

TYPES AND HYPODIGMS

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ABSTRACT. As pointed out by Simpson, traditional attitudes toward the functions of type specimens, particularly in paleontology, seriously impede accumulation of knowledge about natural groups of fossil animals and plants. Until collections of specimens are viewed as co-equal members of a statistical sample, taxonomic species and subspecies will not closely correspond to natural groups. Simpson has introduced the term "hypodigm" for the statistical sample of a population. This sample can, and should gradually expand, and from time to time should be revised. The purpose of the present discussion is to call attention to certain limitations and principles that should govern the use of the hypodigm concept. Certain categories of types which would be abandoned by Simpson have, I believe, real curatorial value which argues for their retention.

INTRODUCTION

ESTABLISHED practice in the taxonomy of fossil organisms involves the use of type specimens to a much greater extent than with living species. Probably only a small proportion of living species are based on extant type specimens. The majority of kinds of animals and plants are too perishable to permit the use of types. Also, the teeming abundance of authentic duplicates in most cases has made the use of a single set of reference standards, such as a holotype or type collection, unnecessary. The situation is different with fossils. Well preserved *unquestionably authentic* representatives of a species in addition to the original type collection hardly ever are generally available. For this reason the original type series on which thousands of fossil species are based are unique in that they alone possess one or both of the following attributes: 1) In some examples the type specimens are the only well-preserved specimens known; 2) because of vague records, or inaccessibility of the exact stratum from which the original types were obtained, they commonly represent the only obtainable specimens definitely referable to a given time level. Hence, all additional specimens almost certainly belong to populations and races younger or older than those from which the types were collected.

Many paleontologists confronted by variation in time and space induced in organisms by evolution and ecological modifications generally have been impressed by the difficulty in

assigning limits to a given species. Lacking statistical data on the variability of practically all paleontological species, they have in practice, although perhaps unconsciously, assumed that in the last analysis the only "authentic" representatives are the holotype and specimens similar to it from the same locality and horizon (topotypes). The original types then, together with any additional conspecific specimens from the type horizon and locality, constitute a final court of appeal for purposes of comparison. According to this viewpoint the original types and topotypes, beyond any reasonable doubt, belong to a single or at least to very closely related populations, and they alone are incontrovertible. Comparison of other suites of specimens with these is subject to individual interpretation.

This method was necessary and useful before quantitative methods were applied to paleontological problems. Statistical analysis is still not widely employed in paleontological studies. We may be sure, however, that the ultimate requirements of refined stratigraphical and paleobiological studies call for recognition of persistent, obscure differences and real "identities" in separate fossil populations regularly demonstrable *only* by quantitative methods. These tend to reduce confusion arising from the play of individual judgment and experience, and will permit for the first time in the history of the science, cumulative increase in significant knowledge of species and subspecies. In the past, descriptions and revisions that do not include the original types, or topotypes of a species, have not been generally regarded as authoritative, hence, knowledge of these lower taxonomic categories under this system scarcely could expand.

In an inspired resumé of the type problem, George Gaylord Simpson recently has fired the first round in an attack on the traditional views toward types held by most paleontologists (Simpson, 1940). Like the majority of thoughtful taxonomists, he deplores the absurd extremes reached by existing terminologies of type specimens. By his tabulation these include more than 51 separate kinds of "types." According to the most elaborate schemes practically all collected specimens would belong to one or more categories of types.

The purpose of the present paper is to explore some of Simpson's proposals for a greatly simplified scheme that will

harmonize modern taxonomic theory with paleontological practice.

FUNCTIONS OF TYPES

Type specimens in ordinary paleontological practice have served as 1) bases for definitions, 2) as standards for comparison, and 3) as fixed biological points in variable populations to which binomial names are attached. According to Simpson, "the modern conception of taxonomy as involving the inference of population characters from samples makes it impossible for the same items properly to serve all three of these purposes. . . . The newer theory of taxonomy as a system of group concepts based on inferences about populations from samples . . . is decisively incompatible with this use of 'types'." (*Op. cit.*, p. 413.)

The three-fold function of types still generally in use in paleontology is a natural heritage of the "type" concept in neontology, only recently generally abandoned by students of living organisms. It is inevitable that the paleontologists, following the lead of zoölogists and botanists, will eventually learn to view their collections of specimens as *samples of populations*. As such, collections cannot individually define the characters of species. They can serve only as useful and valid measures of the particular populations to which they belong, provided, of course, that they are properly analyzed.

Species and subspecies are real in nature. They are groups of individuals that are closely related and that vary between limits, however vague and arbitrary.¹ Our concepts of species and subspecies are, of course, subjective and probably never can be more than rough approximations of the true species in nature. Nevertheless, one of the main objectives, perhaps the chief goal of the taxonomist, is to learn as much as possible about the subspecies or species, and every effort should be made to accumulate accurate and adequate information about their characters. Most forms are far more variable than commonly is recognized. An elementary statistical analysis generally is needed for a valid quantitative statement

¹For example, it is probable that evolution in time is generally or invariably a continuous process. Limits of species are drawn at convenient gaps in the fossil record. There is no reason to believe, however, that these gaps are universal, and annectent forms found after species boundaries are arbitrarily set must be dealt with just as arbitrarily.

of that variability. Likewise, two subspecies of a given species may be clearly and regularly separable only by means of appropriate quantitative methods.

THE HYPODIGM

Traditionally, the original or type collection is the basis for defining and limiting species. Individual variants which fall well outside the artificial limits set by the type specimens necessarily fall in some other category (species, subspecies, or "variety"). Under these circumstances the types *are* the taxonomic species. Clearly, species established on these premises have very little in common with species in nature. Furthermore, there is no provision in this method for accumulating new knowledge about natural species.

Simpson (1940) has shown by means of his *hypodigm* concept, how collections of specimens can provide significant data on natural species and this knowledge can be cumulative as new specimens are acquired. The hypodigm is the *population sample* by which characters of the entire population are assessed. The composition of the hypodigm changes as new specimens are added to it, and as original types or other specimens are removed as required by revision. At the time of description of a species (or subspecies) the hypodigm consists only of the type lot.² Subsequent critical studies of the species based on additional specimens should add to knowledge of the species *by increasing the size of the hypodigm*. The hypodigm then is really a statistical sample. As this sample increases in size by acquisition of new collections (by various workers at various times) the appraisal of the whole population, if *uniformly based on quantitative methods*, gradually approaches the facts in nature. The taxonomic species

² It appears to me that the type lot includes *all* of the specimens referred to the new species, subspecies, or "variety" by the describer in the original publication. If no holotype is selected all of the specimens are syntypes (cotypes). If a holotype is designated all of the remaining specimens are paratypes. A limited survey of usage, however, shows that some paleontologists adhere to the view that paratypes or syntypes must also be separately designated. According to this view specimens unspecified in the original publication are not types at all. I know of no authority for this, and it seems to me basically unsound. Even those specimens not referred to in the description and not critically studied enter into the author's impression of his species and influence the result. Hence, they form part of the type lot.

then will be objective and will resemble natural species composed of one or several whole populations.

The possibilities inherit in this concept are overwhelming in implication, and should lead to complete revision in paleontological thought and procedure.

FOSSIL POPULATIONS

There are practical difficulties and limitations in use of the hypodigm which I believe require careful consideration. The function of the hypodigm is to enable us to learn as much about natural populations as possible through the use of samples from those respective populations. Unfortunately, it is not at all clear how a fossil population may be defined or recognized.

A brief survey of neontological literature indicates that a population, amongst living organisms, is an effectively interbreeding aggregate which forms a gene pool more or less apart from other closely related aggregates. Through isolation, which may be of several degrees and kinds, a population may acquire distinctive gene properties. Under these conditions a subspecies may arise, being co-extensive with one or more populations. Further evolution may produce separate species, which generally comprise a large, but variable number of populations. In space, populations tend to be segregated geographically, or ecologically. In time, however, they certainly must occupy points in a continuous process of organic change. For this reason the vertical boundaries of fossil populations are vague in the extreme. Elsewhere (Newell, 1947, p. 163) I have tried to define (living and fossil) populations in time. "We may speak of past or future populations, or of successive populations. Thus, a population does not have time duration. A subspecies certainly does have time duration (because its vertical limits may be arbitrarily fixed), hence, a subspecies is composed of a succession of gradually changing populations."

It will be seen that only under closely limiting conditions can a hypodigm of fossils be restricted to specimens from a single population. Approximate contemporaneity in a collection of fossils cannot always be proved, and it is probable that most accumulations of fossil skeletons represent an appreciable span of time. At best then all of the specimens in

a hypodigm clearly should be closely related, and should exhibit approximately the random variation characteristic of single or very closely related populations. If the hypodigm is not critically assembled, significant errors through contamination will enter into the cumulative results. By definition "every specimen definitely referred (in publication) to a species is, or has been, part of its hypodigm" (Simpson, *Op. cit.*, p. 419). That is, every specimen studied and definitely referred by an author to a species is part of his statistical sample for that species, *i. e.*, is part of *his* hypodigm. Other authors, using additional material, will of course, have somewhat different hypodigms. Successive descriptions will progressively lead to refinement of elimination of spurious data, and there will be an overall tendency for the hypodigms to become more comprehensive and taxonomic boundaries will be extended with discovery of new specimens. In this way knowledge of variation in natural groups is cumulative rather than static as in the "type" method of comparisons with fixed standards.

Homogeneity of the sample is, of course, one of the primary objectives of the hypodigm. It is not implied that a fossil species or subspecies should be co-extensive with single populations. The hypodigms, even of living forms, include materials that are not strictly contemporaneous, and only approximate contemporaneity can usually be claimed for any two fossil individuals. A hypodigm is sufficiently homogeneous for taxonomic purposes if it displays approximately the random variation of the normal curve of frequency distribution. At least approximate contemporaneity of the individuals forming the hypodigm lends additional valuable evidence that the sample is not contaminated with homeomorphs or examples of parallelism. In most cases, an effort should be made to limit hypodigms to narrow stratigraphic units, or to single bedding planes in order to recognize the smallest stages in the evolution of a group. This may not be adequate or feasible in all cases. In the more slowly evolving animal stocks, species commonly are reported to range through an entire series or system. Careful work on such forms may show that collections from several horizons may profitably be joined into a single hypodigm which better reveals the group characters than do collections from a single horizon.

QUALIFICATIONS OF HYPODIGM SPECIMENS

One characteristic of paleontological materials in general is that they tend to be fragmentary or relatively rare. There are many exceptions, of course, but commonly it is impossible to assemble a large number of individuals from *a single horizon and locality*. Hence, a majority of fossil species were founded on "mixed samples," that is hypodigms which contain specimens certainly not of a single population. Less commonly, the original hypodigm contains representatives of two or more species, as every reviser well knows. This hazard should be recognized and noted, but probably it is not in itself adequate grounds for eliminating from consideration instructive isolated specimens if the original hypodigm is very small. It should be self evident that obscure but real and persistent morphological differences between two subspecies sometimes are recognizable only by means of adequate quantitative analysis. Hence, isolated individuals in such circumstances cannot, with certainty, be ascribed to the proper subspecies.

In consequence, any type collection which is composed of specimens from several horizons and localities is likely to lead to incorrect inferences, since it may not represent any natural group. In such an original hypodigm, I believe, contrary to Simpson's conclusion, that the members of the hypodigm should not be of equal rank. For the needs of revisers they should be clearly differentiated. One of the most convenient methods, that is already in general use, is the application of special terms to the most significant categories of "type" specimens.

TYPE TERMINOLOGY

For new work and review Simpson proposes abandonment of all type designations except the following: (Simpson, *Op. cit.*, p. 424);

Hypodigm—the statistical sample, distinguished from types and discarding the idea of types as bases for species and for comparisons.

Type—the single name-bearing and anchoring specimen. In review and revision only Simpson favors retention of the following:

Syntype—one of two or more specimens to which a single name was equally attached in the original publication.

Lectotype—a syntype subsequently selected to be sole name-bearer.

Neotype—a specimen substituted as name-bearer for one not now assignable to a definite hypodigm.

These are basic categories, but they do not satisfy all needs, in my opinion. In general it seems to me that a very useful function is fulfilled by a few additional kinds of types.

In the original type lot, or hypodigm, it is desirable to stress the circumstantial evidence that indicates which specimens possibly belong to the same subspecies or population, and which ones probably do not. It would seem sound practice to segregate the name-bearer, the holotype, or type as it is simply called by Simpson, together with all of the topotypes. This fraction of the hypodigm is likely to remain as a permanent part of the hypodigm; other specimens may be removed by a subsequent reviser. I agree fully with Simpson that paratypes (unless they also are topotypes) should be accorded no more significance than any other representative of the group in evaluating the species. In my opinion paratypes do play an important rôle. The merit in applying the term paratype to supplementary specimens in the original hypodigm is that the designation carries some prestige and is some insurance that the hypodigm will not be broken up for exchange purposes. It also stresses the published documentary value of the specimens. Implicit in the hypodigm concept is the idea that a large collection will tell more about a species or subspecies than will a small collection, and that a single type specimen will reveal very little about the natural group to which it belongs. For this reason it is urgent that large collections of a species be kept intact. I would term paratypes that come from *precisely* the same horizon and locality as the holotype topoparatypes, to distinguish them from the much less useful stray paratypes. It is clearly understood that the holotype and paratypes do not reveal any more information than subsequently described specimens of the group. Subsequently described additional specimens, in my opinion, are best segregated and designated in order to show that they also are part of a hypodigm. They are the hypotypes. To leave these published specimens without special designation en-

dangers their future preservation. The term diplotype³ for holotypes and lectotypes of genotype species is meritorious, it appears to me. As a name-bearer this category is pre-eminent, and a distinctive term as a safeguard is of great value for curatorial purposes.

In summary, I would recommend expansion of Simpson's list as follows:

Hypodigm
 Diplotype
 Holotype
 Topotype
 Paratype
 Topoparatype
 Hypotype
 Syntype
 Lectotype
 Neotype

³A few writers have consistently misused genoholotype for Knight's "diplotype." Genoholotype is the *type species*, it cannot apply to a single specimen.

REFERENCES

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