Phenetics and Numerical Taxonomy Applied to Systematic Nematology[1]

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Numerical taxonomy and the phenetic approach to classification have aroused considerable interest and debate among taxonomists in recent years. It will not be possible here to examine the controversy in any depth, but a few comments on certain aspects of theory and methodology may be helpful in considering their relevance to systematic nematology. References to pertinent articles dealing with these and additional aspects are included in the bibliography (8, 12, 13, 14, 16, 19, 23, 27, 33, 50, 51, 52, 53).

PHENETICS

The phenetic approach to the classification of a set of organisms or objects involves the establishment of inter-object similarities based on all available data from the objects, with resultant groupings purposely left unmodified by speculation on their evolutionary history. Essentially, a phenetic study attempts to recognize groups based on data, rather than on inferences from data. The desired product of a phenetic study is a "natural" classification (16), a set of groupings based on a maximum of shared characters. Such classifications are generally assumed to possess both a maximum information content and a higher predictability than classifications based on fewer, heavily-weighted characters deemed to have evolutionary significance, although there are reasons for suggesting that this assumption need not always hold true, as discussed below.

The phenetic approach is nothing new; taxonomists have been processing their material phenetically for centuries, by intuitively grouping together individuals sharing a majority of characteristics in common. The congruence between many of the newer classifications obtained by computerized methods with earlier classifications obtained conventionally is therefore not surprising, as phenetics is a major component of most orthodox classifications. Since the time of Darwin, however, it has been considered desirable to describe the results of biological classifications in an evolutionary context.

In contrast to cladistic methods that attempt to classify on the basis of presumed common ancestry (regardless of phenetic similarity or dissimilarity) (9, 24, 26), and phyletic ("evolutionary") approaches that combine a vaguely-defined mixture of phe-

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netics and cladistics (32), phenetics is a relatively straightforward, "here-and-now" sort of approach aimed at determining present-day similarities, regardless of how they might have come about. The fact that the organisms to be classified are the products of a process of organic evolution is certainly of interest, but the *fact* of evolution's occurrence need be neither pertinent nor useful in the determination of phenetic similarities (2). Evolution is without argument a central, unifying concept of biology. However, although it is true that a knowledge of evolutionary processes and pathways can be gained through analysis of phenetic data, it is also true that the actual course followed by evolution will be known with certainty for a vanishingly small number of biological groups to be classified; and this statement is particularly true for the Nematoda. The unravelling of possible or probable evolutionary pathways in this context is a stimulating intellectual exercise, but it can be little more than that. A classification that reflects presumed evolutionary pathways is a theory (31), but a theory that is not testable other than in terms of itself (2). There is no observer of the entire phylogeny of a group to whom we can turn and say, "Does our classification correctly express the phylogeny of this group?". Accordingly, even with a moderately complete fossil record, any evolutionary classification is based on speculation from phenetic data, and cannot be objectively confirmed (13). We may be able to predict that additional, as yet undiscovered, taxa will fit into the categories that we have erected, and that additional characters will be found to show trends concordant with characters used previously. However, the fact that such (phenetically) agreeable taxa and characters may indeed be found proves nothing about the congruence of the classification with the actual phylogeny, although it may indicate that the groupings recognized are natural, phenetic assemblages.

To a person engaged in a phenetic study, the fact that a character may be present in three recognizable character states, A, B and C, is certainly of interest, and his aim will be to group together those objects with identical character states. The fact that state A might be considered "primitive" or "ancestral" or "plesiomorphic" by a phyletic worker (and the same state very likely "specialized" or "derived" or "apomorphic" by another) is a consideration outside the defined scope of a phenetic taxonomy. Despite the fact that many phenetic workers are interested in aspects of evolution as they pertain to areas outside of taxonomy, it has been suggested that pheneticists are opposed to inferences on evolutionary processes because of their refusal to attempt to classify in an evolutionary context (30). This criticism is analogous to saying that a man is anti-water because he drinks water, but refuses to try to walk on it!

NUMERICAL TAXONOMY

Numerical taxonomic studies attempt to recognize similarities and establish classifications by means of operationally-defined, numerically-oriented procedures (56). Most numerical studies are purely phenetic, although some attempts have been made to carry out phyletic studies operationally and numerically (9, 10, 22, 29, 58, 60, 61).

Some of the most bitter disagreements in the history of systematic biology have accompanied the introduction and application of numerical taxonomy (NT), as recent issues of pertinent journals such as *Systematic Zoology* and *Taxon* will witness. Heralded as a panacea by its proponents, NT has been condemned as an abomination by its critics. It appears likely that both sides have an element of truth. There is no doubt that many existing, conventionally-derived taxonomies have a significant content of valuable information, and will not be swept away by the application of numerical approaches. At the same time, there are ways in which NT can considerably clarify taxonomic situations muddled by conflicting phyletic opinions based on different, heavily-weighted character complexes, as well as by variations in descriptive technique. In addition, NT offers a variety of stimulating, new ways of attacking systematic problems and of visualizing their results.

In view of the controversy surrounding NT, its admitted drawbacks in some areas, and the fact that the field is still in a considerable state of flux, a reasonable question for a nematode taxonomist to ask with reference to NT is: "Why bother?"; and there is no easy answer to this question. There are both theoretical and practical objections, as well as advantages, to the undertaking of a phenetic, numerical study, and the potential worker should be aware of these before committing himself.

THEORETICAL CONSIDERATIONS: On the theoretical level, NT has been roundly criticized by respected workers with considerable taxonomic experience (6, 30, 45, 47, 48), and a prospective numerical worker should be aware that he is risking "an excursion into futility" (46). However, a careful reading will show that the majority of such criticisms can be consigned to three categories: the semantic, the emotional, and the double-edged. Semantic quibbling and emotional, dogmatic outbursts against the use of computers and the intrusion of operational, mathematically-oriented procedures into the "art" of taxonomy are sometimes amusing and frequently frustrating, but certainly do little to advance the cause of systematics; Gilmartin (23) discusses this in some detail. In addition, many criticisms of NT, though valid, are as much or more applicable to conventional taxonomy. As an example of a double-edged criticism, NT has been condemned (32) for not being able to separate phena (sample[s] of phenotypically similar specimens; or, more usually, groups recognized in a phenetic study) from taxa ("taxonomic group[s] sufficiently distinct to be worthy of being distinguished by name and to be ranked in a definite category"); and this is quite true. The fact that several individuals form a distinctive, phenetic group in a numerical study provides few clues as to whether or not the group is an intraspecific population, a species, a genus, etc. Such a decision must be left to the taxonomist carrying out the study. This weakness would seem a formidable deficit of numerical phenetics; yet is the conventional taxonomist in any better position? In fact, he is not. In recognizing groups above and below the species level, the conventional taxonomist must rely predominantly (or entirely) on phenetic data, usually morphologic; at the species level the conventional taxonomist may have recourse to the biological species concept, if he can apply it to the preserved material that serves as the basis of classificatory conclusions in most groups of organisms (e.g., Nematoda), but in most cases he finds himself in the same position as a pheneticist. In a way he may be even worse off, since he is very likely recognizing his groups phenetically, but non-operationally, and while claiming to be using unspecified, evolutionary criteria.

Nevertheless, it is quite true that a methodology as much in its infancy as NT has flaws, and a prospective user should not expect to receive the final answers to his problems along with output from the computer. Sometimes problems only begin at this stage!

PRACTICAL CONSIDERATIONS: If one can overcome his qualms about the theoretical bases of NT, additional, practical hurdles lie ahead. First and foremost, the methods of

NT are time-consuming. Several conventional studies can usually be done in the interval it takes to carry out a comparable numerical study. There are indications that numerical studies are more repeatable (36), but again this advantage must be weighed against the time element. Progress toward optical scanning is encouraging (44, 55), but in the absence of such equipment much effort must be expended in searching for characters, listing them, and in the recording and punching of data. On the other hand, the time spent defining and searching for characters can be most rewarding. It is only human nature to seize on the most obvious and reinforcing characters when assessing relationships, but by so doing one may unconsciously overlook more cryptic sources of information that could provide entirely new insights into taxonomic structure. This, of course, is a major advantage to an approach that both allows and forces one to look for as many characters as possible. In addition, the preparation of tables and character lists provides a basis on which a colleague can constructively criticise one's results, a basis usually lacking in conventional approaches.

An additional hurdle is the problem of where and how to process data. There are several alternatives: one can write his own programs, convert programs obtained elsewhere to local facilities, or take or send data to a center of NT activity where up-to-date, sophisticated program systems are available. From personal experience, the last alternative is by far the most preferable, unless one has considerable programming experience or enjoys working with computers.

METHODOLOGY: Assuming that all worries about theory and practicality have been laid to rest, the next obvious question to be asked by our novice NT worker is, of course: "How does one do a numerical taxonomic study?".

The basic steps involved in carrying out an introductory study have been documented elsewhere (56), but can be summarized here briefly as: the choice of a group of objects (OTUs: Operational Taxonomic Units) to be classified; the selection of characters that differ among the OTUs and cannot be further subdivided logically; the standardization of characters to assure equal character weighting; the computation of similarity coefficients between OTUs; and, finally, the grouping together of OTUs with high mutual similarities.

The group to be classified should be rather small in an initial study. Workers vary in the speed with which they grasp the fundamentals, but fewer OTUs tend to reduce any possible confusion factor. For an initial study, a group of perhaps ten to twenty OTUs seems reasonable. Additional reasons for restricting the number of OTUs are given below.

The selection of characters and the number of characters to use in a numerical study are matters still under debate. It is an axiom of conventional taxonomy that some characters are more important than others; unfortunately, the reasons why this should be so are rarely explained in any detail, and operational methods for rejecting less important characters are rare. Initial recommendations for phenetic numerical studies assumed, in the absence of logically defensible schemes for weighting, that all characters are of equal value in recognizing relationships; therefore, all characters should contribute equally in the computation of similarities. Subsequent work (35, 40, 57) has shown that some characters do seem to contribute less information than others: they may vary randomly, show high variability, be difficult to measure or completely correlated with other characters, etc. Exclusion of some characters in favor of others can be justified in a numerical study, but the worker should make extremely clear the grounds on which such exclusions took place; for example, Bird and Mai (5) recommended the omission of characters shown to have high coefficients of variation and Farris (20) suggested a method of assigning lower weight to such characters. Of questionable value are studies such as that of Kendrick and Weresub (28), who began an NT with both a large number of characters and firm convictions as to what their final groupings should be. When many characters did not produce the desired groupings, the number of characters was gradually reduced until only a selected few remained; these, fortuitously, gave exactly the results desired: a classification based on a few, heavily-weighted characters. The circularity involved in such a study is evident.

Some workers have introduced logical, operational schemes for character weighting (20, 29, 38). In the absence of such schemes, however, it remains an axiom of NT that characters should contribute equally. For this reason, character standardization is generally recommended as an integral part of a numerical study.

It is difficult to recommend how many characters to use in a numerical study, although attempts have been made to do this (56). In groups with reduced morphology one may be hard pressed to find a dozen characters, while in others one may be literally overwhelmed. In time it may be possible to issue recommendations based on the group to be studied, the number of OTUs and the kinds and mix of available characters (quantitative *vs.* qualitative). It may be possible to predict the number of characters needed by means of sampling experiments, such as those carried out by Rohlf (41), in which random samples of characters might be analysed to indicate how many additional characters would be needed to reach an information plateau. On the basis of at least three studies to date (21, 34, 41), a certain amount of leeway exists with regard to character sampling, as well as errors in recognizing homologies and in the recording of data. Put slightly differently, it would appear that the basic data structure will tend to come through once a certain minimum number of characters is attained; this structure will tend to be maintained as additional characters are added, but may be affected somewhat adversely by the addition of characters showing random trends.

A computed table of OTU × OTU similarity coefficients is the closest approximation to the "truth" obtainable in an introductory numerical study, in that this table represents similarities between all possible combinations of OTUs computed on the basis of all included characters. Unfortunately, a table of numbers can be rather difficult to interpret, and this difficulty tends to be compounded drastically as the number of OTUs increases. For this reason various techniques such as graphic and cluster analysis have been devised to aid in grouping together those OTUs with high mutual similarities.

Graphic analysis (7, 34, 62) places the OTUs on graphs, in positions relative to their similarity values, to produce a 2-dimensional picture of relationships. Cluster analysis, which is also a device for portraying relationships in two dimensions, generally starts by grouping OTUs with mutually highest similarities, and proceeds from there to add OTUs with somewhat lower similarity values. The manner in which unclustered OTUs are added to existing pairs and groups varies according to the method. The results of cluster analysis are generally presented in the form of a dendrogram of phenetic relationships or phenogram (30, 52). Unfortunately, phenograms are prey to numerous ills, including their resemblance to conventional phyletic trees, and their tendency to accumulate distortions as one progresses from tips to base (43). Methods have been developed to aid in detecting phenogram distortions (34, 54), but their application can be time-consuming and they do not always work as well as they might (15, 37). Suffice it to say that the relationships pictured in a phenogram should not be accepted at face value, but should be analysed carefully for their correspondence with relationships present in the original matrix of similarity values.

Additional methods of portraying OTU relationships have been suggested. Barraclough and Blackith (1) computed discriminant functions and generalized distances among ten groups of eelworms (*Ditylenchus*), including males and females of *D. myceliophagus* Goodey and larvae, males and females of three races of *D. dipsaci* (Kühn). Relationships were illustrated in the form of a 2-dimensional projection of a 3-dimensional model.

Quite recently, workers such as Rohlf (42, 43), Hendrickson and Sokal (25) and Oxnard (39) have applied rather sophisticated techniques of principal components, centroid factor analysis, and canonical analysis to the study of taxonomic relationships. Their methods produce various kinds of output, including 3-dimensional models, and represent some of the most intriguing approaches to taxonomy ever devised. Rohlf (43) has shown that while cluster analysis of similarity values provides a clearer picture of relationships at high levels of similarity, i.e., *within* phenetic groups, factor analysis and related techniques provide a better picture of relationships at lower levels of similarity, i.e., *between* phenetic groups. Accordingly, the application of both approaches can provide complementary results and a more balanced analysis of taxonomic structure than either method applied by itself.

SOME RECENT APPLICATIONS

Few numerical taxonomic studies have been attempted on helminths, so it would be unwise to draw too many conclusions from the existing literature. However, results obtained so far seem encouraging.

Ukoli (59) used NT to analyse morphological relationships among fifteen species of the genus *Apharyngostrigea* Ciurea, 1927, and found several distinct groups. Pertinent changes in nomenclature were proposed as a result.

Bird (3, 4) and Bird and Mai (5) obtained satisfactory results from numerical, phenetic studies of twenty-four species in the genus *Trichodorus* Cobb, 1913, as well as a detailed analysis of various populations, geographic and ecologic, within *T. christiei* Allen, 1957. In order to obtain a good phenetic sample of a taxon, they recommended wide sampling of living populations from different geographic and ecologic situations, with analysis of morphometric and allometric characters for degree of variation.

Moss and Webster (37) in a preliminary study of a group of selected strongylates examined representatives of seven species in five nominate genera. Two studies were carried out, involving individual character readings (27 OTUs) and average character readings (7 OTUs). Distance and correlation coefficients gave very similar results in these studies. Cluster analysis produced phenograms that were extremely accurate in their presentation of results initially present in the similarity tables, and which showed exceptionally good definition of groups. Our groupings tended generally to be close to those recognized earlier in conventional studies by Dougherty (17, 18), and the implications of this are discussed elsewhere (37).

Findings of more general interest arising from the strongylate study included further evidence for the inapplicability of the phenon

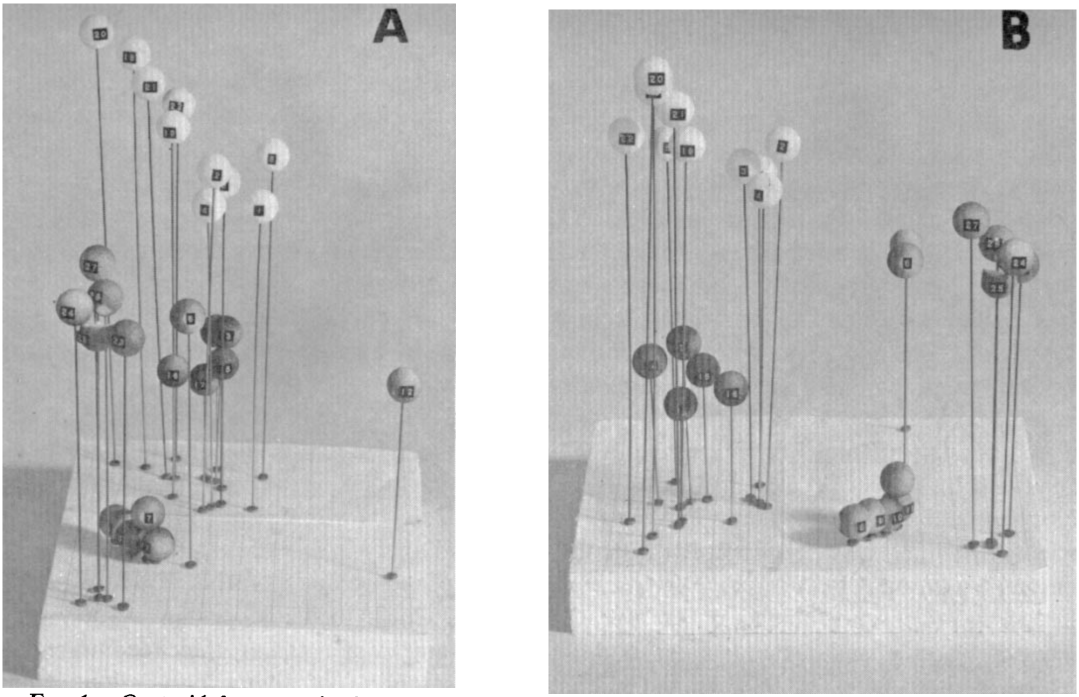

FIG. 1. Centroid factor projection model of 27-OTU strongylate study. **A.** viewed along first factor axis; **B.** viewed along second factor axis. OTU number codes as follows; 1–5 = *Crenosoma canadensis*; 6 = *Metastrongylus pudendotectus*; 7–11 = *Skrjabingylus magnus*; 12 = *Pneumostrongylus tenuis*; 13–17 = *Dictyocaulus viviparous*; 18–22 = *C. vulpis*; 23–27 = *M. apri.*

line (a line drawn at right angles across a phenogram for the purpose of recognizing taxa); and indications of the suitability of using either individual character readings or average character values for each OTU. The problem of whether to recognize an aberrant OTU as a distinct taxon, as opposed to placing the OTU with its closest phenetic relative, was encountered and discussed, but not solved, indicating a need for more operational expressions of relatedness in taxonomy.

Further work on the strongylate material, using centroid factor analysis and the projection technique of Rohlf (42) on 27 OTUs resulted in the construction of a 3-dimensional model (Fig. 1) and stereogram (Fig. 2). Groupings shown in these figures are most closely comparable to those of the distance phenogram obtained by Moss and Webster (37); the correlation between the original set of distances on which our phenogram was based, and the set of distances computed directly from the model of the OTUs in 3-space was 0.863. It is interesting to note that three dimensions were needed to separate the *Crenosoma* replicates from those of *Dictyocaulus*, and the *Metastrongylus* replicates from those of *Skrjabingylus*. The meanings assignable to the three factor dimensions are uncertain, but it is unlikely that any dimension represents size, as in a similar study (34); all measurements in the present study were expressed as ratios (37).

If formal groupings were to be assigned as a result of the centroid study, our conclusions would likely differ from those of Dougherty (17, 18), Skrjabin *et al.* (49) and Chabaud (11). The close approximation of *Dictyocaulus* and *Crenosoma* in the factor projection model is certainly not con-

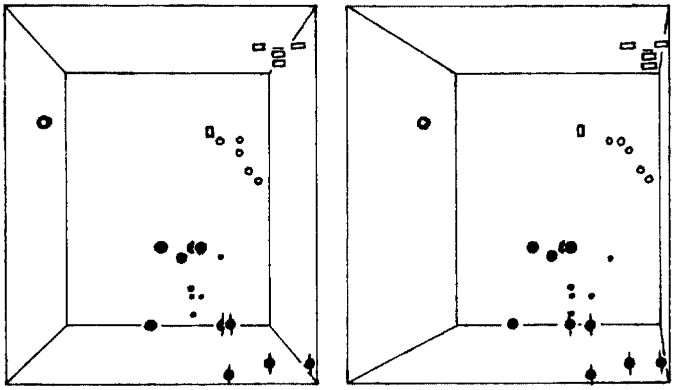

FIG. 2. Stereodiagram of relationships obtained by centroid factor analysis (Rholf's method). The first factor axis runs across the width of the page, the second from top to bottom. The third axis is at right angles to the plane of the page and the positions of the 27 OTUs along this axis become visible when the two views are superimposed by means of a stereo viewer. OTUs coded as follows: small, solid dots = *Dictyocaulus viviparous*; large, solid circles = *Crenosoma canadensis*; large, solid circles with vertical bars = *C. vulpis*; small, open circles = *Skrjabingylus magnus*; large, open circle = *Pneumostrongylus tenuis*; rectangles with longer axis running across page = *Metastrongylus apri*; rectangle with longer axis running length of page = *M. pudendotectus.*

sistent with the separation of *Dictyocaulus* into a superfamily distinct from that containing the remaining genera (11, 49), nor is the separation of *Pneumostrongylus* and *Metastrongylus* and the close approximation of the latter genus and *Skrjabingylus* in our study consistent with the recognition of the families Metastrongylidae (containing *Pneumostrongylus* and *Metastrongylus*) and Trichostrongylidae (including *Crenosoma, Dictyocaulus* and *Skrjabingylus*) (17, 18). However, in view of the fact that ours was a preliminary study with limited representation, intended primarily to test the applicability of the method to systematic nematology, we are not at this time overly concerned with the congruence, or lack of congruence, of our results with existing systems. For this reason we have likewise refrained from the formal recognition of taxonomic groups. It is our hope to carry out an expanded strongylate study, using representatives of additional nominate taxa, in order to obtain a broader picture of relationships. For example, it is possible that the incorporation of additional, more "typical" trichostrongylid material might appreciably affect the degree of relationship between *Dictyocaulus* and *Crenosoma* shown in the present study (cf. similar results in Moss, 35).

We believe that the discreteness of the groupings recognized by numerical approaches in this and our earlier study (37) is quite promising in terms of subsequent characterization of taxonomic units within the Nematoda.

CONCLUSION

It should be clear from the above that there are no uncluttered avenues of escape from taxonomic problems via numerical, phenetic approaches; their use requires a knowledge of where the problems lie, an intelligent input of data, and a careful analysis of results. The few nematological studies attempted so far have been encouraging, but have also raised questions pertinent to theory and methodology; this is, of course, as it should be. A worker with experience in conventional taxonomy will certainly find it extremely stimulating to examine his views on the basis and practice of classification in the light of numerical phenetics. Definite benefits can accrue from attempting a numerical study and, as Gilmartin has noted (23), the worker who evaluates a method from the viewpoint of a participant can bring more of value with his comments than one who merely criticizes from the sidelines.

Regardless of whether or not phenetics and numerical taxonomy prove to be the wave of the future, they have certainly contributed greatly in recent years to a belated verbalization of taxonomic principles and methodology, and should continue to generate interesting hypotheses for testing in the future.

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