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THE ADDRESS OF THE PRESIDENT

THE TAXONOMIC UNIT

T. C. STEPHENS

The retiring president is expected to follow the custom of addressing the Academy upon some subject of general interest. Fortunately, custom does not require that such an address shall embody one's own research or investigation; but it may consist of a survey, or of reflections of a general nature.

It so happens that certain fields in which I have been somewhat interested have brought me to a study of the problem of the taxonomic unit in biology.

One difficulty which concerns many working biologists, and which seems to be becoming more and more acute, is the determination of the living forms upon which they work.

Insofar as zoological and botanical work is to have a permanent value in science it must at all times be open to verification; and it must at all times be possible to relate observations precisely to the natural forms upon which they were made. The necessity of stability in nomenclature is obvious to all.

Our studies in nature have proceeded so far, and differentiations are becoming so refined, that the problem of nomenclatural stability is becoming one of concern. In fact, there may be no such thing as stability; in which case the problem would be to build up a system that would cause the least amount of confusion in its operation.

The "species question" is not new to you; and to most of you who are concerned with the biological field, at least, the tendencies are familiar. I have been loath to present to you a discussion of the species question, partly because of its venerable theme, and partly because it has received the attention of some of the most illustrious biologists, both of the past and of the present.

In fact, I think it was Darwin who exclaimed "How painfully true it is that no one has the right to examine the question of species who has not minutely described many." With this warning a wiser soul might hesitate to proceed further. And yet, the subject is one that cannot be evaded, and is one which cannot be solved for us by the science of any previous period.

In its philosophical aspects the species question is of interest; but from that point of view there is no pressing need of solution. As a scientific problem, however, it affects our daily work, and may become a barrier to progress.

Much has been said of the ideality versus the reality of the species concept. While the conception of a species may be purely a matter of the mind; and while there may still exist the debatable question as to whether the group or the individual is the real unit in nature; yet the fact remains that in practice we must have a unit.

When we endeavor to trace the historical development of any general idea in science it is customary to look as far back, at least, as Aristotle for a starting point. But in this case we do not find that Aristotle possessed any clear and defined notion of what we now call species. He recognized, and had names for, the different kinds of animals and plants, of course; but these differentiations were probably not based upon any generalized notions.

The first definition of species is usually attributed to John Ray, the Englishman, who lived in the seventeenth century. The dominant principle in Ray's conception was community of descent. As interpreted by Hertwig, Ray's definition of species was as follows: "For plants there is no other more certain characteristic for determining species than their origin from the seeds of specifically or individually like parents; that is to say, generalized for all organisms, to one and the same species belong individuals which spring from similar ancestors."

The next important contribution to the subject was made by Linnaeus, who said: "There are as many different species as there were different forms created in the beginning by the Infinite Being." ("Species tot sunt diversas formas ab initio creavit infinitum ens.") The problem in Linnaeus's time was to establish the reality of species and their immutability, rather than to examine critically the criteria by which they might be recognized.

Buffon's definition was: "A constant succession of individuals similar to and capable of reproducing each other." DeCandolle defined a species as "an assemblage of all those individuals which resemble each other more than they do others, and which are able to reproduce their like, in such a manner that they may be supposed by analogy to have descended from a single being or a single pair."

Johannes Muller and De Quatrefages followed in the same line of thought. The former referred to a species as "a living form represented by individual being, which reappears in the product of generation with certain invariable characters, and is constantly reproduced by the generative act of similar individuals." While De Quatrefages defined species as "an assemblage of individuals more or less resembling one another, which are descended or may be regarded as being descended, from a single pair by an uninterrupted succession of families." In these earlier years the conception of species was dominated by the principles of immutability and discontinuity.

More recently there has been a tendency to emphasize the value of physiological functions in the diagnosis of species and varieties. This seems to be an especially easy point of view for the student of bacteria and smaller fungi. The metabolic processes of the bacteria, for instance, seem to be more readily distinguished, if not more constant, than the structural peculiarities. And, of course, a very excellent case can be made out for the specificity of such physiological characters. It must be borne in mind, however, that back of every physiological process there must be a morphological organization which carries the same specific peculiarity. The same may be said of peculiar and characteristic secretions, such as gums, oils, alkaloids, etc.

During the early part of the preceding generation there was a trend away from the Linnaean conception of species. Thus, Huxley expressed his conception of species in this language: "When we call a group of animals, or of plants, a species, we may imply thereby, either that all these animals or plants have some common peculiarity of form or structure; or we may mean that they possess some common functional character."

Haeckel says that the word species "serves as the common designation of all individual animals or plants which are equal in all essential matters of form, and are only distinguished by quite subordinate characters."

In this latter group of definitions we will observe that the principle of structural similarity is dominant. Nothing can be more evident to the biologist, who is compelled to deal, even superficially, with the nomenclature of organisms, than that fundamental concepts and terms are in marked process of change. Half a century ago Professor Owen remarked: "I apprehend that few naturalists nowadays, in describing and proposing a name for

what they call a 'new species,' use the term to signify what was meant by it twenty or thirty years ago."¹ It may be agreed that concepts must change with the development of knowledge, but it would seem that scientific terminology ought to remain as near constant as possible.

After this rather brief historical survey of the species concept it will be germane to inquire as to what concrete criteria have been, or can be applied. The analysis shows that there are three such criteria, viz., the genetic, the physiological, and the morphological.

The idea that hereditary descent is the essential test of specific rank seems to be the oldest and original point of view. As intimated, this was Ray's conception. This criterion is definite, but it fails in allowing for no expansion, no evolution. By virtue of continuity a species is always the *same* species. And this is manifestly in contradiction to the modern viewpoint. This criterion furnishes the basis for the modern principle of intergradation.

The criterion of relationship can have little value, because all forms and all groups, including subspecies, species, genera, etc., are related in this sense. So that relationship is a common property, and not a differential character. Furthermore, in nature it is usually impossible to know the parentage of forms.

The physiological test of species has had a long and honorable past. Many older writers were quite firmly convinced that true species could not interbreed. So that, interspecific sterility was accepted as a true test of a proper species. Time has shown, however, that it is not.

There are recorded cases of sterility in hybrids; there are recorded cases where sterility results from a cross in one direction, and fertility results from a cross in the other direction; there are recorded cases where fertility results from a cross in both directions; and there are, apparently, a few cases in which the hybrid shows a greater degree of fertility than in normal fertilization.

Such facts indicate, no doubt, that all species do not possess the same degree of difference, physiologically, at least. But they also show that there is no constancy in the matter of sterility in hybrid offspring, and that such a criterion cannot be used in the test of species.

Aside from the matter of reproduction some functions have been regarded as having specific value; for example, in the pro-

¹ "On the Osteology of the Chimpanzees and Orangs." Trans. Zool. Soc., 1858.

duction of certain secretions, such as gums, alkaloids, etc. Most especially, in the study of large groups of minute parasitic organisms, like the bacteria and other fungi, the effects of their metabolic activities upon living hosts or upon culture media not only are characteristic, but are quite easily discerned. The minute size of many of these organisms makes the application of the morphological test somewhat difficult. And while expediency may justify the use of physiological characters in such cases, this should not blind us in recognizing the inadequacy of this principle in general.

We may now consider the morphological criterion, viz., that similarity of structure brings individuals within the limits of the specific group, regardless of ancestry — known or unknown.

It goes without saying, almost, that we can have no other criterion for extinct species, whose only remains are structural. In the examination of structure we are able to measure and compare. All of the data are present. It remains but to fix the limits and bounds. Such a criterion of species harmonizes with the conception of a variable and mutable species.

But when the species varies or mutates beyond the confines of the defined species it becomes something else, under our eyes, just as we assume others have done in the prehistoric past. For, in the words of L. H. Bailey, "This notion that a species, to be a species, must have originated in nature's garden, and not in man's, has been left over to us from the last generation."²

The taxonomists of the present generation in science have not entirely graduated from the Linnaean conception of species, particularly as it includes the idea of fixity; although they are prone to look with disdain upon his meager binomial vocabulary. They mistake continuity for fixity and immutability. In their laudable efforts to harmonize classification with the probable phylogenetic history they forget that all groups above the individual are, in a measure, artificial and arbitrary, and of necessity must be, since we have no authentic record of their phylogenesis.

Our conclusion is, then, that the only true and scientific criterion of species is the one based upon morphology.

To what extent may the differentiations of living organisms be useful to science? What degree of difference should be recognized taxonomically? We may readily understand that where such living forms are under experimental observation for the purpose of determining genetic relationships, considerable care in cataloguing minute variations may be necessary; but where

² Survival of the Unlike, page 110.

individuals are taken at random in nature, the same thing is not true.

It is interesting to learn that new forms in a single group (birds) are being recognized and named at the rate of about one thousand per decade in a single zoo-geographical region (Africa).³ Many of these newly described forms are, doubtless, subspecies. The subspecies is a modern refinement of the older unit, the species, with the drawback that it is far more difficult to handle, requiring a considerable amount of material and a degree of skill possessed only by the specialist. The subspecies unit is being introduced not only in Africa, but also in America, and not only among birds, but in other groups of vertebrates and invertebrates, and in many of the groups of plants. The question as to the serviceability of this modern unit is, then, germane.

The subspecies lacks even the capacity for exact definition that is possessed by the Linnaean species. The only characteristic of subspecies is *intergradation*. The only avowed justification, on biological grounds, for recognizing and cataloguing subspecies is to provide for the possibility of detecting incipient species.⁴ That it may be done on other grounds cannot be denied.

But, in order to provide for the very probable possibility of discovering incipient species some taxonomists, and others, seem to be willing to submerge the whole nomenclatural system into confusion and chaos. Perhaps it may be said, without injustice, that at the present time there are certain groups of both animals and plants whose taxonomy and nomenclature have reached such a state of confusion in about a direct proportion to the attention these groups have received from taxonomists — and this mostly a result of multiplication of subspecies.

When a group has been pretty thoroughly worked over for all the subspecies it will yield there will be nothing left for taxonomists to do but to make further revisions with the admission of hypersubspecies to be designated in tetranomials, and so on.⁵

³ *The Auk* (XXXVI, page 452) quotes *The Journal fur Ornithologie* (January, 1918) as authority for the statement that 979 new forms of birds have been named for Africa during the years 1905 to 1914.

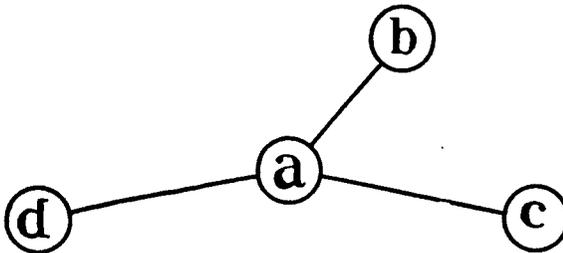
⁴ A clear-cut discussion of this question is to be found in certain papers in recent numbers of the *Journal of Mammalogy*. Dr. C. H. Merriam attacks the principle of intergradation and defends the morphological test. (Volume I, No. 1, pp. 6-9, 1919.) Mr. P. A. Taverner defends the principle of intergradation. (Volume I, No. 3, pp. 124-127, 1920.)

⁵ I am indebted to my colleague, Dr. A. W. Lindsey, for the following contemporaneous entomological example of taxonomic excess: F. E. Watson (*Journ. N. Y. Ent. Soc.*, XXVIII, page 232, 1920) described and named the following aberrant form of an Hesperiid, viz., *Poanes hobomok* form ♀ *pocahontas* ab. *friedlei*. *Pocahontas* is merely a melanic unisexual dimorphic form of *hobomok*, which varies considerably in the extent of its pale maculation. *Friedlei* is merely the darkest form of *pocahontas* yet recorded, and its christening seems to carry the matter to an unnecessary and objectionable degree. And, worst of all, the single type specimen

There is no logical reason for stopping short of this, and no law to prevent it. It would seem that the tendency here referred to is a result of a perverted specialization. One is led to wonder whether such a practice is designed to further the ends of science, or to furnish an occupation.

The whole problem of the determination of specific rank has been in the tentative stage from the beginning, and there is some reason to suspect that it will always be a matter surrounded with difficulty and variance of opinion. What is to be gained, therefore, in attempting to establish another hypothetical unit below the species?

There are two possible conceptions of specific variants. These variants may be regarded as due to fluctuating (continuous) variations, and their relationship should be represented by some sort of a radiate pattern, thus:



Or they may be due to orthogenetic variations, and should be represented in a linear system, thus:



In the latter case, no matter where we assign the ancestral type in the system, it need not have *direct* continuity with all of the other forms. So that, if A, B, C, and D are named forms of subspecific rank, and if A is regarded as the prototype, then B may be a subspecies, but not so with C and D. C might be called a hypersubspecies.

It might be supposed that D would differ from A to such an extent as to justify specific rank; but, according to a principle which has grown up in modern systematic zoology, so long as intergrading forms exist between A and D, the latter cannot be

of *friedlei* was reared artificially, and under such environmental conditions as produced also an unusually dark male; but the aberrantly dark male escaped a christening. To some this procedure will seem to be a prostitution of the purposes of taxonomy and nomenclature.

assigned to specific rank. Thus, no matter how unlike A and D may become, the presumption of common origin, as evidenced by intergrades, prevents their recognition as distinct species. This principle (of intergradation) is untenable from a general biological viewpoint because it is inconsistent with the doctrine of evolution. It is, in fact, a vestige of the discarded doctrine of immutability of species. How specific rank can be granted to *Lynx canadensis* and *Lynx ruffus*, for instance, and then denied to the extremes of variation in the Great Horned Owl, merely because of the existence of intergrades, is a puzzle which puts a strain on one's logical faculty.

On the other hand, if the study of any group of subspecies or varieties would permit their arrangement into a radial system, the explanation would be in harmony with well-understood biological principles, and with the facts of continuous variability. This system requires a prototype, hypothetical or known, upon which the name may be bestowed. The radial variates, continuous variations, are designated simply as varieties when it is necessary to distinguish them at all. Theoretically discontinuous variations produce species at once, and leave no intergrades.

I believe that ornithological taxonomists have found it usually impossible to determine prototypes among subspecies; and they have been satisfied merely to catalogue different forms which individual opinion may regard as having subspecific rank.⁶

What is to be gained, of value, by naming continuous variations, or any particular assemblage of continuous variations, such as a variety or geographic race? Will it not weaken an otherwise fairly satisfactory system of nomenclature? It is quite true that any one of them may represent an incipient species. And it is easily conceivable that any one may proceed in the development of still further unlikeness from the form with which it may be most closely related. The incipiency of this sort of thing seems to be too small a matter to be provided for in a nomenclatural system. As Loomis says, "In trying to manufacture a nomenclature for birds of remote ages, past and future, are we not putting an impediment in the way of the study of existing birds?"⁷

⁶ It is true that a committee of the American Ornithologists' Union has acted as a court which accepts or rejects proposals of new forms of North American birds; for some years the rulings of this committee were satisfactory and generally accepted. More recently the committee has not, apparently, been functioning. It is assumed that the flood of "revisions," with a perplexing array of newly proposed subspecies, has laid upon this committee an impossible task. It seems, at least, that such must be the inevitable outcome of the application of the principles of intergradation, subspecies, and trinomial nomenclature.

⁷ *The Auk*, XX, page 299, 1903.

Along with the subspecies unit comes trinomial nomenclature. The greatest objection to this lies, perhaps, in the difficulty involved, and the consequent restriction in use. It will not help to say that subspecies and trinomials are for the use only of taxonomic experts, and that others may be content with the species unit. There must be a common ground in order to promote coöperation and prevent misunderstanding and confusion. The taxonomist has no license for erecting a system which is unrelated to other biological fields. It must be emphasized that taxonomy and nomenclature are tools of the biologist, and not a branch of science *sui generis*; they serve no useful ends apart from their relation to other branches of biological knowledge. Thus the biologist has a right to discuss the manner in which taxonomy is helpful, or otherwise.

Other objections which have been offered to the subspecies unit and trinomial nomenclature may be summarized as follows:

(a) There is usually a variance in the judgment of the experts on the relative value of the minute characters upon which subspeciation is based.

(b) Subspecies and trinomials represent no stopping place, but lead directly to tetranomials and polynomials.

(c) Such ultra-refinement thwarts the purpose of any system by introducing uncertainty and lack of precision in the ends which taxonomy is designed to serve. For the sake of argument we might grant that the expert taxonomist might be able to work precisely even with subspecies, but we would immediately reply that that, in itself, would serve no useful end. When we split our subspecies one or more times we will be back to the good old pre-Linnaean days when, as pointed out by Loomis,⁸ the Mockingbird was distinguished by the name of *Turdus minor cinero-albus non-maculatus*. Yet this is simplicity in comparison with the multiplicity of trinomially designated forms which only a half dozen persons in the world, perhaps, are qualified to determine.

(d) As urged by some of the British ornithologists when the trinomial system was proposed by the American school, perhaps the greatest objection is its liability to abuse. That such abuse has been practiced one example will suffice to show. In the recent pages of the leading American ornithological journal a new subspecies of teal duck was described, in which the differential character was the extension of a white crescentic patch from the

⁸ *The Auk*, XX, pp. 294-299, 1901.

front of the head around to the mid-occipital region, where the two white bands fused.⁹ In the next issue of the same journal a writer reported that a duck of the same supposed subspecies, which had been kept in captivity in a public park, had molted a splendid example of the species.¹⁰

Finally, and in summary, the preceding remarks may be interpreted as a protest against the substitution of the subspecies for the species as a taxonomic unit. It seems unnecessary to offer evidence that there is a strong tendency in this direction.

Simple binomial nomenclature permits the designation of subspecific forms (i.e., varieties) where necessary in biological investigation, by the use of the term "variety" (usually abbreviated) followed by the varietal name. By this method no attempt is made to establish a new unit, and yet it provides a means of distinction where such is needed. By it incipient species may be recognized without jeopardizing the usefulness of the specific unit. In other words we would return to the *status quo* prior to the use of the trinomial system.

⁹ *The Auk*, XXXVI, pp. 455-460, 1919.

¹⁰ *The Auk*, XXXVII, pp. 126-127, 1920.