

## Numerical Taxonomy: Its Value to Mosquito Systematics

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Nielsen's (1969) article in the last issue of this Newsletter motivated me to write the following comments. It was not because he criticized numerical taxonomy (NT), but rather, in my opinion, he criticized aspects of NT that either a) no longer need to be criticized, or b) are not the fault of the methods of numerical taxonomy but of the people who use them, in this case, Steward (1968). Like Nielsen, I was not impressed with Steward's article when I first read it. But some of our reasons are not the same.

My purpose in the following paragraphs is I) to clarify some misconceptions about NT, and II) to suggest how the methods of NT might be used to enhance mosquito systematics. I write as a systematist, not as a statistician who is interested primarily in the methods for their own sake. As such, I feel that the methods of NT hold sufficient value for systematics to warrant close study of its techniques. Only in this way can we gain the confidence in NT necessary to use it in our research. Most of my published work in NT (e.g., Crovello 1968a, 1969) attempts to estimate its robustness at various stages of the process. My purpose is not to criticize anyone, be they numerical taxonomists or culicidologists. Rather, I wish to clarify some misconceptions about the NT of today and to channel some of the reader's finite resources into the constructive use of NT in mosquito systematics. Presented in terms of a question, the reader's attitude should be, "Can any part of NT help me in any way to obtain further insight into systematics (sensu Simpson 1969)?"

### I. Some Misconceptions

There is a unique NT method - Wrong. The NT text by Sokal and Sneath (1963) is out of date. Although numerous alternative techniques are presented, systematists now can use it only as a starting point into the mushrooming literature on NT. Unfortunately, many practitioners think that NT is only one technique. In one sense it is (compare the definition in Sokal and Sneath 1963:48). But in any operational sense it is not. For example, one technique may standardize characters and another may not; one may produce a phenogram by one method and another may use a different algorithm. Some practitioners who use NT appear to me not to be critical enough of NT when interpreting their results. Conversely, systematists who do not use or study NT at all appear to me to be too critical of NT. I can only agree with Nielsen when he criticizes Steward in his choice of some characters and of character states. Nielsen correctly stated that Steward's description of the state of a character in some species was incomplete, e.g., presence or absence of a white ring on the proboscis. I might have erected two ad hoc classes in Aedes nigromaculis, one with the white ring present and one with it absent. I emphasize that this does not mean formal recognition. Rather, this is one way to take within-species variation into consideration. Clearly, Nielsen's criticism of the handling of the above character is not a criticism of NT, but rather a valid criticism of a particular use of it by a particular systematist.

Steward also used a relatively imprecise method of graphical summary, the phenogram (discussed below). Even the estimates of how well the four phenograms agreed with each other relied only on visual examination. Summary statistics, such as the correlation between each pair of phenograms and between each pair of similarity matrices together with the mean and standard deviation of each matrix would have provided a more accurate comparison of the different analyses.

The methods of NT are phyletic - Wrong. All NT methods are phenetic since they deal with analysis of phenotypic information. They become phyletic for a particular scientist only when he is willing to accept as an axiom that some kind of phenetic relation reflects some kind of phyletic, or more narrowly, some kind of cladistic relation. The essential point is that the user decides whether some method of NT is a reliable phyletic tool. The responsibility lies on the user's shoulders. I use NT for one purpose: to describe the phenotypic pattern of variation among a group of organisms or taxa. I find this useful in my systematic work and in understanding evolutionary phenomena. Mayr (1965), Sokal et al. (1965) and others have distinguished clearly between the purposes of phenetics and phyletics. Most of NT is numerical phenetics (see Wilson, 1968). Only recently have systematists (e.g., Farris 1966, 1968, Throckmorton 1968) become interested primarily in numerical cladistics. A most promising field involves the use of numerical methods on information from such macromolecules as DNA and proteins. I am sure that many readers of Steward's paper and of Mosquito Systematics Newsletter hold that the taxonomic system should reflect phylogeny when possible. If that is your purpose, then you may not consider NT results very useful. Results like Steward's are phenetic results and should not be criticized for not reflecting current ideas of phyletic affinities. I disagree with Nielsen when he says that, "Steward's work clearly demonstrates the fallibility of numerotaxonomic techniques." Rather, his work and Nielsen's comments demonstrate that we must be careful not to make unwarranted phyletic inferences based on NT results. Specifically, inferences about phyletic affinities based on phenetic results may be unwarranted and lead to erroneous conclusions.

There is only one kind of character weighting - Wrong. Character weighting first occurs when certain characters are selected for use in an NT study. Methodologists of NT readily admit this. I use NT, but I would be a poor scientist if I did not use the findings of previous taxonomists who worked on the group to help me to delete those characters that are either too variable, or completely invariant. But the most controversial weighting (equal weighting) occurs in later stages of the NT process. Nielsen is distressed because Steward gave equal weight to the characters, wing length and number of basistyle lobes. But how much more should Steward have weighted the latter than the former; two times, ten times, or two hundred times? Two solutions are obvious but perhaps not desirable. The first is to weight them as the inverse of their variance within each species. This is similar to Nielsen's definition of reliability. But such a technique is more germane to discrimination among established taxa rather than in defining taxa. The second solution is to use only characters that reflect phylogeny. But this may not be germane to numerical phenetics. Also, it presumes that the systematist can identify the relative phyletic importance of characters. I was not upset with Steward's choice of characters (I was upset by his choice of character states) because I considered his report a phenetic, not phyletic study.

There is an absolute standard in taxonomy - Wrong. In early NT work, much time and print were devoted to comparing NT results with the taxonomic results obtained by non-numerical techniques. Today, most workers realize that the "true" phenetic relationships among taxospecies, say, are unknown and perhaps unknowable. As a result, given several different suggested taxonomic hierarchies, some based on NT and some based on conventional taxonomic methods, we cannot say that A is better than B and C. Rather, all we can say is that A is more like C than B is, or some similar statement, in attempting to depict phenetic relationships. One guide that seems reasonable is the assumption that if one has two phenograms, the one based on more characters may at times be a better estimate of phenetic relationships. Steward used his Figure 1 as a standard. But he gave no information on how he estimated the relative lengths along the abscissa, except in a general way.

Phenograms give an accurate summary of phenetic relationships - Wrong. Serious distortion is caused by the reduction of the number of dimensions necessary to depict phenetic relations accurately down to the one meaningful dimension in a phenogram. For example, assume that we have information on 20 species for 50 characters. I could plot the phenetic positions of the 20 species with respect to the first two characters by constructing a regular 2-dimensional scatter diagram. But this uses information from only 2 of the 50 characters for which I have data. We cannot plot it, but we can imagine a 50-dimensional scatter diagram that would use all of the available information. Just as a 2-dimensional scatter diagram cannot depict precisely the relations in the 50-dimensional space, neither can the phenogram. Hence, systematists who decide to try NT should not accept the resulting phenogram as an accurate reflection of phenetic, let alone phyletic relations. A much better summarization technique involves the simultaneous use of a method like principal components analysis and a network that indicates by lines who is the nearest neighbor. The lesson to be learned from this discussion is that NT can be used by anyone who has access to the proper computer programs. But superficial use of NT, such as the study of one or two phenograms, may not be very useful to the systematist. Furthermore, given our experience with phenograms, Steward's are relatively poor summaries of the similarity matrix, even for a phenogram. Steward acknowledged this himself when he wrote that the cophenetic correlation coefficients were all less than 0.750. No one should consider Figures 2-4 as anything but a rough approximation.

NT is just another source of new data - Wrong. Usually NT adds no new data to the character by OTU (e.g., species) table of taxonomy. Rather, regardless of the kinds of data in the table, it provides a repeatable and efficient set of techniques for its analysis. In a way NT is like mathematics in general. It has no real world content. For example,  $Y = a + bX$ , the formula for linear regression, has no content until we assign values to X and Y, such as hours since hatch and larval body length. NT can process the data that we systematists are accumulating at a high rate. As such it will not supplement morphological, chemical, or other data; it will enhance their value.

## II. NT Can Enhance Mosquito Systematics

Given the above comments, let me suggest some of the ways that NT can be of value in taxonomy proper and in systematics (sensu Simpson, 1961) in general.

NT forces us to be complete when we accumulate data - Simply because the data are processed by a computer that has no knowledge about mosquitoes except that read in, we are compelled to provide it with as complete a character by species table as possible. It simply demands that we be the good taxonomists we claim to be.

NT is an efficient summarizing technique - The ability to summarize phenetic relationships among species in an efficient manner (graphically and statistically) is perhaps the most important contribution of NT. For example, assume that a young culicidologist knows nothing about Canadian species of Aedes. Given a superficial examination of representative specimens of each species and a series of NT results (phenograms and principal component summaries), he can gain insight into the salient patterns of variation presented by Canadian Aedes. While we would not wish to base a formal taxonomic decision on male characters only, or chemical characters only, knowledge of how the species compare in each of these character sets would be useful to a more complete understanding of the phenetic pattern of variation among these taxa. NT can provide these summaries in a most efficient manner.

NT can help taxonomists prepare keys and maps - Once taxa have been agreed on, NT and related techniques can search the original set of character by species data efficiently and find that subset of characters that should best discriminate between the taxa. Similarly, if locality data were recorded, distribution maps can be generated quickly. Much work along these lines is being done in connection with the Flora North America project.

NT can serve to generate evolutionary hypotheses - Although the taxonomist who wants to use NT directly to make formal taxonomic decisions is upset when analyses based on different characters give different results, the systematist interested in evolution can study how they differ and ask why. Have they evolved adaptations to different hosts, to different breeding sites, etc.? Along these same lines, one can take the same character by taxon tables and the same computer programs and cluster characters to try to delimit adaptive character clusters that have been selected for in the taxa under study (Crovello 1968b).

NT can be a stimulus to the creation of an automated Mosquito Data Bank - One important byproduct of any large NT study is a deck of punched cards that is available to other mosquito workers for further analysis by itself, or in connection with data to be gathered in the future. I believe that we are at the beginning of a period that will allow us to use the data present in articles, monographs and faunas. It has always been there, but its efficient use has not been possible.

Concluding Remarks

I have discussed some misconceptions about NT and some of its uses in systematics. Neither list has been exhaustive. My only purpose has been to motivate the reader to examine his own research interests and (ignoring extreme claims by some that it is a taxonomic panacea, and ignoring published examples of its misuse) ask whether some aspects of NT can be of value. On rereading Steward's article, especially the opening and closing paragraphs, I think that he had the right attitude. He admitted that his methods were not the best, but wanted to get a preliminary idea of how NT might be used. Unfortunately, when people see phenograms formally published in a quality journal, they are hard pressed to look at it as a progress report. My own feeling is that Mosquito Systematics Newsletter would have been a better place to publish Steward's article. Then Nielsen and others, including numerical taxonomists, could have provided constructive criticism on the methodology. Steward then could have carried out an improved analysis that would have benefited mosquito systematics further.

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