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Remarks on the Species Concept in Paleontology Author(s): C. W. Drooger Reviewed work(s): Source: The Micropaleontologist, Vol. 8, No. 4 (Oct., 1954), pp. 23-26 Published by: The Micropaleontology Project, Inc. Stable URL: <u>http://www.jstor.org/stable/1483957</u> Accessed: 17/07/2012 05:06

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Notes

REMARKS ON THE SPECIES CONCEPT IN PALEONTOLOGY

C. W. DROOGER

In the July issue of The Micropaleontologist, Esteban Boltovskoy raised the question of the species concept and related problems in the study of foraminifera. His article clearly shows the disadvantages of space limitations, as it deals with so many topics that the schematic treatment is sometimes in danger of being misunderstood. Nevertheless, Boltovskoy's article may be very useful for those who ignore the neontological species and subspecies concepts. Some very valuable warnings are given, although their background has to be necessarily very vague. At the risk of being equally terse, I would like to comment on some of the points raised by Boltovskoy.

First, the point concerning systematics and the meaning of species: Boltovskoy lists the four principal points of view, which are, unfortunately, so briefly defined that it would be difficult to find adherents of any of them. As they stand, I can find some truth in all four of them, as, in my opinion, they are not mutually exclusive. As to the first point of view, although I accept the natural basis of species, I can imagine numerous instances where a specific name is justifiable even though it is merely "a label invented for the sake of convenience." With regard to the second point of view, I think that species are not identical in zoology and in paleontology. In zoology, species (and to a lesser degree subspecies) are naturally defined units. In paleontology, the time factor necessitates the setting of limits that are subjective and more or less arbitrary, and in any case different from the limits in zoology. Finally, Boltovskoy differentiates systematics based on morphology alone from systematics based on phylogeny alone, but I am not aware of any clear contrast, since morphology and phylogeny are on different planes. Pure morphologic systematics must ignore all probable relationships and any hierarchy of characters with regard to their systematic values, and as such it seems to me to lead to utter confusion. On the other hand, phylogeny is a conclusion drawn from observations, mainly of the morphology. In itself, phylogenetic systematics is an ideal that may be achieved only when all morphological and other data concerning some group of fossils have been assembled, and even then its components must be expressed in morphologic terms. Classification is based on a variable mixture of morphology and phylogeny, in which morphology is primary.

In order to be able to estimate the relative influences of genetic and environmental factors on the observed morphologic characters, we must look for analogous Recent organisms and for conclusions drawn from evolutionary changes already observed. In this way, we can establish a hierarchy of individual characters with regard to their systematic values. The more correct the hierarchy, the better the classification will agree with phylogeny.

As for the species concept, I do not believe that it is recommended or even possible to prescribe a uniform rule for (micro)paleontologists. Of course, the paleontologist must approach the neontological concept as closely as possible, in so far as the available material allows him to do so. For the species in neontology, we may take, for example, Mayr's definition (p. 120): "Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." This obviously contains factors that can not be used by the paleontologist. Morphological details of the fossilized parts of organisms are, for the most part, his only data. But these data may enable him to recognize fossil populations by the unimodal frequency distributions of measurements of characters of the individuals in his samples. This allows him to establish morphologically the average (or the mode) and the range of variation of the original populations. With increase in the amount of such data on some groups of fossils, the populations tend to lose their distinctness as the discontinuities between them disappear. This consequence of the time factor, unknown to such an extent in neontology, necessitates the drawing of species limits within a continuous series of populations. These species limits, which will not usually be comparable between different groups of fossils, can best be established by the application of statistical methods to the hierarchy of characters. Some theoretical and practical approaches may be found in the literature (Burma, Sylvester-Bradley, and Drooger, among others). The paleontological species established in this way are, in my opinion, the closest to neontological species.

Subspecies in paleontology are still more difficult to deal with. Their neontological definition is of almost no use to us. Geographic separation alone can be clearly established by direct observation, but synchronism is much more difficult or impossible to ascertain. I do not see the latter fact as an objection, however. It favors the extension of the subspecies concept in paleontology to include series of populations at a single locality in the course of time. As a result, subspecies in paleontology may be smaller morphological steps in the change from one species to another, as well as geographically separated groups of populations that differ in characters of a lower rank in the hierarchy than those used in discriminating species. For the paleontologist, subspecies can stand only for groups of populations that differ from other such groups by differences that are smaller than those between species. Both species and subspecies in paleontology are arbitrary units than can best be established in monographic studies. The necessity of such work is more and more recognized nowadays, in micropaleontology as well as in other fields.

But what about the vast majority of cases, in which data are not yet complete enough so that species (and subspecies) limits can be set? We cannot ignore them because of our incomplete knowledge. The constant use of open nomenclature for them may, in the end, be even more of a nuisance than a wealth of specific names with variable bases which has accumulated from numerous faunal descriptions. Often an experienced paleontologist can predict population variation and even species limits fairly well, without possessing all the data that would be necessary to establish them the most accurately. There can be no objection to such species, provided all the available data have been given.

Two great disadvantages in micropaleontology are our frequent lack of knowledge of the hierarchy of the relatively few morphologic characters, and the difficulty of measuring them. In descriptions, this necessarily leads to enumerations of inexact data (in terms such as "more, less, rather," etc.), of different but often obscure importance. The next step, that of comparing such descriptions, entails a highly subjective evaluation of the systematic value of the observed differences. In these comparisons, much stress is automatically laid on the visual element, that is, on the few figured specimens, which can only poorly reflect the existing variation. A single individual, therefore, receives too much prominence, especially when the author has described only this one specimen (a wrong and condemnable application of the necessity of designating a holotype). In many groups of fossils, species have thus become arbitrary, ill-defined groups of individuals around a figured mean, a practice which furnishes the opportunity for "narrow" or "wide" interpretations. Relationships to the actual populations are mostly obscure, partly because of the author's neglect, and partly because of their inability to ascertain or to express these relationships adequately. In many cases, however, authors cannot be held responsible for their incomplete data; however, this fact does not exempt them from criticism for the many shortcomings.

Inability to give a clear description of highly variable populations has led to the practice of defining this variation by means of a number of types, between which all degrees of intermediate forms may have been found. This is the basis of many so-called varieties. I agree that numerous described varieties might better be called subspecies, but others represent artificial clusters in populations, which are equivalent to the species designated by similar arbitrary circles around holotypes. Of course, this is theoretically entirely wrong, but it is wiser to face the fact than to behave as if we were dealing with and describing only correct species and subspecies. The relatively small number of morphological characters in foraminifera and other simple organisms is no doubt responsible for the fact that the "variety" is a more persistent category in micropaleontology than it is in the systematics of higher organisms.

Both formally and theoretically, Boltovskoy is right in condemning the variety. The International Rules of Zoological Nomenclature do not allow for the use of it, and populations are more reliable units in systematics than are individuals. But individuals are an objective truth as components of populations. So if their occasional separate recording is the clearest way to approach the population, it does not seem prudent to neglect them on formal grounds. Giving them names as used in Linnean nomenclature is often preferable to non-Linnean indications. At the risk of being regarded as a heretic, it is my opinion that the variety had better not be ignored or denied, even if it may possibly be extended to include growth stages or ecophenotypes. When correctly employed and distinctly stated, it is a valuable aid in practice. It does not seem to overburden systematics with its names, since there are as many or more specific names required for populations that are in various ways composed of a group of varieties. This is especially true when variants haphazardly appear and disappear in time and space, probably without significance in evolution, but important in stratigraphy and ecology. They further may permit a more exact designation of the frequent discoveries of single (or a few) individuals, in cases where we do not know the position of the average of the original population. The recognition of varieties may also restrict their frequent and incorrect elevation to specific rank, a practice which tends to obscure the relationships between taxonomic units.

In short, so long as we are mainly accumulating data, the variety may still find a justifiable place. This is equally true in practical work such as stratigraphy. I think it preferable to use (with the utmost care) these special methods for our fragmentary paleontological remains, rather than to employ blindly prescriptions from neontology. In this way, we state the facts more clearly, and we are probably better able to avoid chaos than we would by attempting to attain a perfection that is still beyond our reach.

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PUBLISHING ON FORAMINIFERA

JAN HOFKER

When the author, as a young student, published his first paper on the Protozoa (*Protozoa van de Zuiderzee*, 1922), he included notes on many foraminifera. Many of his determinations proved to be erroneous, and had to be corrected in later publications. Quite the same can be said about the earlier works of Cushman on the smaller foraminifera.

Every advanced student of the small foraminifera knows that the task which he has set himself is an extremely difficult one. Gradually he learns to distinguish the multitude of forms with which he is dealing, and it often happens that his first impressions prove to be wroug.