, there has been, throughout the past century, an undercurrent of objection to Darwinian and neo-Darwinian ideas among biologists with a temperamental antagonism to theoretical and deductive ideas. Philosophically, the numerical taxonomists of the 1960's are very close to the conservative late-Victorian systematists who preferred typological to phylogenetic methods. The proponents of strictly empirical approaches to biology have sometimes played a very useful role in restraining excesses of phylogenetic speculation by those in the Darwinian camp. But the extreme operationalist point of view not only carries with it the dangers of shallowness and superficiality but is fundamentally anti-evolutionist in emphasis, despite assertions to the contrary. I agree with Ehrlich and Holm that "perpetuation of today's theory as dogma will not encourage progress toward more satisfactory explanations of observed phenomena." Unfortunately, in view of their methodological bias and paucity of theoretical principles, it is difficult to see how they are going to be more successful than other biologists in studying the "pattern in which organisms are related in space and time." To judge from the magnitude of operationalist achievements so far, it would seem premature to knell the demise of the biological species concept and to proclaim the approach of a "non-Euclidean" theory of classification. In the words of Rothstein, a hard-boiled operationalist (*11*): "we believe that lack of progress in non-physical disciplines where attempts have been made to introduce operational definitions results from the lack of well-defined laws. . . . Operational definitions . . . are necessary rather than sufficient conditions for progress."

GRADY L. WEBSTER

Department of Biological Sciences, Purdue University, Lafayette, Indiana

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We admit that our thinking, like that of virtually all present-day scientists, has been influenced by the writings of Bridgman. This does not mean that we embrace operationalism as a philosophy of science, for it does not represent a philosophy and was not proposed as such. Our attitude is well summed up by Rothstein: operational definitions are necessary but not sufficient conditions for progress. Much useful theoretical structure in biology (for example, various ideas about the origin of life, the general theory of evolution) is not amenable to direct operational analysis. However, valid concepts which are formally integrated into such a theoretical framework must be verifiable empirically. Such empirical verification requires operational definition. The interesting assessment of operationalism by Lindsay does not seem germane to this discussion. Concepts such as "species," "niche," and "community" have not been used by biologists as abstruse theoretical constructs linkable only indirectly (or perhaps not at all) with observations. It would be entirely fair to say that many biologists are under the impression that species, niches, and communities are *things observed.* If these concepts are to be useful to biologists, their operational definition is a *sine qua non.*

It is obvious to anyone that words such as *community* are acceptable and useful in many contexts (as we discussed with reference to *tundra*). It is when they are used, as they almost inevitably seem to be, as labels for presumptive general units that operational definitions must be formulated. That this is a problem should be clear in view of the prevalent discussions of community "migration" or biome "phylogeny." The problem is no less difficult with respect to "species." There are numerous definitions of biological species in the literature, but none is operational, since they all include the idea of "potential interbreeding" and this cannot, by definition, be tested. Indeed, theoreticians have been unable to establish a satisfactory measure of actual interbreeding, although one might hope such a standard may eventually be devised. Many modern taxonomists "feel" that biological species exist (at least in diploid out-crossing organisms); they take the point of view that the principal difficulty is in finding or delimiting them (although virtually every well-studied case turns out to be "borderline" or "a problem"). The attempt to force all organisms (including apomictic and allopolyploid plants) into the "biological species" is as common as it is indefensible.

The problem of typology has been dealt with in great detail by Sokal (*1*), who points out that it is improper "to attach automatic derogatory implications to the adjective 'typological,' since it is only those aspects of typological procedure which cannot be defended or maintained today that would merit such a connotation." Daly (*2*), in another analysis of the problem, states, "It is now clear that the phyletic approach has perpetuated the most undesirable attributes of classical typology: the need for a fundamental character and the intervention of personal judgment in the event none can be discovered." The typological approach has been employed in biology in many different ways. It is clear that when it forms the basis of a philosophical system seeking to establish the existence of nonmaterial "types" it would have little appeal for the modern biologist. However, a statistical average is a type, but this does not limit its usefulness, make its use old-fashioned, or align the statistician philosophically with Plato.

We must agree with Webster that increased objectivity and repeatability are great advantages of numerical taxonomy. Indeed, a discipline which does not achieve such goals to a reasonable degree does not merit the appellation "science." This, in part, is "what has been gained . . . for all the time and expense of data programming and computer analysis." (We might point out that numerical taxonomic computer programs are available at no charge, and that many major universities make computer time available to faculty members without charge if no funds are available. For many studies the cost of computer time would be much less than $100.)

We must also point out that the techniques of numerical taxonomy hold promise of doing much more. For instance, it seems that developmental questions such as whether or not the system of phenetic relationships among larval beetles is congruent with that among adult beetles will finally be settled. As another example, the study of relationships of individuals (as in the much-maligned pilot study mentioned later) may permit the creation of a "population phenetics" which will add new dimensions to the study of microevolution. Perhaps the most fortunate aspect of numerical taxonomy is that it may open the door to a general taxonomy—one not restricted to classification of organisms but applicable to such diverse things as soils, automobiles, stellar systems, or any other collection of objects one desires to classify on the basis of any set of characteristics.

Webster's statement that phenons "may be 'rigged' at the proper percentage level to make them *approximate natural taxonomic* groups" (our italics) is very revealing. It is only possible to "rig" something when one has a preconceived idea of what it should be rigged to fit. Numerical taxonomists urge that groups be constructed without the use of intuition or of preconceived notions of phylogeny. Once groups are established they may be scrutinized in an attempt to discover the biological reasons for their existence. The basic data of the taxonomist are the similarities of the entities with which he deals. Preconceptions should not be permitted to bias the gathering of these data. At any rate, the phenon concept in numerical taxonomy is a device for avoiding long, meaningless discussions revolving around what status should be given to a group (is it a genus, subgenus, subfamily, and so on?). Phenon level, therefore, has nothing at all to do with the "naturalness" of groups, and the phenon level may be "rigged" as convenience dictates. Indeed, phenons could be established in a classification based on the frequency with which various letters appear in the scientific name of the organism—a system which almost all biologists would consider "unnatural" because of the extreme paucity of biological information that it would contain.

The contention by Webster (and Edwards) that Ehrlich judges the biological species concept on the basis of an analysis of 13 specimens is very difficult to understand. In the paper in question (*3*) all 94 genera of North American butterflies are discussed, as well as information from other animals and plants. The section dealing with the 13 specimens is introduced with the statement, "In order to test the hypothesis that numerical analysis will not cluster individuals by population, a pilot study was undertaken in which the similarities of an array of individual butterflies were evaluated." In other words, this pilot study was undertaken merely to discover whether individuals within a local population were all more similar to each other than they were to any individual from outside that population. As soon as an individual is discovered to be more similar to an individual from another population than to one from its own population the question is answered. Thirteen individuals were ample for a pilot test of this hypothesis, as the addition of more individuals to the study would merely have expanded the *Q*-matrix, not altered any of the values in the original matrix. These individuals were not considered samples from a larger set of items, they were the units being compared.

Weighting of characters has been dealt with extensively in the literature (for example, *1*, *4*), and no logically defensible system of weighting has yet been advanced by the proponents of the idea that some characters are a priori "more important" or "more basic" than others. There is no reason why information from the genetic system cannot be used in numerical comparisons. However, at this stage it must be asked, In what way is degree of chromosome pairing "more important" than degree of hairiness? It is known that, in diverse organisms, the first may be controlled by a single gene (*5*), as may the latter. But inasmuch as single genes, as well as balanced polygenic systems, may affect gross morphological characters we find it hard to see how such evidence may be employed in a system of weighting. Are we to imply from Webster's letter that the "sound theoretical basis" for weighting of characters is the "experience of most competent systematics"?

Few taxonomists (classical or numerical) have attempted to remove the environmental component and deal only with the genetic variation in their material, for obvious practical reasons. Webster seems to feel that taxonomy ideally would deal only with additive genetic variance, but there is some theoretical question as to whether this would be desirable even if it were practical.

In no place do we suggest a " 'non-Euclidean' theory of classification," although the idea may have merit. We have suggested that the present strong interlocking of taxonomy and evolutionary theory may inhibit the development of a "non-Euclidean" theory of evolution. This does not mean that we decry the existence of taxonomy or repudiate the present theory of evolution. We would not, however, wish to be placed in the position of having to affirm a "belief" in evolution.

Today biological evidence seems overwhelmingly in favor of the neo-Darwinist view of evolution. Therefore it is especially important for us continually to re-examine its most fundamental tenets. In our article we wished merely to point out that certain problems might be viewed in different perspective. We had no intention of retroactively supplanting one approach with another, even if that were in some way possible. When it appears that a road is blocked because the cart is before the horse, there are two possible courses of action. One is to blow up the horse and cart. The other is to send an exploring party up a nearby path while the road is being cleared. We wished to suggest the second alternative.

PAUL EHRLICH
RICHARD W. HOLM
Division of Systematic Biology, Stanford University, Stanford, California

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A Grain of Skepticism

"What is really needed is more of that healthy skepticism which generates the key idea . . ." [*Science* **138**, 75 (1962)].

Allow me to apply a germ of skepticism to this statement. At just what point did skepticism generate a key idea in the xenon tetrafluoride synthesis case?

I suspect that Neil Bartlett would report that skepticism as such had nothing to do with it. How was the key idea generated? It would be interesting—and surely it is important—to know.

BURNETT CROSS
170 East Hartsdale Avenue, Hartsdale, New York

. . . one must agree that "the essential ingredient in discovering xenon tetrafluoride was not money or equipment," but one must conclude that an essential ingredient was people—17 of them.

J. W. WETZEL
Hotpoint Division, General Electric Company, Chicago, Illinois

. . . seventeen scientists signed their names to an article that required only "a few hours of effort and a germ of skepticism." I am sure that the salaries for 17 scientists come to a very much greater figure than many elaborate pieces of scientific equipment.

JULIUS H. COMROE, JR.
San Francisco Medical Center, University of California

I suppose that I am not alone in feeling that the editorial "The need for skepticism" points a finger at me, along