A Critique on Numerical Taxonomy

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In a recent issue of Systematic Zoology (1968, 17:426-431. Numerical Classification of the Canadian Species of the Genus Aedes), C. C. Steward attempted to classify the 42 species of Canadian Aedes by numerotaxonomic techniques. A total of 82 alternative characters were used, 30 adult female and male, 14 male terminalia and 38 larval. Seventy-six characters were morphological, three were ecological, two were physiological and one geographical. Steward stated "I believe they will be accepted by most specialists as good and reliable." Unfortunately, Dr. Steward's untimely and regrettable death in September, 1968, makes it impossible for him to defend this statement. It is highly doubtful that many specialists familiar with these species will agree with the reliability of many of the characters used. At least 16 of the adult, 2 of the male terminalia and 20 of the larvae are unreliable. That is, the character and its alternative can both be found in the same species. For example, the first adult character listed is ... Proboscis with white ring +; white ring absent -. One of the Canadian Aedes with a white ring on the proboscis is nigromaculis, a species in which a significant number of individuals lack this ring. Three alternative characters on comb scale number are used, comb scales 1-12 or not, 13-30 or not, more than 31 or not. This is a particularly unfortunate choice of characters. At least 28 of the 42 species of Canadian Aedes have comb scale ranges which overlap two of these characters and one species, fitchii, has a range of 10-36 which overlaps all three.

After computerizing the results by the Sokal and Sneath matching coefficients method Steward prepared dendrograms of the adults only, larvae only and adults plus larvae and compared these with a dendrogram of the "natural" classification of Canadian Aedes based on Edwards' 1932 classification of adults. He then concluded that his results from adults only or adults and larvae showed good agreement with Edwards' conclusions but that results from larvae only were not satisfactorily correlated. It is not the intent of this review to judge Steward right or wrong on the basis of his similarities and differences with Edwards' classification. I do not know of any mosquito systematist who is satisfied with Edwards' classification or for that matter with any system thus far proposed. What I would like to do is point out some of the highly questionable conclusions reached by Steward on the basis of the equal weighting of 82 characters, of which almost one-half are unreliable. There are other more reliable characters that could have been used and which had they been used would have significantly changed some of Steward's results. The discrepencies and argumentative points on the placement of species on Steward's dendrograms are too numerous to be considered completely here. I will consider some which should be especially obvious to workers familiar with these species.

Steward's results indicate that 4 members of the punctor complex, aboriginis, hexodontus, punctor and punctodes are so similar that they deserve no more than subspecific rank on the basis of adult characters. It is true that these species are closely related and in existing keys are separated most reliably by larval differences, but there are good adult, morphological and behavioral characters which separate them (none listed by Steward) and each species is sympatric with one or more of the others in a significant portion of its range.

Some of the species wich appear to be the most improperly placed include niphadopsis, nigripes, flavescens and trichurus. I will consider only the first here. Aedes niphadopsis is a common dark-legged univoltine species in the Great Basin of the western United States, but is rare elsewhere and has only recently been collected in western Canada. It is a species we have studied in detail in Utah. It belongs to the communis group and appears to be most closely allied to cataphylla, a species it closely resembles in the adult female and male terminalia and in many larval characters. The two species also have some significant ecological and behavioral similarities. Steward in his adult dendrogram places it next to excrucians (a white-legged species, usually assigned to the stimulans group) but stated it could just as well be placed alongside of sticticus (a dark-legged species usually assigned to the communis group); however, in his adults plus larvae dendrogram he places it alongside of campestris (dorsalis group) and trivittatus (scapularis group) and in the larvae only dendrogram he places it next to abserratus (punctor subgroup). His treatment of niphadopsis strongly suggests a misidentification of material or a serious lack of knowledge concerning the taxonomic characteristics of this species.

Aedes niphadopsis seems to be an enigma to numerical taxonomists. Rohlf in his numerical taxonomic study of Aedes classification (1963, Ann. Ent. Soc. Amer., 56:798-804) placed niphadopsis in a combined dorsalis and stimulans group . Having done a considerable amount of research on the taxonomy and biology of most of the species in the dorsalis and stimulans groups I can think of few Ochlerotatus species more unlike the species in these two groups than is niphadopsis.

Steward's work clearly demonstrates the fallibility of numero-taxonomic techniques. The work thus far done on mosquitoes has been characterized by many inaccurate conclusions concerning natural affinities. This has been due primarily to the equal weighting of all characters and the use of an insufficient number of reliable characters. The bias of numerical taxonomists against the weighting of characters is difficult to understand when one considers that most of the characters they have been using are the result of a careful selection or rejection by classical taxonomists and therefore would not require a priori weighting. Sound taxonomy has been repeatedly demonstrated to be feasible only when an investigator is thoroughly familiar with the characters of the group studied and of their phylogenetic significance.

For example, a systematist familiar with mosquitoes would certainly realize that Steward's character ... wing length greater than 5mm or less than 5mm ... is less indicative of natural affinities than ... basistyle with two lobes or with one or none .... Yet both characters are counted equally in Steward's results.

All mosquito systematists certainly agree on the need for more characters to help in understanding natural relationships.

But we must face up to the fact that despite the great amount of work that has been done on mosquitoes we do not yet have enough information to establish a really satisfactory natural classification. We all recognize a knowledge of the distribution of genera, subgenera and species is vital if we are to determine natural relationships, migration patterns and rates of evolution. Yet we actually suffer from extreme deficiencies in our knowledge of the distribution of species and subgenera on a world wide basis, and even in as restricted and studied an area as the United States we have important gaps in our knowledge of species distribution. Mosquitoes apparently originated in the tropics, and yet here is where some of our greatest gaps occur and where many undescribed species exist. That is why some of the most vitally important mosquito studies at the present time are such long term projects as J. N. Belkin's study on the Mosquitoes of Middle America and the Southeast Asia Mosquito Project under the direction of Dr. De Meillon. Dr. Belkin estimates, probably conservatively, that the Middle America project will take 10-15 years to complete.

There are many other sources of phylogenetically valuable characters that have been inadequately studied. The eggs of mosquitoes represent a stage that has been comparatively neglected even though Craig and Horsfall more than 10 years ago pointed out Aedine mosquito eggs as being of phylogenetic importance (1958, Proc. 10th Int. Congr. Ent., 1956, 3:853-857). Fortunately, there appears to be a renewed interest in eggs and two significant papers demonstrating the potential of eggs in establishing species relationships have appeared during the last two years (Myers, 1967, Can. Ent., 99:795-806 and Kalpage and Brust, 1968, Can. Jour. Zool., 46:699-718). The internal anatomy of mosquitoes has been shamefully ignored. Landa (1959, Proc. 15th Int. Congr. Zool. 54:1-2) has demonstrated that the internal anatomy of the excretory, tracheal, nervous and digestive systems in mayflies yield highly significant data of phylogenetic value. In our studies of ovarian cycles in mosquitoes my students and I have noted some distinctive generic and subgeneric differences in the structure of the ovarioles. Mosquitoes certainly are worthy of detailed studies of the internal systems. There is a need for more studies on chromosomes, larval mouth parts, physiological, behavioral traits, etc. Doubtless, each of us could think of additional possibilities. Numerical taxonomy may someday be a useful supplementary source of information. However, numerical taxonomists are likely to contribute significantly to an understanding of mosquito relationships only when they are willing to use the accumulated knowledge available for properly selecting and weighting characters and are aware of the fact pointed out by Throckmorton (1968, Systematic Zool., 17:355-387) that common possession of plesiomorphic (primitive) traits is of a different magnitude of significance than common possession of apomorphic (specialized) characters in grouping related species together.