

## SOME ASPECTS OF THE SUBSPECIES QUESTION.

BY WITMER STONE.

WHEN Linnaeus devised his binomial system of nomenclature, a species no doubt seemed to him a very definite thing about which no one could have the least doubt; but ere long we find him marking certain forms with an "a" or "b," etc.—forms that seemed to be worthy of recognition by name but which in some way, did not seem to measure up to the others in the sharpness of their definition.

These were the forerunners of the subspecies, although earlier polynomial authors were not entirely ignorant of their existence!

Ever since then the problem of species *vs.* subspecies has been an attractive, if not always fruitful, one for discussion. It may seem foolish to take up the theme again but it possesses a lure that seems to challenge one's wits, and after all it may not be out of place once in a while to revive it to see if any progress has been made in its solution.

Furthermore to some of us it recalls the days when master minds at A. O. U. meetings waged wordy wars in the discussion of its pros and cons. How many of our members, I wonder, remember Dr. D. G. Elliot's eloquent presidential address on "The Inheritance of Acquired Characters," or have read the discussion in 'Science' for 1897, participated in by no less authorities than J. A. Allen, C. Hart Merriam and Theodore Roosevelt?

When these discussions were occupying our minds the geneticists had hardly begun *their* investigations into the origin of species and such everyday terms as chromosomes, hormones, gametes and zygotes were unknown—and doubtless the word geneticist as well! Systematists concerned themselves wholly with the operation of external environmental factors in the formation of species and subspecies.

Since then, however, immense strides have been made in genetics and the study of the germ cell, with the result that a new light has been thrown on the species *vs.* subspecies problem and a new opportunity for difference of opinion opened up, splitting the geneticists and systematists wide apart, on a problem not even thought of when Drs. Allen and Merriam argued on the proper way to distinguish species and subspecies. To state the case briefly I cannot do better than quote the words of Dr. Percy R. Lowe and Mr. Macworth-Praed,<sup>2</sup> two ornithologists who embrace the theory of the geneticists. They say: Species and subspecies differ radically; species are mutational variants, presenting characters which are directly derived from the action of "factors resident in the germ plasm and which are therefore heritable."

---

<sup>1</sup> Read at the Fifty-second Stated Meeting of the A. O. U., Chicago, Oct. 24, 1934.

<sup>2</sup> *Ibis*, 1921, pp. 344-347.

"Subspecies are mere environmental, unstable, and essentially superficial variations which would quickly disappear if the organism were transferred from its normal environment to some other of a different nature."

The majority of systematic ornithologists, on the other hand, claim that species and subspecies are similar in origin and potentialities and differ only in that species are completely isolated from one another, while subspecies intergrade, and further that subspecies are incipient species; a species first disintegrating into several subspecies through various environmental influences and these eventually becoming distinct species through further differentiation or isolation.

Upon these rival claims we have recently received much light through the painstaking experiments of the eminent geneticist, Dr. Francis B. Sumner. His investigations, involving the rearing of many generations of several geographic subspecies of White-footed Mice transferred to environments different from those in which they occurred naturally, are familiar to us all. Briefly, he found "that the peculiarities of the geographic races or subspecies are wholly genetic and that the environment may have a well marked directive influence upon them [variations] is the belief of many students of distribution."

While Dr. Sumner's researches constitute one of the most important contributions to this subject and strongly support the stand of the systematist he does not solve the less important but more widely discussed problem of the difference between species and subspecies in actual practice. This was the topic involved in the Allen-Merriam-Roosevelt discussion, and the one with which systematists have been most concerned.

Dr. Merriam, summarizing the statements in the A. O. U. 'Code,' says:

"Forms *known* to intergrade, no matter how different, must be treated as subspecies and bear trinomial names; forms *not* known to intergrade, no matter how closely related, must be treated as full species and bear binomial names." *Science*, May 14, 1897, pp. 753-758.

He then states his proposal for what he regards as an improvement upon this plan:

"Forms which differ only slightly should rank as subspecies even if known *not* to intergrade, while forms which differ in definite, constant and easily recognized characters should rank as species even if *known* to intergrade." [Italics mine.]

In other words the old criterion of "intergradation" as the touchstone of trinomialism is changed to one of degree of difference, and Dr. Merriam adds that a knowledge of the degree of difference between related forms is infinitely more important than a knowledge of whether or not the intermediate links connecting such forms happen to be living or extinct.

It was the hope of those formulating the A. O. U. 'Code' that the criterion of intergradation would eliminate the personal equation from the question of which forms were species and which subspecies, but Dr. Merriam very truly points out that authors usually exercise their individual judgement as to the probable existence or non-existence of intergrades, thus introducing the personal equation it was hoped to avoid.

Dr. Allen, always the valiant defender of the 'Code,' was of the opinion that Dr. Merriam's proposal to use degree of difference as our criterion would enlarge to the widest possible extent the personal equation element.

The truth is that the personal equation figures in any plan that has been suggested and cannot be eliminated.

At the A. O. U. Meeting in Washington in 1902, the late Dr. Nelson presented a paper on the evolution of species and subspecies as illustrated by certain Mexican Quail and Squirrels and, as I recall it, he found it necessary to reduce several supposedly well marked species to subspecific rank. Dr. Merriam and the present writer on this occasion advocated allowing them to remain as species regardless of the intergrades that had been found; and after thirty years I am still of the same opinion.

Let us look at the facts in cases similar to this and at the character of, and variations presented by, both species and subspecies, using the term "form," as is usually done, to indicate either group.

We have some forms in a genus which are so different from one another that they have always been regarded as species; they may or may not occupy the same or overlapping territory during the breeding season. The Downy and Hairy Woodpeckers, for example, or the Song and Swamp Sparrows.

We have other forms with identical breeding ranges (to some extent at least) but which differ from one another very slightly and yet do not intergrade. These too have always been considered as species, as the Olive-backed and Gray-cheeked Thrushes; the Acadian, Least, and Alder Flycatchers. Then we have forms occupying different but usually contiguous breeding areas and intergrading in the strip lying between their ranges. These constitute the great majority of our subspecies.

Still other forms have completely separated ranges but their characters overlap in one or more details and these are also usually regarded as subspecies. They include (a) European and North American representatives of a wide-spread species; (b) island forms, which are representatives of close-by mainland species.

Now in the course of consistent application of the criterion of intergradation we are often forced through the acquisition of additional material to reduce many formerly respectable species to the rank of subspecies and in some cases we are confronted by a series of related forms which at one end

of their combined range react as species while at the other end they intergrade. Thus we have recently been forced to regard Woodhouse's Jay and the California Jay as subspecies though they do not intergrade and probably would not if their ranges were brought together, yet they are connected through a long line of Mexican forms.

So the status of many forms is constantly changing back and forth either through the accession of more material, or through the different mental attitude of the last reviser of the group.

Now let us consider what we actually do in deciding the status of a given form and how far we base our decision upon intergradation which we think is our criterion.

If it has a breeding range identical or partly identical with that of a more or less similar form we regard it as a species. If on the other hand its range is distinct but contiguous we either find intermediates or *infer* that they exist, and denote it as a subspecies. I venture to say that we infer in the vast majority of cases if the difference is slight. If it is more marked we hesitate to infer and often let it stand as a species awaiting more material. In other words degree of difference looms large in our decision. Have we not all commented at some time or other on a form as a "*mere* subspecies," obviously with the idea of degree of difference uppermost in our minds. And when we describe birds from foreign countries with only a few, or even one specimen available, do we not invariably judge of its specific or subspecific status on the basis of degree of difference? More than once I have heard the comment "Oh that is *very* different, that is a *species*." Evidently no question of intergradation came up there!

The proposed method of designating very distinct "so-called subspecies" as species, is of course a matter of arbitrary judgement, *i. e.* personal opinion. But so is our present method. In passing on the status of North American and European representatives of the same type of bird for the 'Check-List' there was every sort of variation of opinion expressed by members of the Committee and the results are neither consistent nor dependent upon intergradation.

In the case of island forms, as those off the coast of California, the decision as to whether an island form is worthy of a distinctive name of any sort is based upon the degree of difference, and so also in deciding whether a proposed new genus is to be accepted as distinct from an old one.

If we make use of the degree of difference criterion to such an extent, why not go a bit farther and recognize many well-marked subspecies, usually former species, as full species even though some intergrades do exist—and how are we to be sure just when the last intergrade becomes extinct?

We must realize that by no means all subspecies as at present recognized, are of the so-called "millimeter" variety, some of them are far more different

from one another than are many species, but the fact of intergradation compels us to regard them as subspecies.

The big Aleutian Song Sparrow is a subspecies according to our present criterion; the pale Seaside Sparrow of Cape Sable is a species; yet both, I have little doubt, are of almost, or quite, identical status from an evolutionary point of view.

Now what do we gain by substituting degree of difference for intergradation in such cases? We are able, in the first place, to put the wide-spread criticism of subspecies squarely upon the category of subspecies against which it is really directed, and free a number of forms which are sufficiently different from their closest allies to be readily distinguished even in the field. We also make much clearer to those interested in general ornithology how many *kinds* of birds there are. For example a gentleman anxious to form a representative collection of North American birds recently told me that he did not desire *any* subspecies, having evidently formed his idea of subspecies from some of the races which can only be separated by experts with abundant material. When shown a Boat-tailed Grackle and an Aleutian Song Sparrow he said: "There must be some mistake, surely those are not subspecies!"

From a purely technical point of view it matters very little what rank any form may be given, since its identity and its individual name (either binomial or trinomial) are always preserved, but for the broad zoologist and the general body of ornithologists it is far more useful and practical to have the readily distinguishable forms of bird life in one category and the very closely related forms in another.

Many German writers, carrying out their idea of the "formenkreis" or evolutionary group, found it quite practical to associate species and subspecies in a single group without altering the names, just as we associate them in our genera, and after all our aim should be to try to find some way by which we may indicate phylogeny or genetic relationship without destroying the permanency of the name of the organism. The main trouble with our present system of nomenclature is that we try to give an object a name by which it may always be known and then continually change that name to indicate the evolution of the organism or its genetic relationship. In other words we try to use a name for two quite different purposes.

It has been argued against the arbitrary designation of certain forms as species when we know that they intergrade, that there will be a number of specimens which cannot be definitely relegated to one or the other but we have exactly the same situation in the case of subspecies where the intergrades cannot be referred definitely to either race.

Now let us look at another side of the question. It would seem that many ornithologists have already departed from the intergradation criterion

so that we are faced with two sorts of subspecies to the further confusion of systematic ornithology. This is attributable to the "Formenkreis" idea so popular in Germany and many writers in attempting to emphasize the genetic relationship of a group of forms, including both species and subspecies, make them all subspecies of a single species. The result is the exact reverse of the plan I have advocated and leads to the multiplication of subspecies and the reduction in the number of species. These writers have departed entirely from the idea of intergradation but have gone in the wrong direction!

Dr. Hellmayr in his admirable 'Birds of the Americas' (Part VII, p. 5) makes *Corvus caurinus* Baird from the northwest coast of North America, a subspecies of the Fish Crow (*C. ossifragus*) of the Atlantic coast of our southern states; the California Jay (*Aphelocoma californica*) a subspecies of the Florida Jay (*A. coerulescens*); and the San Lucas Robin (*Turdus confinis*) a subspecies of *T. migratorius*. There is no question of intergradation in any of these and his comment in the last case that *T. confinis*, is obviously "merely an excessively pale race of the Robin" seems to indicate that degree of difference *only* was in his mind.

A still more conspicuous example of this sort of thing is seen in Dr. B. Stegmann's recent review of the larger Gulls of the World<sup>1</sup> in which he reduces all of them to subspecies of five species; our Slaty-backed and Western Gulls (*Larus schistisagus* and *occidentalis*) being made subspecies of the Black-backed Gull (*L. marinus*), and the Iceland and California Gulls (*L. leucopterus* and *californicus*) of the Herring Gull (*L. argentatus*). Obviously there is no question of intergradation here and how such an arrangement could result on the basis of degree of difference it is hard to understand. If there were ever sufficient degree of difference to constitute a species, surely it is to be found in the case of these Gulls which Dr. Stegmann has joined together!

If the subspecies idea is to be carried to such an extreme, we had better return to Bowdler Sharpe's plan of designating every form of bird by a binomial (specific) name no matter how much or how little it differs from its nearest relatives, or in what manner.

As a matter of fact there is so much difference in the ideas of different writers as to what are subspecies and of which species a given form shall be regarded as a subspecies, that it is often difficult to know where to look for the race in which we may be interested, while the confusion created in the arrangement and labelling of museum collections and in indices to published journals is enormous.

Another aspect of the subspecies problem is seen in the attempt of certain authors to abandon the use of subspecies, more especially in papers based upon field identifications. It is claimed that where actual specimens are not

<sup>1</sup> Jour. für Ornith., July, 1934.

obtained it is impossible to be certain as to which race we may be studying, and that the use of the subspecific name of the race known to occur in the region is unscientific, therefore we should use only the specific or binomial name. The chief objection to this practice is that the binomial name has been used in so much of our literature to indicate the so-called typical form that it is very confusing to use it for some other race. For example, to record *Melospiza melodia* from the coast of British Columbia when the bird we have called *M. melodia* (more properly *M. melodia melodia*) is well known to be restricted to the Atlantic slope of the United States. A far better practice would be to write *Melospiza melodia* subsp., as is often done.

The practice, however, seems to be unnecessary unless it is known that several races are likely to occur in the region. It resolves itself into a question of our ability to identify a bird in the field. Many subspecies as already stated are as easy to identify in the field as are many species and we could just as logically say that we should not record any sight records of the Thrushes or small Flycatchers except by the generic name! When we know that a certain subspecies is the one occurring at a given locality there is a very slight chance that the individual we have seen there belongs to some other race. When an author uses only the binomial name of a bird in the heading of a note while in the text it develops that he has specimens and has made the necessary subspecific determination (and this has been done in some recent publications), he is creating trouble and annoyance for anyone who wishes to consult or quote his paper and is simply shirking his duty.

There is the same desire in some quarters to abolish English names for subspecies and to provide one for each specific group and the recent 'Check-List' has been blamed for failure in the latter case, the critics apparently overlooking the fact that no names for specific groups have ever been provided in *any* of the editions of the 'Check-List.' Furthermore if they were to try it they would realize the difficulties of the proposition!

Were the more distinct subspecies recognized as species and a check put upon the relegation of perfectly distinct species to the rank of subspecies such a plan might be feasible without too much violence to historic nomenclature, but it would seem undesirable and conducive of no possible benefit to abolish such time honored names as Boat-tailed Grackle, Red-breasted Sapsucker, Gambel's Sparrow, etc., not to mention California Gull, California Jay, Yellow-billed Magpie, etc., etc., simply because, for one reason or another, they are considered to be subspecies.

A writer in 'The Condor' (1934, p. 245) says that subspecies "belong to the serious student of systematics and animal distribution and in this type of research the scientific name is sufficient." In this we agree but we doubt if the collectors of eggs, who value the sets of rare subspecies at high figures,

would concur in this opinion, or would care to dispense with English names for them. They would have to learn a vast number of scientific names for the subspecies which they now know by the historic English names handed down for several generations. The same writer in commending Dr. Grinnell's note on revision of English bird names (*Condor*, 1934, p. 165) says, "descriptive or geographical names are far preferable to the present hodgepodge of meaningless personal names."

I very much doubt, however, whether anyone will profit by changing "Barlow's Chickadee" to "Santa Cruz Chestnut-backed Chickadee" or "Grinnell's Chickadee" to "Idaho White-browed Chickadee" as Dr. Grinnell has suggested. It is practically impossible to use such names on museum exhibition labels and before one could call his companion's attention to one of these birds in the field, by such a sesquipedalian name, the bird would probably have flown! More seriously, however, is it not just as important to perpetuate the names of our ornithologists in our bird names as to coin new geographic or descriptive terms? The former are not "meaningless" and really mean just as much if not more than the latter and may stimulate the "beginners" to ascertain who these men were and what they did. After all a name is a name and experience in every language shows that the shorter it is the better and the more likely to be used. This discussion of English names, however, is somewhat apart from my thesis and I would only add that inasmuch as our technical names must needs change so long as we try to make them express evolutionary relationships as well as to serve as a handle to let others know what we are talking about, then by all means let us maintain stability, so far as possible, in our English names and not coin any more new ones when our literature possesses such a large proportion that have been maintained for from fifty years to a century.

To summarize my main contentions regarding subspecies: I should advocate regarding as subspecies all geographic races differing but slightly from one another and whose ranges join (i. e. the majority of our subspecies of the A. O. U. Check-List); also island forms and representatives of European or Asiatic birds which differ very slightly from mainland, or Old World forms (these are for the most part now regarded as subspecies on the grounds of overlapping of characters although actual intergradation is manifestly impossible because of geographical isolation).

I should regard as species forms which differ markedly from one another; and other forms which differ only slightly but whose ranges are more or less identical with no crossing or intergradation, such as the smaller Thrushes and Flycatchers (such forms are now recognized as species); also very distinct subspecies even though intergrades are known to exist. I should strongly oppose the reduction of such distinct forms as the California Gull, Yellow-billed Magpie, Boat-tailed Grackle, California Jay, etc. etc., to subspecific rank on the ground of genetic relationship.



While I do not wish to appear iconoclastic, I believe that serious consideration should be given to the present status of the subspecies and the tendencies of the day in this connection, which seem to be more likely to produce chaos than system. Certainly no improvement or reform can be attempted in either technical or English nomenclature until we decide a little more definitely which forms are to be regarded as species and which as subspecies.

*Academy of Natural Sciences of Philadelphia.*