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THE SPECIES CONCEPT

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INTRODUCTION

The species concept is focal in evolutionary studies and, indeed, in all biological thought. Its endless discussion is sometimes boring and seemingly fruitless, but is not wholly futile. In the course of such discussion the concept has been clarified, comprehension and a consensus have tended to develop, and the concept has changed in a significant way. There have recently been two more flurries of attention to this perennial topic. One, mostly in *EVOLUTION*, by Burma (1949a, 1949b), Mayr (1949), Dunbar (1950), Elias (1950), and Gregg (1950), was originally concerned with whether the species is a "fiction" or is "objective," but also treated such matters as the relationships of neontological and paleontological species concepts. The other, in the *Journal of Paleontology*, by Weller (1949), Jeletzky (1950), Bell (1950), and Wright (1950), was concerned with the bases and practices of paleontological systematics and also with "morphological" versus "phylogenetic" or "natural" versus "unnatural" classification. These papers, among others, and an attempt to grapple with the whole problem for a class in systematics have inspired the following remarks.

I agree with most of what all the authors just cited have said. I believe, however, that it is possible to say much of this in a somewhat different and therefore possibly clarifying way, to combine some of their apparently but not really conflicting views into one consistent statement, and to add a few significant considerations not explicit, at least, in any of their papers.

Parts of the discussions cited and some of the apparent conflicts are primarily semantic. By a ponderous application of symbolic logic, Gregg sought to show that the issue raised by Burma and Mayr is not a genuine taxonomic problem or, at least, that if it does relate to a taxonomic problem it does so in the wrong words. It is, of course, important that words be used as accurately as possible and that they do not obscure properly taxonomic questions. Nevertheless, Burma and Mayr (as well as subsequent discussants) were considering a genuine taxonomic problem, in words perhaps not logically impeccable but, taken in context, adequately performing their main semantic function, that of communicating understandably among colleagues.

The semantics of the systematists' vocabulary is a fascinating subject, which

surely does have its own importance but which has the danger of merely diverting attention from the systematists' proper business, systematics. I believe that most of the purely semantic confusion on the present subject can be avoided if such terms as "real," "natural," or "objective," and opposite or contrasting terms, are not applied to taxonomic categories or methods of classification, and if the two terms "arbitrary" and "non-arbitrary" are used in specially defined senses.

Definitions of taxonomic categories, such as a species, specify the sort of data or of inferences from data that are to be used in assignment of organisms to a group ranked in that category. For instance, the category definition of a species as a group of "actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr) specifies that data and inferences as to interbreeding and its absence are to be used. In some cases the data or inferences used will indicate essential continuity among the organisms to be grouped, and in other cases they will indicate essential discontinuity. Under the preceding genetic definition, actual or potential interbreeding is continuity and reproductive isolation is discontinuity. With a morphological-associational definition, continuity would be overlap in variation between compared populations and discontinuity the absence of overlap. Essential continuity or discontinuity in geographic, ecological, or temporal distribution has obvious meaning.

I propose to call taxonomic procedure arbitrary when organisms are placed in separate groups although the information about them indicates essential continuity in respects pertinent to the definition being discussed, or when they are placed in a single group although essential discontinuity is indicated. Conversely, procedure is non-arbitrary when organisms are grouped together on the basis of pertinent, essential continuity and separated on the basis of pertinent, essential discontinuity. Of course no stigma is meant to attach to

taxonomic procedure thus defined as arbitrary. A completely non-arbitrary classification is impossible. It would be possible to extend discussion to such points as the precise definition of "essential continuity" or other parts of these definitions, but I think their meaning will be clear to all taxonomists, now or as discussion proceeds, and that semantics may be dropped at this point.

TYPOLGY, MORPHOLOGY, AND GENETICAL GROUPS

The typological concept of a taxonomic group is that the group corresponds with an abstract or ideal morphological pattern. Variation may be dealt with by a fixed or intuitive standard as to allowable deviation from the pattern, in which case the grouping is arbitrary. (It may either include discontinuities or draw a line across continuity.) Or, somewhat less naively, at a given level, usually that of species, the criterion of continuity in variation around the pattern may be used, a non-arbitrary procedure for that category.

The typological concept is pre-evolutionary and non-evolutionary. It still underlies a great deal of taxonomic practice but is now seldom favored in theory. Arkell (1950), an experienced paleontological taxonomist, seems to be accepting it when he says that, "Theoretically, at least, the number of species named reflects the number of forms, and so is more or less an objective matter," but he was mainly concerned with the highly laudable desire to keep super-specific categories conveniently manageable. The only serious modern theoretical support for frankly typological taxonomy comes from those few students who believe that species arise by abrupt morphological change from one "morphotype" to another, notably Schindewolf (1950).

Most of the data actually used in the practice of taxonomy are morphological. It is therefore not surprising that practical taxonomists suggest from time to time that classification should be morphologi-

cal, in principle, as Weller (1950) has recently done. But a purely morphological classification would be based strictly on degrees of morphological difference between organisms, and this is really so impractical that no one, not even Weller, really tries to do it consistently. It is a commonplace that the degree of morphological difference within what everyone, morphologist, geneticist, or other, calls a single species is frequently greater than that between what all call separate, related species. It is also quite impractical to obtain a valid, over-all measure of total morphological difference between two organisms. Characters are always selected, weighted, and interpreted. As Wright (1950) pointed out in criticism of Weller, the usual and meaningful basis for selection, weighting, and interpretation is phylogenetic. Even typological classification, more strictly morphological than others, requires definition of the morphotype from characters in a group already set up on grounds not, in practice, purely morphological. Typological or not, practical morphological classification starts with some sort of grouping and in most practice this is usually an attempt to recognize what is (whether so called or not) a genetically defined population. Thus Bell (1950) cogently argues the value of stratigraphic evidence in paleontological taxonomy because it bears on pertinent and useful biological taxonomic criteria that are not morphological.

The fundamental point here for taxonomy is the modern idea that it is populations, not specimens, that are being classified. Newell (1948) has stressed this point for invertebrate paleontology in criticism of the practice of naming variants which are not populations. Jeletzky (1950) also emphasizes this point of view and its usefulness (one might say, necessity) for phylogenetic classification, although his argument is greatly weakened by his statement that variants are "natural groups" within the population and by his contrasting of phylogenetic with

statistical methods, as if statistical methods were not a means of reaching conclusions about populations and hence about phylogeny. I have also insistently recommended population concepts in taxonomy, and so have many others. A few paleontologists have been mentioned first because, on the whole, paleontologists have been rather slower to grasp or accept the population concept of taxonomic groups. Despite some conservatives and reactionaries, the concept is widely accepted among neontologists (in botany, e.g., Camp, 1951; or in zoology, e.g., Mayr, 1942).

If classification is to start with populations, category definitions at and below the species level should refer to populations which, further, should be meaningful biologically. It seems to me, and few systematists are likely now to question this, that such groups should likewise have evolutionary significance. Here is the most serious fault of typological or of purely morphological definitions. Unless by chance or unless a hidden genetical criterion is actually used, they do not define biological populations or have clear evolutionary significance.

Attention to biologically significant populations is the basis and justification for the now usual neontological definitions of the species category in terms of interbreeding and reproductive isolation, i.e. of genetical factors, like the definition already quoted from Mayr. As Wright (1950) has mentioned, the fact that a species, as a group, is actually diagnosed in morphological terms, does not conflict with definition of the species, as a category, in genetical terms. The basis for definition of a category is quite different from the evidence available for decision as to whether a particular group of organisms meets that definition. And although the evidence used is mainly morphological in practice, it also almost always includes other sorts of data as well: distribution or association, at least, and preferably also other information.

The genetical definition of a species as

a group of actually or potentially interbreeding organisms reproductively isolated from other such groups is non-arbitrary both in its inclusion and its exclusion. Its criteria are reproductive continuity and discontinuity. The group defined is co-extensive with the continuity and bounded by the discontinuity. A species under this definition is the largest group with non-arbitrary exclusion and the smallest group with non-arbitrary inclusion. By the criteria of this definition and in cases to which it applies, infra-specific groups are non-arbitrary as to what they include (being reproductively continuous, by definition), but more or less arbitrary as to what they exclude (having boundaries without full reproductive discontinuity, by definition). Under the same criteria and circumstances, supra-specific groups are arbitrary as to inclusion, because by definition they do or may include two or more groups between which there is discontinuity, but non-arbitrary as to exclusion, because their boundaries coincide with the non-arbitrary boundaries of included species.

Thus under this particular concept and in the particular cases to which it applies, the species is defined as the one taxonomic category that is non-arbitrary both in exclusion and in inclusion. This is another way of expressing what is clearly intended by statements that the species (so defined) is the "objective" or the "real" taxonomic unit. If my usage of "non-arbitrary" is accepted and discussion of the meaning of "objective" or "real" is avoided, it should not be seriously questioned that the statement of the first sentence of this paragraph is valid. Objections, which may also be entirely valid in their own terms, are of five principal sorts:

1. The genetical concept of species is not the only one possible, and for certain groups and in particular circumstances it may be less desirable than some other.
2. Application of the genetical definition to actual cases, even those to which

it could theoretically apply, sometimes turns out to be vague or impractical.

3. There are many groups of organisms, or circumstances involved in their taxonomic grouping, to which the stated genetical definition does not apply even in theory.

4. The genetical definition implies but does not adequately state or overtly take into consideration more definitely evolutionary criteria on which it does or should depend, criteria as to the evolutionary role of a lineage, to be discussed below.

5. Application of this or of related evolutionary concepts of the species does not correspond with past and current usage in certain groups and by certain taxonomists.

It seems to me that all these objections have considerable force, more force than is granted them by some students whose taxonomic work is in the circumscribed fields where the genetical definition is in fact most practical or those whose interests are not primarily taxonomic. Yet I do not think that the objections invalidate the genetical concept or remove it from a central and basic position in taxonomic theory. They merely require that it be modified in certain applications and that it be supplemented by other concepts to meet situations to which it does not properly or practically apply. The rest of this paper is devoted mainly to discussion of some desirable or necessary modifications and supplemental concepts. One pertinent subject not directly discussed, because of limitations of space and ability, is the taxonomy of asexual groups, clones, apomicts, agamic complexes, and the like. Some of what is said below bears inferentially on this subject, and it has been briefly but ably considered by Stebbins (1950) with references to older literature.

GENETICAL AND EVOLUTIONARY SPECIES

As Mayr (1946, 1950) has emphasized, the usefulness of the genetical concept in taxonomy and the non-arbitrary defini-

tion of the genetical species (its "objective reality") are most evident in what he calls "non-dimensional species," those established in biotas living in one place at one time. Under such conditions, discontinuities in morphological and associated physiological variation are usually evident. In sexually reproducing groups it is almost always easy under these circumstances to establish by observation, experimentation, and inference which morphological discontinuities reflect reproductive discontinuities and to designate these as species boundaries.

But, as Mayr has also recognized, the fact that genetical species are usually rather obvious under these special limitations does not mean that they are equally clear and the genetical definition equally adequate under other and perhaps more important conditions. Populations do have extension in time and space and a non-dimensional taxonomy cannot cope with many essentials of life and of its evolution. With extension in space, the criteria of genetical continuity and discontinuity, of actual or potential interbreeding or its absence, cease in many cases to be absolute and clearly non-arbitrary and become merely relative. The similar and related local populations may not in fact interbreed over a period of years and yet may reasonably be considered as still having that potentiality. On the other hand, quite extensive interbreeding may occur between adjacent populations which nevertheless retain their own individualities, morphologically and genetically, so clearly that any consensus of modern systematists would call them different species. In some groups of plants, even though species are defined and considered as genetical entities, occurrence of some hybridization between adjacent species may be the rule rather than the exception. In such cases the species are in part arbitrarily bounded even though the gene flow is less between than within species, and the genus may become the most fully non-arbitrary unit (a thought expressed in other words by

Camp, 1951). A rigidly genetical zoologist might then insist that such botanical genera equal zoological species, but evidently most botanists feel that in some way their species *are* analogous with zoological species and they can make out a good, even though not an absolutely clear-cut, case. (See Stebbins, 1950.)

In practice, even by zoologists who adhere strictly to genetical concepts of taxonomic units and who work on groups to which the concepts are applicable, it is often clear that the criterion of interbreeding or its absence is not taken as wholly decisive. Species may be distinguished even though they interbreed (hybridize) to some extent, and populations may be referred to a single species even though there is evidence that they are not in fact interbreeding. Other criteria are given weight additional to that of their evidence on interbreeding, e.g., morphological divergence, partial or full intersterility, and especially occurrence with discontinuity in the same area.

The genetical definition is meaningful because it is related to the evolutionary processes that give rise to the groups being classified. Yet the genetical criteria are not related to evolutionary change directly but only, as a rule, by implication. The following seems to be the strictly *evolutionary* criterion implied: a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution. The genetical definition tends to equate the species with such an evolutionary unit. Most of the vagueness and differences of opinion involved in use of the genetical definition are clarified, at least, if not wholly resolved by taking the genetical criterion, or interbreeding, not as definitive in itself but as evidence on whether the evolutionary definition is fulfilled. Thus the species as actually used by many progressive systematists in both animals and plants does tend to approximate a unitary phyletic lineage of

separate evolutionary role even though in both cases outbreeding, hybridization, may occur and in some groups of plants this is widespread and usual. Emphasis on unitary evolutionary role may even resolve the theoretical difficulty of defining species in asexually reproducing groups.

This redefinition, or shift of emphasis, or revealing of the implicit basis of much modern evolutionary taxonomy, introduces the element of time into the concept of species, even in the so-called non-dimensional situation. It designates the species, including the "non-dimensional" species, as a unit which has been evolving separately, or which will do so, or, as a rule, both. Decision that populations will evolve separately involves prediction. Such points as wide geographical discontinuity (especially with a strong intervening barrier), morphological divergence, sympatric occurrence without interbreeding, and intersterility are clearly items of evidence for this sort of prediction. Their bearing seems to me more meaningful in evolutionary terms than in the definition of actually or potentially interbreeding populations, although of course the evolutionary species usually is also such a group. The special importance of intersterility, even though no modern taxonomist makes it an absolute requirement for specific separation, is, for instance, evident in this context: intersterility makes the prediction of separate evolutionary roles certain.

THE SPECIES IN PALEONTOLOGY: DATA AND DISCONTINUITIES

Part of the endless discussion on species concepts is concerned with the relationship between neontological and paleontological species. Opinions vary from the view that the two usually are quite different (e.g. Elias, 1950) to the view that they are usually essentially the same or that one is only an extension of the other concept (e.g. Mayr, 1950). Both views are correct in the sense that species just

like those (by any definition) of neontology do occur in paleontology, but that actual practice regarding them may be more difficult or, at least, necessarily somewhat different in paleontology and that there also occur in paleontology taxonomic groups to which no strictly neontological species concept can properly be applied.

That paleontological data and materials are different from neontological is well known and sometimes overstressed. Direct genetical methods are unavailable in paleontology, but they are very rarely used in neontological taxonomy. The paleontologist usually has parts, only, of the organisms concerned, but the neontologist commonly uses parts, only, of recent organisms. Different parts may be available or used in the two cases, but inferences from them regarding populations may nevertheless be closely analogous or actually identical. Nearly or exactly the same general sorts of data, morphological, distributional, and associational, are frequently used in the practice of paleontological and neontological taxonomy. (Fuller discussion of these points was given in Simpson, 1943.)

The "non-dimensional" species is encountered more frequently in paleontology than in neontology, in spite of the fact that paleontology is inherently more multidimensional than neontology. The neontologist is seldom forced to confine himself to collections from one locality, and is never justified in doing so unless forced. Much paleontological taxonomy is necessarily and properly based on quarry collections or mass collections from one local stratum, associations without appreciable dispersion in space or time and ideally non-dimensional. In such cases neontological concepts and definitions of genetical and evolutionary species apply without modification. (Even Elias, 1950, outspoken opponent of the current rapprochement of neontological with paleontological systematics and of both with genetics, admits that in such cases paleontologists "may be obliged to resort to

neontological concepts of taxonomic terms.”)

Discontinuities are more frequent and of more varied sorts in paleontology than in neontology. This has certain disadvantages for paleontological theory and interpretation, but it also has some practical advantages. Discontinuities of observation, only, due to inadequate sampling of local populations or inadequate distribution of sampling stations, occur in both fields but are generally harder to fill in when paleontological. Discontinuities of record, that is, in the organisms actually present and available for sampling in the field, are a particular paleontological problem and may concern both time and space. When samples have been obtained from different localities or horizons, rocks and fossils intermediate between them may not exist. Such discontinuities are, as of now, facts in nature. Their use to delimit taxonomic groups is non-arbitrary, by definition. Yet they do not necessarily coincide with any particular sort of discontinuity that existed when the organisms were alive. Hence their relationship to the sorts of units defined in neontology may be and remain ambiguous.

The special questions involved in succession or sequence will be discussed separately, but it should be noted here that paleontological samples discontinuous in space are often also discontinuous in time and that the possibility can seldom be discarded. With such samples of similar organisms it is always difficult and it may be quite impossible to determine whether:

(a) They represent local populations that were genetically continuous, and hence infraspecific groups by genetical and evolutionary definition.

(b) They represent separate phyletic lineages, and hence distinct genetical and evolutionary species.

(c) They represent ancestral and descendent populations, and hence a special

and peculiarly paleontological situation discussed below.

In such a case, the preferred practical procedure is:

1. To consider the two (or more) lots of associated specimens as samples of different local populations and to derive from them estimates of morphological variation in those populations.

2. If the population estimates indicate no significant mean difference, to consider the samples as representative of essentially a single population and hence taxonomic group.

3. If the population estimates indicate significant mean difference but overlap in range of variation, to consider the samples as drawn from different subspecies of one species.

4. If the population estimates indicate no overlap in range of variation (for at least one well-defined character), to consider the samples as drawn from different species.

Species recognized in this way are non-arbitrary in exclusion and inclusion by combined morphological and distributional criteria. They are morphologically similar to most genetical and evolutionary species. In many cases they will in fact be genetical or evolutionary species, but under the stated conditions it is virtually impossible to determine this equivalence with any high degree of probability.

THE SPECIES IN PALEONTOLOGY: SUCCESSION

Succession on a small scale and involving short periods of time occurs in some neontological data and there involves some special taxonomic problems, but on the whole succession is distinctively paleontological.

Discontinuities of observation and of record are frequent in paleontological study of successive populations. They frequently correspond with discontinuities of time, already mentioned. Diastems, geologically brief intervals of non-deposition (with or without erosion), are abun-

dant in most stratigraphic sequences. They represent local discontinuities in time, but may be considered taxonomically unimportant if there was no significant change in the populations being studied or if intervening fossils of the same or closely similar populations are available from other localities. Larger and regional stratigraphic unconformities are also, although less, common and they usually represent taxonomically significant discontinuities in time.

Discontinuities in succession may also be caused by migration, by change of (biotic, and commonly of correlated stratigraphic) facies, or, frequently, by a combination of both (see especially Bell, 1950, also Newell, 1948). Such discontinuities often coincide with discontinuities in time but, as Bell has stressed, they need not do so. For instance figure 1 shows diagrammatically a situation in which there is a discontinuity of facies, with fossil populations as limited by facies successive wherever found, but really contemporaneous and without discontinuity (or, indeed, regional succession) in time.

When discontinuities in succession are present in the data, they may be dealt with in practice as outlined above for paleontological discontinuities in general. They may similarly permit non-arbitrary

delimitation of morphological-distributional species which may approximate, but cannot usually be clearly equated with, genetical-evolutionary species. This greatly simplifies paleontological procedures and in many particular cases it averts the special taxonomic problems inherent in continuity of succession.

Essential continuity in sequences long enough to involve significant progression or diversification of populations is far from universal in paleontology. It is, however, frequent and becomes steadily more so as collecting becomes more extensive. The special problems involved therefore do have great and increasing practical importance. They are of supreme importance for paleontological taxonomic theory. No one seriously doubts that the whole of life has factually been a continuum of populations when the whole sequence is considered, in spite of the innumerable discontinuities in the record.

The genetical-evolutionary concept of species is applicable as between different phyletic branches, evolving lineages, especially if they are contemporary but also if they are not. Thus in figure 2A, *a*, *b*, and *c* are three different species, by genetical or, more clearly, by evolutionary definitions, although *a* and *b* are contem-

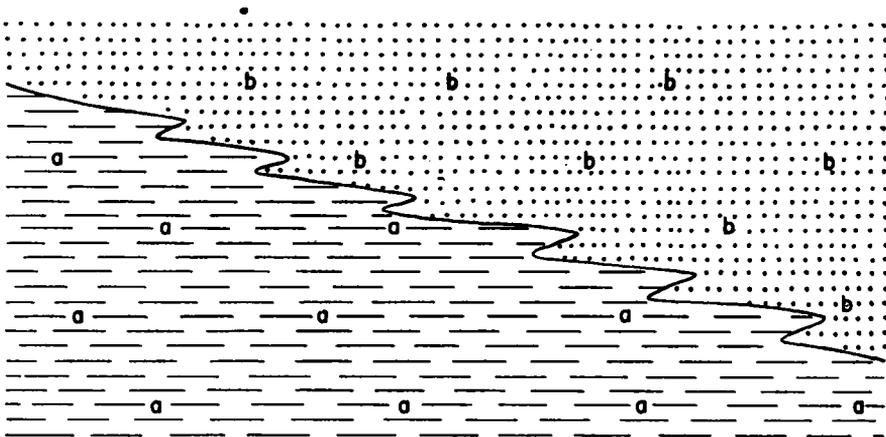


FIG. 1. Diagram of change of facies and fossil succession. Broken lines and dots represent two different rock facies each with a characteristic fossil, *a* and *b*. Although *b* everywhere occurs above *a* in any given local section, the two are, in fact, contemporaneous.

porary with each other but not with *c*. Serious problems in theory, and usually also in practice, arise rather regarding the parts of such a pattern that cannot be distinguished as separate branches.

One possible solution, diagrammed in figure 2B, is to recognize central lines as species and to distinguish branches as other species. This procedure is "correct" from an evolutionary point of view, or, better, the species so designated do fulfill the proposed evolutionary definition even though their delimitation is genetically arbitrary at the points of branching. For rather small groups under exceptionally favorable circumstances the procedure is also practicable and is actually used. Its practicability depends, however, on recognition of an essentially unchanging central line, *a*, and main branches, *b* and *c*. It is, however, more usual even within rather small groups and universal within really large groups and long sequences for all lines to evolve materially. Then it is not practical taxonomy to designate the whole of any one line as a single species, and there is no meaningful criterion for designating "main" or "central" lines and branches. Thus the four alternatives of figure 2C are all equally acceptable interpretations of the same phyletic facts as in figure 2A, in terms of main lines and branches, if all lines are undergoing progressive change. The only reasonable criterion of choice would be designation of certain terminal branches as more important, or somehow definitive, than others. A logical extreme would be, for instance, to take *Homo sapiens* as the supreme species and to consider its ancestry, from the beginning of life (or even before) as the main line, not specifically separable from *H. sapiens*. This arrangement has in fact been seriously proposed by a philosopher (Miller, 1949). Taxonomists will surely agree that this result and the whole procedure involved are impractical if not absurd.

Another possible approach is to recog-

nize each evolutionary lineage as a unitary species until it divides and then to consider the descendent branches as species distinct from each other and from the single ancestral line, as diagrammed in figure 2D. This grouping meets an evolutionary definition of species, although delimitations between adjacent species are arbitrary by genetical criteria. It is, however, both undesirable and impractical. It frequently happens that a population undergoes no essential change even though a branch, a separate species, has arisen from a part of it. •E.g. in figure 2D, *d* and *e* may be genetically and morphologically identical in all essentials. It is then not meaningful taxonomy to designate them as separate species. An even more serious objection is practical: the pattern of branching in a paleontological sequence is gradually discovered, perhaps never fully known, and generally depends as much on opinion as on unequivocal data. The taxonomy of long-known species would be changed every time a new branch was discovered or inferred and would be excessively and unnecessarily subject to personal disagreement. Moreover, a phyletic line may change radically between branches (say within *e* of figure 2D), and it is then not useful taxonomy to classify it as the same thing throughout.

The difficulties involved here are merely obscured by the presence of phyletic branching. They arise, regardless of whether or not branching occurs, from the problem of classifying ancestral and descendent stages in a continuously evolving population. Such a population may be diagrammatically represented, as in figure 3A, by a curve of variation (both genetical and morphological), moving through time and also being displaced as its genetical and morphological characters change. A cross-section represents the population at a particular instant in time, as it would be represented by a fossil sample from a single horizon. Such a cross-section is a genetical non-dimensional species, as seen both in neontology and in paleontology.

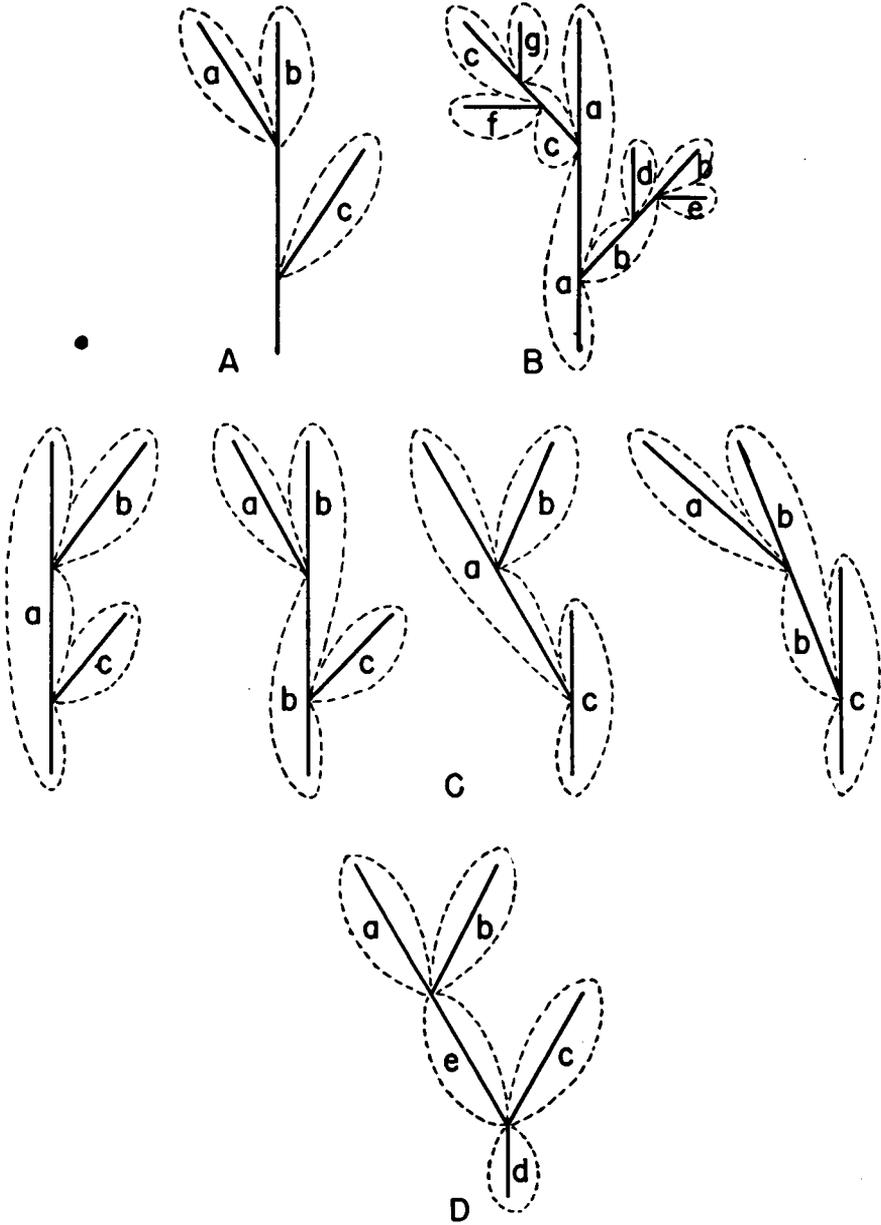


FIG. 2. Classification of successive populations with phyletic sequence and branching. In each diagram, the time sequence is from bottom to top and the solid lines represent phyletic descent. The broken lines enclose phyletic segments classified by various methods as distinct species. A, branching phyletic sequence with three clearly distinct evolutionary species, a-c. B, similar but more branched sequence with main lines and branches classified as species. C, four different possibilities of designating main lines and branches in the same phyletic sequence as in A. D, sequence as in A, with species boundaries set at points of branching. See discussion in text.

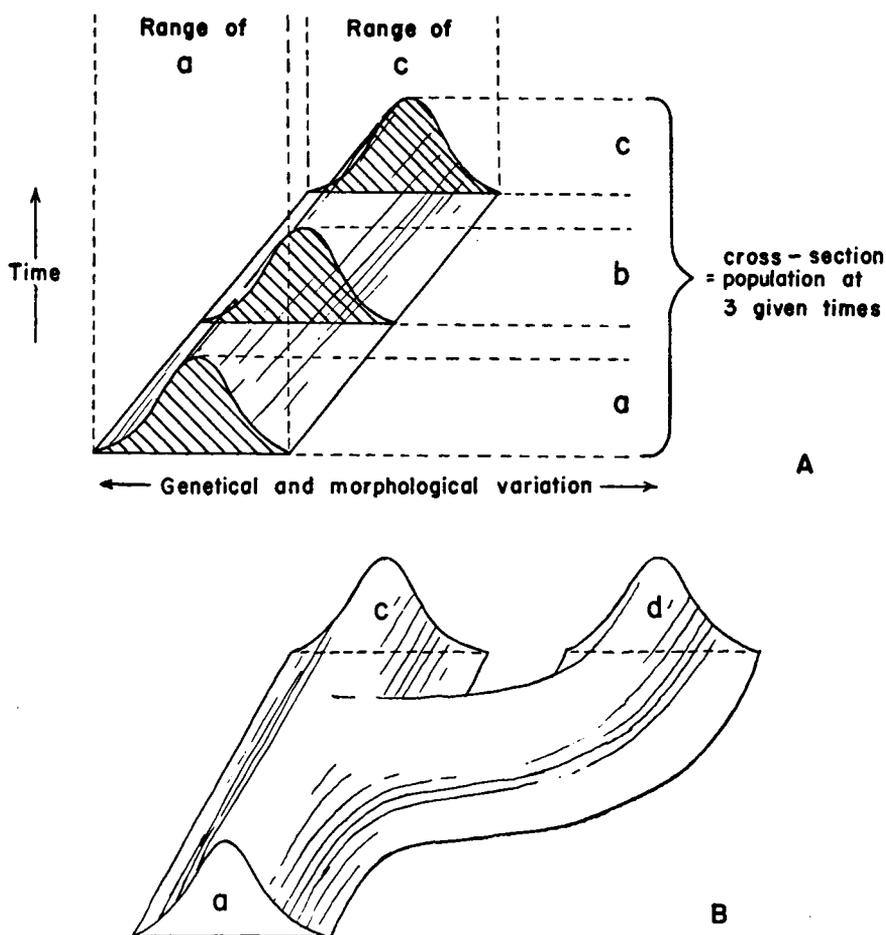


FIG. 3. Phyletic evolution and classification of successive populations. Phyletic sequence in a varying population is represented by a normal curve moving through time and changing in mean character, and by the solid generated thereby. A, sequence without branching. B, branched sequence. See discussion in text.

The whole sequence of populations, *a* to *c* in figure 3A, is genetically continuous and it fulfills the conditions of both genetical and evolutionary definitions of a species, as previously discussed. By these concepts, it is a single taxonomic group, defined as a species. Yet with the passage of time and continuation of progressive evolution, *c* has become quite different from *a*. For purposes of evolutionary study and of practical application to stratigraphy, it is essential that a distinction be made between these populations, which are different.

In practice, the paleontologist calls *a* and *c* different species if, as in figure 3A, the inferred ranges of variation do not overlap. They are *not* different species by the widely accepted genetical criteria or by the proposed evolutionary criteria discussed above. The comparison is clarified in figure 3B in which speciation (in the neontological sense) is represented as also having occurred. In this diagram, *c* and *d* are different species by any current usage; explicitly they are different genetical-evolutionary species and also different species in current paleontological practice.

But *a* and *c* are parts of a single genetical-evolutionary species, although called different species in paleontological practice.

The paleontologist thus uses the designation "species" for two sorts of entities which are radically and fundamentally incongruent. The only way in which the species category might be defined so as apparently to include both sorts of entities would be to abandon any evolutionary significance for taxonomy and to use purely morphological criteria. But this is not a useful solution. The general undesirability and impracticality of *purely* morphological taxonomic concepts have been sufficiently emphasized above. Moreover, the *whole* sequence of organisms represented in figure 3B cannot be classified at all, in morphological or any other terms, if the pattern in time, i.e. the evolutionary situation, is ignored. As static, separate pictures, the morphological difference between *a* and *c* and that between *c* and *d* are of the same sort, but within the pattern of the whole group in time, even the morphological relationships are not the same in the two cases, for *a* and *c* are morphologically (as well as genetically) continuous through intervening populations and *c* and *d* are not. (One might say here, in line with Dunbar, 1950, that *c* and *d* are continuous through the sequence *c-a-d*, but the fact that this involves a reversal in direction of time still makes an essential difference from the sequence *a-c* or *c-a*, which is consistent in the direction of time.)

In the situation represented in figure 3A, the desirable and indeed necessary taxonomic separation of *a* and *c*, whether they are called species or by some other category term, is arbitrary, because through intervening stages they are continuous by all meaningful criteria. The placing of an intermediate population, such as *b*, in one category or the other is, of course, also arbitrary. When the data really reflect the continuity of the sequence, intermediate populations must often be placed by rule of thumb rather than by any more positive and meaningful

criterion. It is in such situations that the frequent occurrence of discontinuities of record, the absence of part of the sequence *a-c*, is practically useful in providing a means of separating *a* and *c*. This is still a separation in what *was* a continuum, but it is non-arbitrary (by the special definition of that word in this paper) as regards the actually available materials being classified.

Since paleontologists are applying the designation "species" to two fundamentally dissimilar sorts of taxonomic categories, it would appear logical that they confine that name to one of them and use a different name for the other. This has also been suggested, but it runs up against another serious practical difficulty: the paleontologist often does not know and has no way to determine which of the two basically different sorts of groups called "species" he has before him.

It is a common situation to have two discontinuous paleontological samples such as *a* and *c* of figure 4A. (It has been noted that if *a* and *c* are discontinuous in space, the possibility that they are also different in time can seldom be ruled out.) By applying the practical methods previously summarized, the paleontologist can readily draw population inferences from these samples, find that variation probably did not overlap in the populations, and define them as different "species." However, he does not know in what sense they are different species, because he does not know whether the relationship is as in figure 4B or as in figure 4C, and unless other crucial populations can be sampled he may have no conclusive way of finding out. In dealing with different samples from closely similar populations, this is one of the commonest situations in the practice of paleontology.

In such cases, a distinction cannot be made in practice between "species" in the basic genetical or evolutionary sense and in the sense of subdivisions in a continuous ancestral-descendent line. I do not

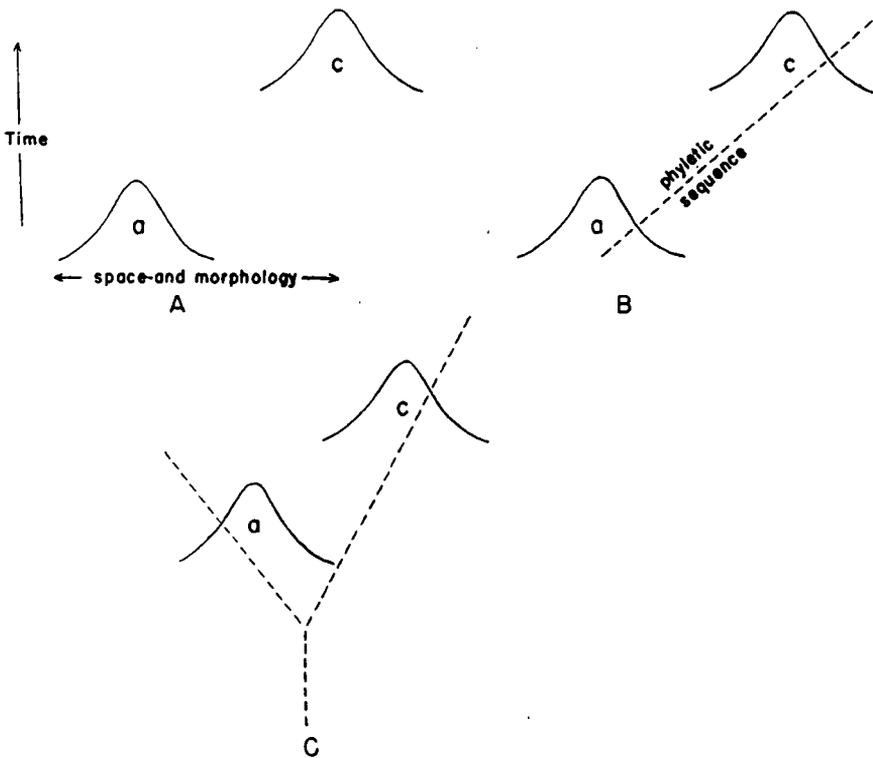


FIG. 4. Diagram illustrating problems of interpretation of two samples of related fossil organisms separated in space and (or, and possibly) in time. The variable populations represented by the samples are represented by normal curves. A, the given situation. B, interpretation as a single phyletic sequence, in which *a* and *c* represent the same species by genetic definition. C, interpretation as a branching sequence, in which *a* and *c* are different species by genetic or evolutionary definition. See discussion in text.

here favor or propose a special term for the latter sort of taxonomic group. I do maintain that it is desirable and useful to realize that these are two quite different things, and that the "species" of paleontological taxonomy may be of either sort.

There are many other pertinent and interesting points that might be considered, such as the problem of dual, partly coincident evolutionary species *a-c* and *a-d* in figure 3B, the uses of evolutionary acceleration and appearance of key characters for separating ancestral and descendent species, or the relationships of subdivisions of choroclines and chronoclines. This paper is, however, sufficiently long already, and the possible extension of its general point of view and

method of approach to other points will probably be evident to most taxonomists.

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