Similarity *versus* Relationship In *Drosophila*

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Introduction

When we consider numerical and orthodox taxonomies, it is immediately apparent that the seriousness of the differences between them, and the possibilities for their mutual agreement, depend finally on the ultimate goals of taxonomy. These goals are by no means as well established as one might think from reading the declarations of leading spokesmen (Simpson, 1961; Mayr, Linsley, and Usinger, 1953) for orthodoxy. If there were unanimous agreement on the aims of taxonomy, the applicability of any proposed method would be readily apparent, or at least unequivocally testable, in which case there would be no controversy over methods. Basically, the real problem that taxonomy faces is that of defining its aims. I would like to defer the problem of aims for later consideration, however, and to devote attention now to various aspects of method. It is at this level that the primary attributes of numerical taxonomy are most apparent, and it is here that orthodox taxonomy is said to be conspicuously deficient (Sokal and Sneath, 1963).

To some degree, the bitterness of the controversy between numerical and orthodox taxonomists has resulted from opposing views as to the aims of taxonomy. Another large part of the disagreement has arisen from a confusion of the issues involved. Up to the present, the lines of argument seem mostly to have been drawn as if it were necessary to choose *between* methods, as if we must have orthodox methods *or* numerical methods. No areas of mutual assistance have been recognized or sought. In reality, we are not faced with the problem of choosing one methodology over the other. We have instead to ascertain the present state of our science and hence to determine the areas open to improvement. In doing this we must ask what, or which, methods are best for the problems we face. We cannot assume that orthodox methods are perfect and simply defend them. Neither can we accept the numerical taxonomists' evaluation of their wares and blindly adopt their methods. We must instead evaluate *both* methods in terms of the taxonomic problems we need to solve.

One of the obvious means for evaluation of methods is the testing of alternatives, and this brings us to a curious impasse. To me, and perhaps to others, one of the strangest aspects of the discussions concerning numerical taxonomy has been the virtual absence of concrete statements of methods alternative to it. For some reason there is no detailed method, comprised of theoretically justified, operational steps, that can stand as *the* method of orthodox taxonomy. Too often, formal explanations bog down with references to art or to experience at precisely the points where clarity is most needed. One cannot help but wonder why. Surely it is not because the method is too complicated. A method that is too complicated to explain is too complicated for reliable use. Adequate methods must be explainable, but inadequate methods may not be. Actually, most taxonomists have learned their science by osmosis or absorption from adjacent taxonomists. Primarily, they have learned or been taught attitudes, concepts, and customs, but not methods. These they have had to produce intuitively, or by imitation of their predecessors. Judging from the shifting patterns of synonymy and homon-

ymy in the literature, not all taxonomists have been equally successful in generating or imitating methods. At least, all methods have not had equivalent results in the eyes of all taxonomists. Perhaps, then, we should not be too surprised at the diffidence of individual taxonomists when it comes to publishing their private methods. All too easily, this could be disastrous. Unfortunately, silence is neither constructive nor convincing, and we can hardly test numerical methods against orthodox methods if the latter are not explicitly stated. Until orthodox methods are clearly stated, we have only the orthodox taxonomists' word for it that their methods are adequate and that they accomplish what is claimed for them. This is an unhealthy state of affairs. It makes it possible for orthodox methods, however admirable, to remain unassailable simply by remaining obscure. We can neither evaluate nor improve methods that are hidden in the minds of systematists, and most taxonomists would probably agree that a clear statement of method could materially benefit taxonomy. It would certainly make recognition of the differences and similarities between orthodox and numerical methods easier. And with it the possible interactions between the two approaches should become more apparent. For this reason we must explore the problem of method. But since orthodox methods are neither well-explained nor followed consistently by all taxonomists, we cannot attempt to describe what *is* done. We must make a different approach, and I would like to do this by indicating the way in which taxonomic method might be developed by a problem-oriented, as distinct from a method-oriented, scientist. In this way we may be able to view both numerical and orthodox positions from a vantage point independent of either.

Phylogeny

Before we can investigate method we must determine its objective. Here we have several alternatives, but the traditional goal of taxonomy has been the production of a classification that reflects phylogeny, and this can serve our present purpose. Now, if one looks at this taxonomic goal as a problem-oriented scientist *must* look at it, the first thing the taxonomist must do is produce phylogeny. Then he must devise a classification that will reflect it. By any other procedure the correlation between the classification and the phylogeny will be accidental, and there is no virtue in being right by accident.

As it happens, phylogeny itself is a compound problem, and the approach to it is determined by where one starts. For clarity, it is simplest to start by assuming that the organisms being studied have never been treated taxonomically. There are then three steps. These are: (1) species recognition, (2) discovery of primary groups, and (3) analysis of relationships among primary groups. Each of these steps is a separate and distinct problem, and the methods appropriate to one are not appropriate to the others. This has been a continuing source of confusion among some taxonomists. I have spoken with individuals who maintained that one uses the same method to group specimens into species, species into genera, and genera into higher categories. If this were true, we would (if we were rational) welcome phenetic–numerical methods enthusiastically, since that is exactly what they purport to do. Unfortunately, real biological problems cannot be solved so easily.

Basically, the problem we have to solve is that of classifying the products of organic evolution. This means that we deal with a unique array of objects, an array that has peculiar properties because of the manner of its production. We cannot proceed by putting extant species into groups. They already exist in groups by descent. Our objective must be to *discover* the groups to which organisms belong. This is a simple distinction, but it has a critical effect on perspective. It signifies that the theory that underlies taxonomic practice today is evolution theory, not some general theory of classification, and our problem is to dis-

cover what has been produced by evolution. Taxonomists should not think of themselves as classifiers. They should instead consider themselves to be students of evolution, with a classification one useful by-product of their activities.

I do not wish to discuss all three of the steps to phylogeny—species recognition, discovery of groups, and the discovery of groups of groups—in detail here. I am most interested in the third step and will devote more space to it than to the others. However, I would like to mention briefly each of the first two steps in order to indicate how problem-orientation affects the way in which we go about solving them. The effects of problem-orientation can be seen most readily in considering the difficulties of species recognition. If we accept the biological species concept, we are interested in recognizing populations that are evolutionarily independent of each other. In the vast majority of cases, however, it is impossible to test reproductive isolation, and we are forced to draw inferences from characteristics of the samples available to us. Formerly, before the biological species concept was widely accepted, taxonomists might approach the problem of species recognition by asking: How *different* are they? Now, the comparable questions are: Do the characteristics of the samples provide evidence for genetic discontinuity between the populations from which the samples are drawn? And, if there is evidence for genetic discontinuity, is the interruption of gene flow temporary or permanent? This does not make the problem of species recognition any easier. It simply places it in biological perspective. As has been emphasized many times by many people, at the species level we are not classifying objects, we are evaluating the properties of gene pools. At the operational level, the species problem is the problem of detecting genetic discontinuity. And one does not use the same analytical approach to discover genetic discontinuity that he uses to answer the question, How different are they? If one asks this last question, and applies it to the problem of species recognition, he will be right, by accident, in a certain proportion of cases. He would be right then, not because of the scientific excellence of his procedures but because the evolutionary system produces, in a certain fraction of the total cases, species that match his preconceptions. We might contrast these two methods as "accidental" and "intentional" taxonomy.

At the species level, the intentional approach has been developed carefully over many years. There has been much space devoted to it, and I do not wish to add anything, either by way of definition or by way of method, to what has already been said on the subject. For my purposes here, the species question, and its ultimate resolution, is an excellent example of the way in which the recognition and formulation of a problem *determines* the method that will solve it. It is also the first problem that must be solved on the road to phylogeny, and eventually to classification.

The second step that must be carried out is that of discovering what I will call "primary" groups. This step and the next are very usefully considered against the background of evolution in the genus *Drosophila*, and hence the title of this paper. The genus *Drosophila* is particularly helpful here because it provides some of the few instances where the results of taxonomic practice, or the validity of taxonomic inference, can be evaluated by independent, non-taxonomic criteria. The case to which I wish to draw attention is that of the species groups and subgroups that have been recognized within the different subgenera of *Drosophila*. Judging from conversations I have had with others, it is apparently not fully realized that these species groups are, for the most part, established on purely phenetic grounds. They are phenetic groups in the same sense as are the phenetic groups of the numerical taxonomists. They differ only in being a restricted type of phenetic group, representing just the ultimate terminal clusters of phyletic lineages. The recognition of these clusters is based,

not on selected or key characters, but on analysis of the total phenotype that is accessible to the investigator. Species are recognized as belonging together in primary groups when phenetic resemblances are so high that the probability of their monophyletic origin, from a single ancestor unique to them, amounts almost to a certainty. Concomitantly, there is a very low probability that any other known species or group originated from among the species in question. There are readily detectable gaps between groups, and the species within the groups are so similar that in many cases they can be distinguished from each other only with difficulty. It has been suggested (Stone, 1962) that these groups are the equivalent of the superspecies of some authors (e.g., Simpson, 1961). Attempts to subdivide these groups would have to be based on such a low number of characters that the implied relationships would be very uncertain. Some persons, not accustomed to such fine discrimination in their detection of phenetic differences, might question the validity or reality of such groups of species, even though one might predict that evolution should produce such clusters. Fortunately, these groups have been validated, unintentionally for the most part, by genetic and cytogenetic studies (Patterson and Stone, 1952; Stone, 1962). Not all groups have been investigated so thoroughly, of course, but with few exceptions among the studied groups, genetic and cytogenetic evidence has only served to confirm the conclusions that taxonomists have drawn from phenetic criteria. Thus, on genetic, cytogenetic, and phenetic grounds, primary groups in *Drosophila* appear to be real groups. They can be recognized by discriminating phenetic studies without the necessary assistance of genetic or cytogenetic techniques, and there is no reason to think that such groups cannot be, or are not, recognizable by taxonomists working with any groups of organisms. Primary groups such as these have a certain utility of their own in classification. I wish to emphasize them now, however, not as a category but as real units, the recognition of which is a very useful if not an essential step in the discovery of phylogeny. If these clusters have reality as the terminal branches of phyletic lineages, and this is what the genetic and cytogenetic evidence indicates, then important deductions and inferences can be drawn from characteristics distributed among them.

Before we continue, we must digress briefly and consider factors involved in taxonomic inference when phylogenetic conclusions are to be drawn. These develop from the fact that phylogeny is a consequence of genetic continuity, and any phylogeny is accurate only to the extent that it indicates the genetic history of the groups involved. Implicitly or explicitly, taxonomic inference, if it is to support phylogenic conclusions, must be genetic inference. It may not be genetic inference to the level where specific anatomical or other traits are correlated with specific alleles, but there must at least be the inference that more similar phenotypes indicate more similar genotypes. For this purpose it is convenient to use the concept of genotypic homology, and to view the problem of phylogeny as that of tracing the genotypic changes that have occurred during the evolution of many individual characteristics.

Genotypic homology is a consequence of the interaction between the replicative capacity of the genetic system and natural selection. If replication were perfect, we might not have any evolution, but in any case we would speak of genotypic identity rather than homology. Homology is a concept that has utility only when we are dealing with attributes that are similar but different. We infer genetic similarity, and genetic similarities are a consequence of genetic replication. Hence they are *evidence* of common descent. In this sense, genotypic homology is a more useful operational tool than conventional homology, since that is usually defined as *due to* descent. Since replication is not always perfect, but nearly

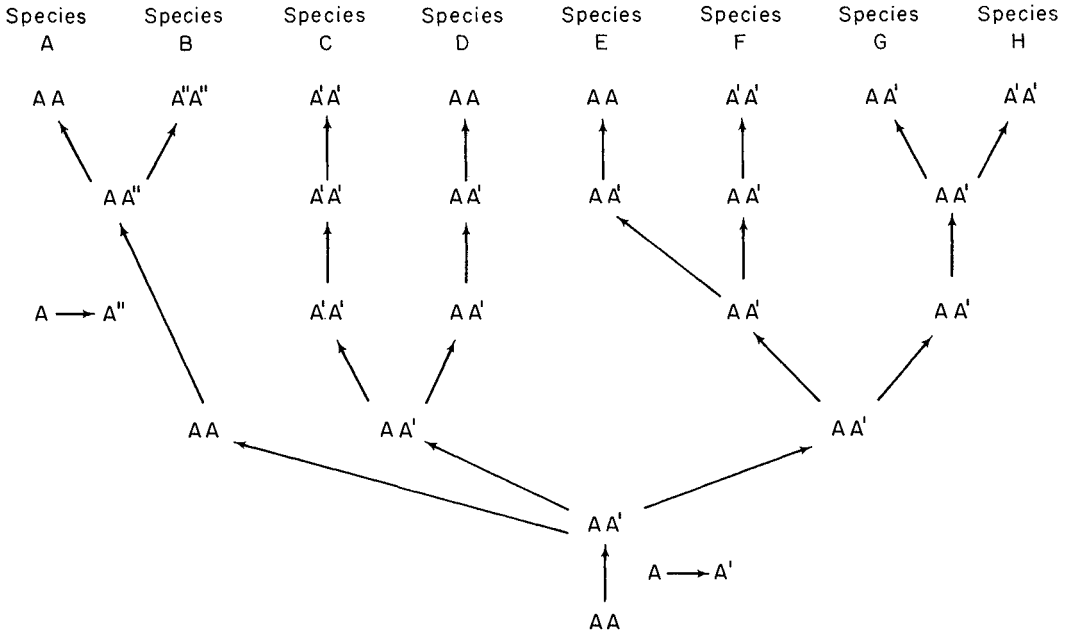

FIG. 1. Evolutionary consequences of heterozygosity.

so, and since natural selection acts on changed products (mutations) to produce slow and gradual replacement of a genotype in time, we must deal with degrees of genotypic homology rather than with the absolutes of gene identity. Since most characteristics are determined or influenced by many loci, we are concerned with evolutionary changes in complex genotypes. These can, however, be simplified for descriptive and predictive purposes.

Some predictions regarding the probable consequences of genotypic change in evolutionary lineages are shown in Figure 1. The emphasis there is on the evolutionary consequences of heterozygosity. In sexually reproducing diploid organisms it is, so far as we know, impossible to go from one character state of an organism to a more derivative state without passing through some genetic intermediate stage. If the two alternative character states are visualized as homozygous (which they need not be), then the transitional stages would include genetic elements necessary to produce *both* the new and the old phenotypes, plus, perhaps, some intermediate phenotypes, depending on the way in which the "new" and the "old" genotypes interacted. Since evolution is opportunistic, the subdivision of a population can occur any time, and not necessarily only when there is little or no genetic variability in the gene pool. In fact, we might expect that gene pools that were rich in genetic variability might more often produce successful descendent species than gene pools with little or none. Hence, persistent polyallelism (heterozygosity) in evolutionary lineages might be predicted as a very probable state of affairs, in which case, there will be, for perhaps a considerable period of time, the possibility for alternative character states to be produced by segregation within descendent gene pools. In the genetic sense, the genotypes responsible for the character states will be *completely homologous,* if not virtually identical; but the character will *appear* many times independently, which is to say that it can occur independently in species derived from species that *did not* show the characteristic, even

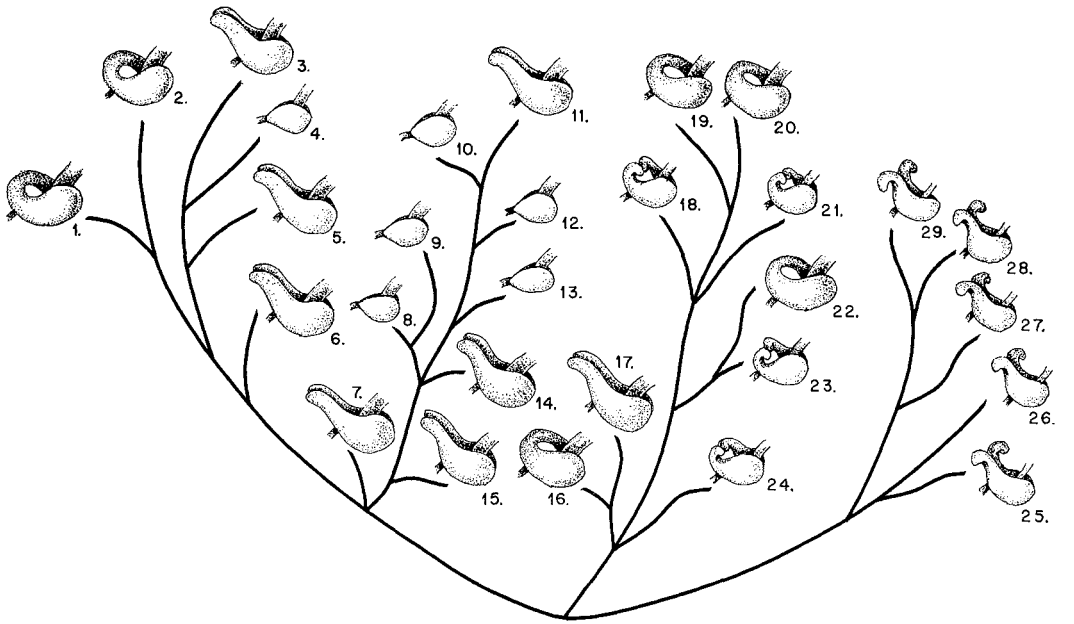

FIG. 2. The distribution of types of ejaculatory bulbs related to the cytological phylogeny of the *repleta* group of *Drosophila*. After Throckmorton, 1962.

though the genotype for the character was potential within their gene pools. This is a critical difference between genotypic homology and conventional homology, since in the latter case one generally insists that a character be present in both ancestor and descendent species before it can be considered homologous. If the character cannot be inferred to have been present in the ancestors and is not traceable back to one common ancestor, it is customarily referred to as a parallelism, or even mistaken for convergence. For genotypic homology, the genotype existed "unassembled," so to speak, in the *gene pool* of the ancestor. Few if any individuals would have had the genotype at that time, and this ancestor probably would not have shown the character. Later the genotype could have been "assembled" many times independently in separate descendent lineages, but it would not have been any the less homologous for that reason. Genotypic homology is determined by the derivation of the genetic *elements* from a common ancestral gene pool, not by the time of assembly of the genotype (Throckmorton, 1962). Consideration of the potentialities of the genetic-evolutionary system, and particularly of the evolutionary consequences of persistent polyallelism in gene pools, emphasizes the essential equivalence of so-called homologies and parallelisms. They can both be used, with about the same degree of confidence, when one infers genotypic histories, which is to say, when one infers phylogeny.

The genus *Drosophila* has many examples of this particular evolutionary phenomenon. Figure 2 shows details of the ejaculatory bulb, a part of the male reproductive system, in relationship to the cytological phylogeny of the *repleta* group. There is one type of bulb (Fig. 2: 1, 2, 16, 19, 20, 22) that is restricted to about six of the more than three hundred species of the genus I have examined to date. All of these species are in the *repleta* group, and four subgroups; the primary groups in this case, are shown in the figure. The species sharing this type of ejaculatory bulb belong to two different cytological phylads, but it would be highly unrealistic to argue that

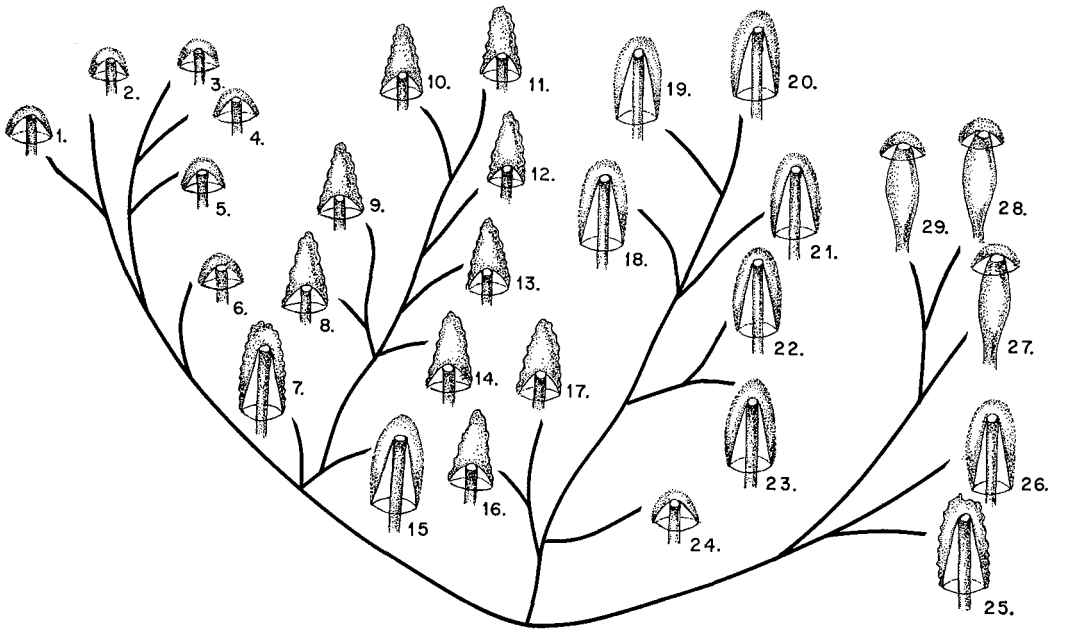

FIG. 3. The distribution of types of spermathecae related to the cytological phylogeny of the *repleta* group of *Drosophila*. After Throckmorton, 1962.

they do not reflect genotypic homology. Their detailed resemblance almost certainly is a reflection of a detailed similarity between their genotypes.

These ejaculatory bulbs also represent parallelism, as that term is commonly used. They do indicate relationship, as we can see from the evidence of cytology, but the relationships they indicate are not the immediate relationships of the species that share them. Rather, they are the relationships of the primary groups to which the species belong. Figure 3 shows much the same thing for another structure, the dorsal seminal receptacle of the female. Here we have several different types (e.g., Figs. 2: 1, 24, and 29; 14 and 16; 7 and 25; 15, 23, and 26), again appearing to segregate (to use this term rather loosely) to several different species in several different phyletic lineages. Here again the presence of a given character state tells us not that the species that share it are very close relatives but that the close relationships are between the primary groups to which these species belong. This provides us with the information on which to base the last procedure in the phylogenetic analysis. It also indicates that we must be very cautious in inferring phylogenetic relationships between closely related species.

In most instances in *Drosophila*, closely related species are complex mosaics of the characteristics of their nearest relatives. They show, individually, very little that is unique to themselves. They show, instead, unique *combinations* of the characters found among other close relatives. When they do share a few distinctive traits with other species, the possibilities of parallelisms are such that these few common traits cannot be given weight as determining the phylogeny *of the species*. It is true that some unique characters are indications of relationship, but we have no *a priori* way of determining which character states undergo parallel development and which do not. Thus, on an *a priori* basis, we cannot determine which characters represent conventional homology and which represent parallelism. If we would have an objective analysis, we must treat all character states

as if they were parallelisms. If we pretend to recognize homologies and group our organisms accordingly, we bias our procedures by our preconceptions regarding the evolution of the groups with which we deal. The operational assumption that characters reflect parallelism is the least restrictive assumption that can be made during a phylogenetic analysis, and it also proves to be a perfectly workable assumption, as shown below.

Parallelism is the rule rather than the exception for *individual characters* in *Drosophila.* There is no evidence from *Drosophila* that parallelism has ever involved extensive character complexes, however, and the genetic and cytogenetic tests are uniquely suited to uncover such a situation, if it exists. For the individual characters, however, "reversals" of character state are common, and ancestral character states recur often. "Reversals" over about three character states are frequent. In genetic terms, this suggests that, at any level in time, the average gene pool could generate genotypes for the character states existing at that time, for those that had been supplanted, and for some that had not yet emerged. Since we deal with complex genotypes, this need not imply polymorphism, although polymorphism could be a manifestation of this phenomenon. The data supporting these conclusions have been published elsewhere (Throckmorton, 1962).

These considerations tend to emphasize, first, that the phylogeny of individual species may be highly uncertain and, second, that the phylogeny of primary groups need not be. Recall that this is the substance of the conclusions from comparing character states within a known phylogeny (Figs. 2 and 3). It is this that requires the detection of primary groups as the second step in the analysis of phylogeny. This step can be carried out very readily, as long as one depends on the analysis of the total accessible phenotype and not on selected or key characters for delimiting the group. Recognition of the need for this step in the analysis of phylogeny could probably come only from a problem-oriented approach. Essentially we have investigated the properties of the evolutionary system, and the characteristics of its products, by prediction (Fig. 1) and by example (Figs. 2 and 3). We have asked what *is* produced. Then we ask what one must do to discover this product. The existence of parallelisms cautions against an approach to phylogeny through the species, and at the same time it indicates great promise for an approach that utilizes primary groups consciously to exploit the phylogenetic implications of parallelisms.

What we need to do next is to derive the gene pools that have existed in the past and from which our existing primary groups are derived. This may sound formidable, but operationally it turns out to be almost alarmingly simple. This type of analysis is described elsewhere (Throckmorton, 1962) in greater detail, and only the bare essentials will be presented here. Technically, one can use all characters available, and the characters are not weighted. I have found by experience that the process is made much easier if one uses the characters in a certain order. Those to be used first are the ones that bring the largest number of primary groups together into groups of groups. The largest possible groups are formed from the character having the fewest states. The steps themselves can be almost mechanical, although some consideration may be given to the direction of evolution when that can be inferred.

The general steps involved are shown in Figure 4. This is a great simplification and shows an analysis based on nine characters and nine primary groups. The primary groups are numbered across the top, and each group includes two species. Each species is indicated by its character state in brackets under the number of its primary group. For this example, I have selected the primary groups and the two species each from those available among the close relatives of *Drosophila.* This example is, therefore, a real but abbreviated case. The steps in the analysis are numbered down

the left side, and the characters used are indicated beneath, together with a notation for the character states and the direction of evolution.

The first step involves the use of the character states of the Malpighian tubules. Actually there are three character states, but practically there are only two since the two more derivative states exist side by side in most of the primary groups. This is the first benefit of working from primary groups. We can often see at a glance which character states show promise of giving phylogenetic information and which do not, simply by their distribution among primary groups. In the present example, the wide distribution of the two more derivative character states of the Malpighian tubules implies that the genotypes for these character states have continued to segregate over a rather considerable period of evolutionary time. Quite literally, it appears that the ancestral gene pools, from which primary groups 1 through 8 were derived, were segregating for the genotypes for the derivative states of this character. It is not unreasonable to assume that these eight gene pools were themselves derived from a gene pool that was also segregating for these genotypes. It is probable that a series of gene pools was involved, judging from the number of groups involved, but the assumption of a single gene pool is most parsimonious at this stage. It presumes the shortest possible time period during which the evolutionary segregation of character states could occur. That is to say, the period during which a gene pool could segregate genotypes for two or more character states is assumed to be short unless and until evidence from other characters requires the assumption of a longer period. Hence, a single division is indicated by these character states, and this division is shown by extending downward the line between groups eight and nine. Primary groups are, of course, indivisible, and the disposition of one species from the group fixes the disposition of all species of the group.

The next character also exists in three states (Fig. 4, step 2), and the sequence of the primary groups must be changed. This change is made by considering the probable contents of the gene pools from which the primary groups were derived and by considering the direction of evolution for the character under consideration, when that can be inferred. In this case, groups 1 and 4 appear to be derived from gene pools that were segregating two character states. Specifically, the species in these groups show either the presumed derivative state of the character or a state of the character that is intermediate between the primitive and derivative states. A segregating gene pool is taken to be evidence (operational evidence, not absolute and unequivocal evidence) of intermediacy in the evolutionary sequence. Hence, groups 1 and 4 are placed between the groups that show only the primitive character state and those that show only the derivative character state. Also, primary groups 1 and 4 include species having a presumed intermediate character state, which tends to support the intermediate disposition of these two groups. The genetic inference here would be that the intermediate character state had been established genetically prior to the origin of the gene pool from which primary groups 1 through 7 were derived. The genotypes for character state C had also become available by this time, but they co-existed in the gene pool with those for state B. Therefore, both character states could (and did) segregate from a gene pool that existed at that time. Groups 1 and 4 were established from this gene pool, and their original gene pools themselves continued to segregate for these two character states. Primary groups 2, 3, 5, 6, and 7 probably also came from this segregating gene pool, but fixation of one genotype (for C) was involved in their derivation from it. I need hardly point out again that these are operational interpretations, but they are working assumptions that are justified in view of what we know of the properties of

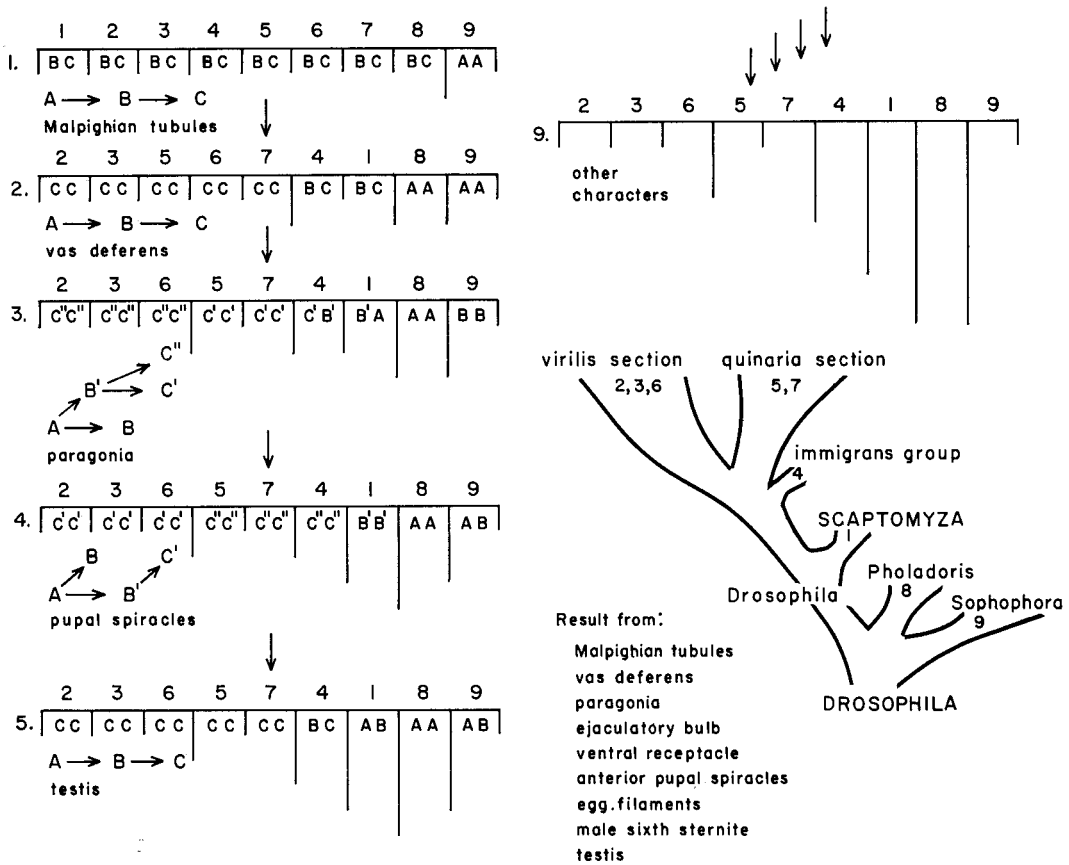

FIG. 4. General method for deducing phylogeny.

the genetic system. The new sequence is therefore adopted, and the additional group divisions (between seven and four, and between one and eight) are indicated.

In the third step, several character states exist, and they do not seem to have a linear relationship with each other. Two different character states appear to have been derived from the primitive. One is found in primary group 9, the other in primary groups 1 and 4. This may be an indication of diverging lineages, but it does not alter the sequence. These groups are already adjacent to the primitive group (8) on the basis of the earlier characters. Again, primary groups 1 and 4 are intermediate when judged on the basis of segregating gene pools. Group 1 is transitional in having members with either the primitive or the intermediate character state. Group 4 is also transitional, but it has the intermediate state together with one of the derivative states (C'), suggesting that it originated somewhat later than did group 1. This, too, is consistent with the existing sequence. Finally, the positions of groups 5 and 6 need to be reversed, to keep the character states grouped as much as possible. The new divisions are marked in as before (between 5 and 6), and when additional evidence for a previous separation is obtained, the line indicating that division is extended (lines between 1 and 8, and between 8 and 9).

By the fourth step no changes in sequence were necessary. Character 4 confirmed the results from the previous characters. The fifth step likewise required no

change in sequence, and it again gave a pattern consistent with the previous interpretations. This analysis was continued up to nine characters, not all shown in Figure 4. After the first three characters, few changes were required by the addition of new characters. For the most part, additional characters reinforced the pattern produced by the first ones. Hence, the order in which characters are used does not seem to be too important. Also, evidence from the additional characters supported the *inferences* on which the earlier dispositions of groups were based. Had the earlier *operational* assumptions for one character been improper, one would not have expected such a marked concordance among all the characters used. The general phylogeny for the groups in the example is shown to the lower right of Figure 4 to indicate how the operational figure may be converted to a typical dendrogram. This type of analysis is designed to produce only sequence (cladistics), so distance and angle in the figure have no significance.

One of the most important features of this approach to phylogeny is that it requires no inferences regarding probable characters of ancestors, and it requires no reconstruction of ancestral types. Technically, we infer only the probable contents of gene pools, and since we have fewer preconceptions about gene pools than about morphology, we gain in objectivity by this procedure. In this approach the most important evidence for intermediate position is the possession, by two or more species in one primary group, of character states that indicate which other primary groups were derived with them from a common and unique ancestral gene pool. In *Drosophila* it has been possible to resolve almost all questions of sequence on the basis of the intragroup variation, and not on individual evaluations of what constitutes morphological intermediacy. The evidence from intragroup variation and that from presumptive morphological intermediacy were consistent with each other in most instances. When there were conflicts it was because some character states were overlooked, in prospect, that appeared as perfectly obvious intermediate states, in retrospect. In short, this method has proved to be a rather powerful one for discovering direction of evolution of different characters.

Phylogenetic Method and Numerical Taxonomy

Up to this point we have been discussing method as it should be developed with a single problem in mind. The problem was to derive the sequence of genetic change that occurred during the evolution of a group of organisms. This is the ostensible aim of taxonomy so long as it makes any pretense of having a phylogenetic basis. The method that has been outlined may seem foreign to some, and the genetic interpretation and justification of the steps may distress others. This last, the genetic interpretation of taxonomic data, is a subject that might profitably be discussed at some later time. At this point it is well to call attention to the ways in which the method just outlined reflects procedures used by orthodox taxonomists. We can note also the extent to which the technical procedures for each level of analysis might be refined by contributions by numerical taxonomists. That is, we can suggest potential interactions and cooperations between orthodox and numerical taxonomists, at least insofar as their methods are concerned.

The first point that needs to be re-emphasized is that, from the problem-oriented viewpoint, the preliminary steps to classification are three, and a different method is required for each. No single procedure, numerical or otherwise, will adequately reduce taxonomic data for classification. The three steps outlined above are the minimum number that can be employed prior to assigning groups to categories. The first step, that of species recognition, requires little comment except to suggest that there is here a fertile field that might be exploited by numerical methods. To date, this level of taxonomic research has been disdained by most numer-

ical taxonomists, and some have even defined it out of existence (Sokal and Sneath, 1963; Sokal, 1964; Ehrlich, 1961). The species problem remains, nonetheless, and the possibilities for refining phenetic techniques specifically for detecting genetic discontinuities between gene pools seems an obvious and potentially fruitful outlet for energetic computers. Such methods, if developed, would be primarily for resolving special and troublesome cases, or for demonstrating as conclusively as possible that in a given instance phenetic analysis could not uncover evidence for species distinction. It would not be expected that computers could give us unequivocal answers to all species problems. Error and uncertainty are inherent in our system so long as we are constrained to depend on phenetic methods to resolve problems that can only be resolved unequivocally by reproductive tests. Still, our responsibilities as systematists must be toward resolving species questions as accurately as possible in as many cases as possible, and numerical methods should help us increase the number of cases where accurate species recognition is assured. At this level of taxonomic investigation, therefore, numerical methods should be supplemental to orthodox methods, just as cytological and biochemical methods are. We do not choose between these methods. We use all of them as skillfully as possible on the problems for which they are best suited.

The second level of investigation, that of the discovery of primary groups, is eminently suited to the numerical approach. Unfortunately, many numerical methods undertake to do much more than this. It is this step that most taxonomists are thinking of when they speak of "classification." It is an obvious and necessary step in any taxonomic procedure, and it is quite obviously a step that is based on estimates of degree of resemblance. Regrettably, many taxonomists have not realized that their only valid inference at this level is that a very high degree of similarity indicates very recent common ancestry and a low degree does not. This allows one to identify the primary groups to which species belong, but it does not allow one to rank species by degree of similarity and infer therefrom their probable phylogeny. The existence of an evolutionary system in which heterozygosity plays a part, however small, automatically entails parallelism and hence precludes the assumption that degree of resemblance is equivalent to recency of common ancestry, except as already noted, when extremely close relatives are involved. The more extensive the parallelism, the less tenable this assumption will be. It is true that in some cases, even in many cases, this assumption may be substantially correct, but if we trust in this we will, again, be right only by accident. Taxonomy, as a science, must have more lofty aims than this! Hence, the need for a third method for evaluating relationships outside of the primary groups.

Numerical methods can make great contributions at this second level, in two different ways: they can refine methods for discovering primary groups, and they can develop methods for evaluating the properties (homogeneity, for example) of already recognized groups. This is an area that should be most actively explored by orthodox and numerical taxonomists alike since it promises to place on a firm and uniform basis the taxonomic category (the primary group, whatever its category designation) that has the greatest practical usefulness, whose phylogenetic implications are least equivocal, and whose predictive qualities are highest. If orthodox and numerical taxonomists would collaborate just to the extent of evaluating some existing groups, we ought soon to have a much better understanding both of what numerical methods can do and of what orthodox methods have done. Some assertions of numerical taxonomists might prove to be incorrect, and some of the skepticism of orthodox taxonomists might prove to be unjustified. It is often remarkable the extent to which simple tests may contribute to the abatement of controversy, and the present case may prove to be no exception.

The last step to phylogeny, that of grouping of groups, is somewhat less utilitarian but of great biological interest. The system outlined here may need some modification before it could be treated as a general method, but in its present form it is objective and repeatable, and it can also serve as a method for the *a posteriori* weighting and evaluating of characters. These are achievements that are often referred to as attainable only through art or through experience. The outlined procedure is a simple way by which one gains experience quickly and objectively. When this is done, taxonomy becomes not an art but a science. The role of computer methods at this level of analysis remains to be determined. The work of Camin and Sokal (1964, and in publication) suggests that there is real hope for progress in this direction.

Classification

Figure 5 shows a phylogeny of *Drosophila* and its close relatives, derived basically in the manner indicated earlier. It provides an example of the extent to which orthodox methods have achieved a phylogenetic classification, and the concordance between phylogeny and the existing classification is not impressive. This figure also provides an example of the magnitude of the problem one faces in attempting to reflect phylogeny in a classification. A major difficulty with this phylogeny is that it shows a pronounced vertical development, rather than the pattern of sequential divergent branching presumed by the Linnean hierarchy. Most of the diversification in this family has occurred by divergence from a single lineage that was itself changing slowly in time. At a given level, several groups may have evolved from this basic type, but they have not all diverged or diversified to the same degree. Thus, species, species groups, and sub-genera separate from nearly common points in the phylogeny. Those that have diverged in their external and traditionally diagnostic features are classified in other genera. Where these same features have remained unchanged, and in spite of other changes, the forms are classified as *Drosophila*. Any attempt systematically and consistently to impose a hierarchical arrangement on such a pattern will result in a wildly asymmetrical product that rapidly exhausts the category and subcategory names available.

There is, then, an observation to note and a point to be emphasized. The *observation* is that orthodox methods have not produced what they claim to produce, that is, a phylogenetic classification. The point to be emphasized is that the hierarchical Linnean system is severely limited as to what phylogenetic information it can carry. The phylogenetic *detail* in Figure 5 simply cannot be reflected by a Linnean hierarchy. This last is not a new point (see Hull, 1964), but it certainly has not been given the serious attention it deserves from taxonomists.

One would like to know the reason for the dichotomy between the principles of orthodox taxonomy and the practices of orthodox taxonomists, as these are revealed by the situation shown in Figure 5. Under ordinary circumstances, in most scientific disciplines, this would be easy. We would simply ask whether the error resulted from improper basic premises, from improper methods, or from the incompetent application of methods that were themselves adequate. As noted in the introduction to this paper, taxonomists have denied themselves this standard procedure of self-evaluation and improvement by the simple expedient of never explicitly defining aims and never explicitly stating their methods. This has led to a great deal of confusion and inconsistency, and this confusion is probably the clearest message that can be read from Figure 5. Whatever the criticisms that orthodox taxonomists may have of numerical taxonomists and their methods, they certainly cannot claim for themselves that they have clear objectives or more consistent and defensible practices. We can readily agree that some taxonomists do have proper aims, and proper methods to achieve these aims. We must at the same time recognize that all taxonomists do not share the same aims or use the same methods, even when they do seem to have the same objectives.

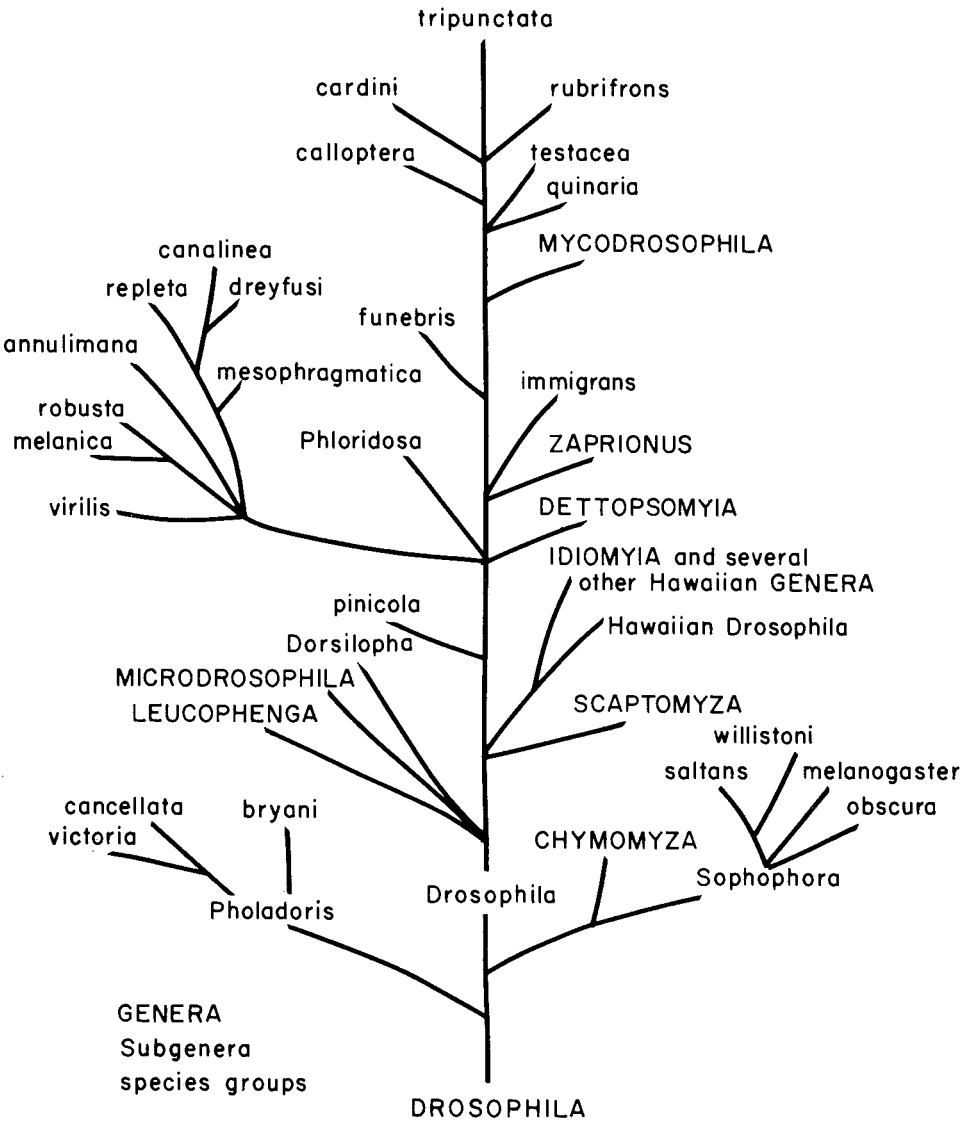

FIG. 5. Phylogeny of *Drosophila* and related genera.

In the last analysis, the major question faced by taxonomy today is not, as implied by the controversy over numerical methods, whether classification should be phylogenetic or phenetic. It is probable that the great majority of biologists agree that a phylogenetic system is preferred. Many taxonomists seem to think that this settles the problem of aims. Unfortunately, the problem still remains as to what constitutes a phylogenetic classification, granting that we will use the Linnean hierarchy to express it.

Considering the problem of phylogenetic classification, there are two basic formats that must be distinguished. One is a classification that is a literal translation of phylogeny. This is what most biologists have been taught to expect of a classification (see for example Grant, 1963:34), even though

such a translation may in fact exist only rarely. It is this form of classification that cannot be impressed on the groups shown in Figure 5. The second major format is one that simply shows groups and diversification within groups. Phylogenetic sequence is not implied here, except in that groups are intended to be monophyletic in a very strict sense. This form of classification would not, and could not, show divergence. It is the only classification that can show, unambiguously, the little phylogenetic information that can actually be contained in a hierarchical classification. The Linnean hierarchy can show gross phylogenetic relationships (if its groups are rigidly monophyletic) and diversification (the number of different monophyletic groups within a larger group). It is suited to show little else.

The existing system of classification seems to be an unwholesome hybrid between the two basic systems, or something else that is neither. The classification of the groups in Figure 5 shows divergence in some parts (apparently in the vain hope that divergence *per se* would have some phylogenetic significance), and diversification in others. Hence, it shows little about phylogeny. It would show more about phylogeny if there had been a reasonable degree of equivalence between degree of difference and recency of common ancestry. As noted earlier, we would not expect such to be the case, and, in the Drosophilidae at least, it certainly is not the case.

Where are we then with regard to the interactions between numerical and orthodox taxonomy? The numerical taxonomists recognized long ago, along with other less vocal taxonomists, that there were inconsistencies in the practices of orthodox taxonomists. They set out to change this state of affairs and have played a major role in stimulating a re-examination of taxonomic methods and goals. This in itself is no mean achievement. Unfortunately, they seem to have interpreted the confusion in taxonomic practice as resulting from a conflict between phenetics and phylogenetics. Hence, they have pressed methods without seriously evaluating problems. It is more probable, however, that the basic confusion in taxonomy is a consequence of discord resulting from a misunderstanding among taxonomists regarding what a phylogenetic classification can and should do, and of how phylogenetic data is to be converted into a phylogenetic classification. This confusion remains. Numerical taxonomy has done nothing to dimish it (phenograms are no more amenable to hierarchical classification than are phylogenies), and it must be eliminated before further constructive attacks can be made on method. Taxonomy today is a hodgepodge of goals and methods. We must settle firmly and conclusively the problem of the aims of taxonomy by specifying the format by which phylogeny will be expressed in classification. If we do this, the problem of methods should settle itself since, as I have shown above, appropriate methods exist for all the critical steps in the taxonomic procedures that precede classification. We must decide what should be done, how it is best done (and what should *not* be done), and then do it. Within this emerging system it is almost inevitable that numerical methods will attain increasing importance for particular problems at certain stages of taxonomic analysis, but we cannot expect them to completely supplant procedures that now exist.

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Notice: International Association

Prof. L. D. Brongersma, Leiden, has informed the Secretary that plans for an international association for systematic zoology have been suspended. This change stems in part from failure to organize the association in an adequate way, and in part from the growth of world-wide membership in SSZ. Prof. Brongersma feels that by joining forces, and by increasing the international membership of SSZ still further, the goals aimed at, when the plans for an international organization were first made, can be reached in a more effective way.

Money contributed by zoologists for the international association has been held in trust and will be returned upon request. The individual sums are rather small, however, and cost of return would use up a substantial portion of the fund. Therefore Prof. Brongersma has indicated that any money not requested within *three months* will be given to the patrons fund of SSZ to increase our society endowment. Contributors to the international association who are not members of SSZ will be notified by mail of the dissolution of the proposed organization.

Funds contributed by North American and Britist systematists are held by the Treasurer of SSZ. Members in these countries who desire return of money should contact Dr. Joseph Rosewater. SSZ contributors from elsewhere in the world who wish their contribution returned should contact:

Prof. Dr. L. D. Brongersma
Rijksmuseum van Natuurlijke Historie
Raamsteeg 2
Leiden, The Netherlands

Notice: Committee on the I.B.P.

A new committee has been formed to work in cooperation with the International Biological Program (I.B.P.) of the International Union of Biological Sciences (I.U.B.S.). The I.B.P. is oriented primarily toward ecology and conservation with the thought that these approaches may contribute toward a more abundant food supply for the exploding human population. The Society's committee is interested in adding to this a further program designed to preserve areas of biological interest for the future or to make collections of endangered animals and plants for preservation in systematic collections so that they will be available for study if the species should disappear in the natural state.

At their meeting in Ann Arbor in April, 1965, the Directors of Systematic Collections passed a resolution to the effect that it was a valid and primary concern of museums and other systematic collections to cooperate to the best of their ability with the I.B.P. in the study of threatened biota. By the establishment of this new committee the Society of Systematic Zoology is furthering this decision.

The committee will welcome correspondence with members concerning the items outlined above and on other points where it is felt the committee may be of service as an advisory group during I.B.P. planning.

The members of the committee are:

Friedmann, Herbert—Chairman
Los Angeles County Museum, Los Angeles, California

Cowan, Richard S.
U.S. National Museum, Washington, D.C.

Emerson, William K.
American Museum of Natural History, New York, New York

Illg, Paul L.
University of Washington, Seattle, Washington

Miller, Robert R.
University of Michigan, Ann Arbor, Michigan

Michener, Charles D.
University of Kansas, Lawrence, Kansas

Peters, James A.
U.S. National Museum, Washington, D.C.