The Subspecies Concept and Its Taxonomic Application

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ELEVEN years ago, Mayr summed up and co-ordinated in his *Systematics and the Origin of Species* the taxonomic principles and methods that had gradually come to be recognized as basic and practical by many of the specialists working with the better-known groups of animals. Founded in the genetical precepts of neo-Darwinian evolutionary theory, Mayr's synthesis dealt most importantly with the nature of the species, which he held to be an objective and definable phenomenon, and with the geographical variation shown by populations composing the species. His species criterion was the occurrence in nature of free interbreeding, actual or potential, between members of a population or between populations; different species, he believed, are those populations possessing any factors intrinsic to their member individuals that will act to prevent interbreeding *between* the populations of a degree as free as that *within* each population. The basic reasonableness and operational advantages of Mayr's criterion struck an immediate wide and favorable response among many segments of taxonomic opinion, and his principle has been applied with considerable enthusiasm and with generally improved results to many and varied groups of Recent, sexually reproducing animals.

Along with widespread approval, this version of "population systematics" has aroused some outright opposition, as well as some more tempered criticism of particular phases of Mayr's argument. The outright opposition comes largely from those who either have not read carefully enough the various expositions of population systematics, starting with Mayr's, or who for some reason have failed to understand what we regard as for the most part a clear and simple thesis. Most of those so opposed, like M. W. de Laubenfels (1953) and Ruggles Gates (1951), insist upon regarding Mayr as having postulated that species are basically separated by *sterility barriers*. Starting with this thoroughly mistaken notion, de Laubenfels, Gates, and their school find it easy to bowl over straw men in all directions. De Laubenfels, for instance, is horrified to note that "Some dictionaries, many lesser zoologists, and the one whom many consider to be the greatest living systematist, propose a criterion of complete genetic isolation for species determination. Already they propose that most kinds of wild ducks are all one species. . . . Even many wood warblers are all one species [References?] . . . . By the geneticist's definition tigers are at best a subspecies of the lion, and bison merely a race of domestic cattle." The case of the lion and the tiger especially is so often used in this connection that we feel it would not be superfluous to make an example of it by pointing out the characteristics that prove these two forms species: (1) the breeding ranges of the lion and tiger overlap broadly in southern Asia, and the two species have occurred, at least in the recent historic past, in closely contiguous territories in India; (2) there is no sign that the Indian lion has been genetically affected through interbreeding with the surrounding tiger populations, or vice versa; (3) our principal reference (Burton, 1933) offers no evidence for any hybridization between lions and tigers in nature; (4) differences in breeding behavior, for instance, while not very well studied, seem nevertheless to be of a kind

that may well act to prevent genetic inter-change between the two species; (5) hy-bridization, even if it did occur, would not justify reducing the two species to races unless it could be demonstrated to be free and introgressive at the zones of actual contact.

Of course, Mayr, Dobzhansky, Stebbins, and many others have repeatedly observed that hybrid sterility is only one of several possible intrinsic mechanisms that can prevent two populations from interbreed-ing effectively. In the place of *intrinsic failure to interbreed freely in nature,* which is Mayr's criterion, de Laubenfels and Gates somehow mistakenly and per-sistently substitute *cross-sterility.* Once the nature of this misinterpretation is fully realized, there is little excuse left for accepting criticism of population sys-tematics aimed in this direction.

Criticism of a more useful sort comes from other sources. First may be men-tioned the objections of the paleontolo-gists (latest reference: Simpson, 1952). These workers place emphasis upon the difficulties arising when population sys-tematics is applied to species-evolution as it occurs through geological time. Obvi-ously, species do arise from units that are not distinct as species, so that the inter-mediate time stages, however brief, de-stroy the sharpness of the species cri-terion. More important is the apparent fact that species populations may evolve new characters in time without undergo-ing any splitting; for instance, one finds a population represented in each of several successive strata by what appear to be slightly and progressively differing species that can only be taken as cross-sections of a continuum. This criticism does not de-stroy the basis of population systematics, but it leads us to re-emphasize an impor-tant qualification that must be made: *species distinctions hold only for the con-sideration of a single time-transect.*

A greater difficulty is expressed in the disagreement of some observers concern-ing the interpretations to be placed upon allopatric populations (i.e., populations with geographically separate breeding ranges) that are not very obviously dis-tinct as species. Most authors rely on taxonomic judgement in treating such populations, but some have tried to apply a rule whereby allopatry uniformly marks either all species or all subspecies. The situation with regard to sympatric versus allopatric populations deserves careful at-tention for the following reasons. If two populations have separate geographical ranges, there may exist between them any degree of interbreeding potential from full to none at all. Thus, theoretically and probably in fact, allopatric populations may show every degree of divergence up to that of full species, and will in this sense blur the fine distinction that char-acterizes the species as a category. If, however, two allopatric populations ex-tend their ranges unto geographical con-tiguity, or otherwise become sympatric, their interbreeding reaction theoretically can be expected to establish very quickly whether or not they have diverged to the species level. If they interbreed freely and produce a hybrid population that is in no way reproductively or selectively inferior to the parent populations, then they are clearly to be regarded as conspecific. If they do not interbreed, or if their hybrids are relatively rare and sporadic or other-wise show a reduced ability to form a self-maintaining population as compared with the parent populations, then the latter must be counted as separate species.

Different populations newly arrived at sympatry after having reached an inter-mediate degree of loss of interbreeding potential will probably go quickly and un-equivocally to either the species or sub-species level: any partial intrinsic bar-riers will be strongly selected either for or against because of the simple fact that it is disadvantageous for the parental populations to maintain the mass pro-duction of inferior or sterile hybrids. There is some evidence that this selective process may be among the most important mechanisms involved in species formation (Dobzhansky, 1952, p. 208). Consequently,

sympatry is more than an observer's criterion for deciding whether two populations are distinct as species; in any given case it may have been the final and essential factor that actually forced the species separation.

Since no such mechanism is operative in the differentiation of allopatric populations, there will be no clear-cut lower delimitation of species. *These populations must be dealt with arbitrarily* by gauging the genetic divergence through observed characters—morphological, physiological, and behavioral—according to standards based on comparison with the observed divergence of related sympatric species populations.

Therefore, Mayr's interbreeding criterion for the species, if qualified by the restriction of absolutely definable units to a single time-transect and to sympatric situations (the "non-dimensional species"; Mayr, 1949), and extended arbitrarily but with obvious justification through the analogy of character divergence to allopatric populations, seems to provide a natural, consistent, and practicable baseline for systematic theory.

Geographical Variation: The Subspecies Concept

Along with his analysis of the nature of the species, Mayr (1942) gave an extensive review of the evidence on variation within the species. He was mainly concerned with variation of populations as correlated with geography, and particularly with the properties and evolutionary significance of the subspecies, a category generally regarded as synonymous with the geographical race. The subspecies were conceived of as genetically distinct, geographically separate populations belonging to the same species and therefore interbreeding freely at the zones of contact. Many populations previously considered species were found to fit these conditions and were combined as subspecies in a single polytypic species. Mayr also extended the racial category to include

closely related but geographically isolated populations, particularly those inhabiting different islands of tropical archipelagoes.

The taxonomic field has not been slow to exploit the opportunities opened up by the general recognition of the geographical race as a formal taxonomic category, expressible nomenclatorially as the trinomial subspecies. At the present time, it is clear that a great part of the total taxonomic effort is directed toward the detection, characterization, and formal nomenclatorial registration of "new" subspecies. This is particularly true in the case of specialist fields dealing with animal groups in which a large proportion of the full species have already been formally described and named, leaving the burden of the unceasing search for novelties to rest upon the subspecific populations.

The past two decades have witnessed an increasing tendency on the part of taxonomists to rely upon the theoretical basis so firmly promulgated by Mayr. With the progressive accumulation of seemingly sound trinomials in relatively well-worked groups such as the birds, there has grown up a complacency in systematics concerning the objectivity and usefulness of the subspecies. Specialists in many less well-worked groups, and especially those where insufficient time and material are available for detailed analysis of geographical variation, have all but forgotten the early claims of subjectivity for the race, and have come to regard it as a concrete geographical population capable of being recognized by one or a few "diagnostic" characters most accessible for study in preserved material. Many massive revisions have of late depended on the authenticity of this notion.

The tacit but very fundamental theoretical assumption most systematists make is that when characters vary geographically, their variation is co-ordinated. In terms of evolutionary genetics, the predominant genome of a given population constitutes a "coadaptive system," an aggregation of genes which are best adapted as a unit to the special environment of

the population (Ford, 1945). As a result, the geographical distribution of genes, and with them the resultant phenotypes, will be concordant.

While this concept of character concordance follows evolutionary theory well, the factual background from which it is drawn does not rightfully inspire the confidence taxonomists as a group place in it. Taxonomists seem to have forgotten the great complexities and disparities revealed in racial patterns by some really thorough analyses of geographical variation made in the past. Most of the prominent commentators on the theory of speciation have been careful to emphasize the inherently subjective and even arbitrary nature of racial limits. Here is a vastly unappreciated statement by Mayr (1942):

We have stated repeatedly that every one of the lower systematic categories grades without a break into the next one; the local population into the subspecies, the subspecies into the monotypic species, the monotypic species into the polytypic species, the polytypic species into the superspecies, the superspecies into the species group. This does not mean that we find the entire graded series within every species group. It simply means that in the absence of definite criteria it is, in many cases, equally justifiable to consider certain isolated forms as subspecies or as species, to consider a variable species monotypic or to subdivide it into two or more geographical races, to consider well-characterized forms as subspecies of a polytypic species or to call them representative species.

From our experience in the literature we are convinced that the subspecies concept is the most critical and disorderly area of modern systematic theory—more so than taxonomists have realized or theorists have admitted. Particular confusion surrounds the drawing of the lower limits of the subspecies category within that spectrum of classes recognized by Mayr as extending from "the local population into the subspecies." The difficulties in this delimitation stem from four outstanding features of geographical variation: (1) the tendency for genetically independent characters to show independent geographical variation; (2) the capacity for characters to recur in more than one geographical area, yielding polytopic races; (3) the common occurrence of the microgeographical race; (4) the necessary arbitrariness of any degree of population divergence chosen as the lowest formal racial level. It is our purpose now to illustrate these four features with the aim of re-evaluating the nature of geographical variation and of throwing new light on the subspecies concept as it is applied in taxonomy.

Independent geographical variation. Abundant examples of this phenomenon can be drawn from most careful analyses of geographical variation in a wide variety of animal groups. In his exceptionally complete work on *"Lymantria" dispar,* Goldschmidt (1940) finds eight characters which vary geographically (excluding chromosome size; cf. Makino and Yosida, 1949), none of which is in exact geographical concordance with any of the others. Several of the characters may be used by themselves to make striking racial divisions by cabinet standards, or they may be used in various combinations to achieve different results. Goldschmidt formally establishes five races by utilizing combinations of characters in size and coloration, while at the same time recognizing that "the number of subspecific types could be greatly increased by going into more and more intricate differences." In fact, Goldschmidt's data affirm that the number of races discernible increases as a function of the number of characters taken into consideration. This classic work is doubly important because it illustrates that physiological characters, such as degree of sexuality, rate of larval development, vary geographically just as do the more obvious adult morphological characters ordinarily used in lepidopteran taxonomy.

Moore (1944) surveys variation of the common leopard frog, *Rana pipiens* Schreber, in eastern North America, giving special attention to the characters stressed by authorities who had formerly divided the species into three geographical groups

(species or races). After a very thorough analysis of these taxonomic features plus some others newly introduced, he plots twelve of them in a table of "population formulas" listed geographically. These show clearly that, over broad ranges, there is essentially no consistent maintenance of groupings of characters from one broad region to the next. One can detect gradual clines, step clines, and sudden mid-distribution cline reversals for each character, and the clines obviously do not all have their axes lying along the same compass directions.

One very dramatic character is that concerning the presence or absence of the oviducts in the male. Moore's map (Figure 3) shows oviductless males exclusively inhabiting the Mississippi Basin and the states to the east, from Long Island to northern Florida, while the populations situated peripherally, in the Florida Peninsula, New England, the northern and far western states, and southern Texas have, with scattered exceptions, males with oviducts. It seems reasonable to conclude that the oviductless condition dominates and is spreading outward from some center of origin, gradually displacing the oviduct-present character. The point here is that the distributional pattern of the character shows an obvious lack of correlation with those of the external "taxonomic" features. Is it to be ignored by taxonomists on this account?

Moore later (1946) detailed his findings after conducting interbreeding experiments between frogs from different populations, and found that impairment of embryonic development reached lethal proportions in crosses between parents from the northern and southern extremes of the area sampled, while those populations separated by smaller distances showed intermediate or no hybrid impairment. North-south differences were emphasized in these experiments, but some limited east-west tests gave similar results.

A further extension of his studies led Moore (1949) to consider variation of characters presumably having a much greater adaptive significance than those external ones earlier studied. The new characters included embryonic temperature tolerances and rates of development, which show a north-south difference of a more or less clinal nature; egg size, showing clinal reduction from north to south, but with a striking reversal in Mexico; and form of egg mass, concerning which data were insufficient and show only that variation may possibly run from east to west as well as from north to south. Combining Moore's studies, it is interesting to note that the most promising of the few possible "correlated breaks" in some of the external adult characters comes to the north of New Jersey in the East, whereas by the criteria of egg size and embryonic temperature tolerance, both demonstrated to be adaptively crucial characteristics, the New Jersey populations are not significantly different from the northern populations and belong with the latter instead of with the southern populations.

Moore quite logically rejects the validity of the former broad racial divisions, and points instead to the more uniform concatenation of characters that may be found within each of the many small, allopatric local populations. We agree that his findings accord with his judgement that "there is no generally accepted and easily applied criterion for recognizing subspecies."

LeGare and Hovanitz (1951), in a detailed study of genetically based adult color variation in Californian populations of the butterfly *Melitaea chalcedona* present data suggesting a racial split between the populations of the Little San Bernardino-Mojave Desert mountain area from those to the north and west. However, larval color varies as much as adult color and shows a different geographical deployment. The larvae from several northern populations are yellow, those from the southwest coast are largely deep black, while those from the desert area show replacement of the black by gray. Despite several confused and contradictory statements on the part of LeGare and Hovanitz

with regard to the relationship of color and size, it is clear that these are poorly correlated geographically. Thus all three characters studied tend to vary independently, and as in the case of *Lymantria*, several racial divisions can be drawn depending on which characters are used and in what combinations.

A simple case of discordant variation involving a pair of characters has been described by Mayr (1942) for the bird *Paradisaea apoda*. This species is distributed linearly in the lowlands around the coast of New Guinea. Coloration of the back lightens in a cline extending around the eastern tip of the island and terminating in the north at Goodenough Bay, while coloration of the plumes lightens in a cline which commences to the northwest at Cape Ward Hunt and terminates at the Huon Peninsula. Mayr uses the resultant superimposition patterns to demarcate at intervals five races. One wonders what new racial lines could have been drawn had other, less obvious characters been carefully analyzed.

Polytopic races. If races are delimited by a single character, it is easily within the realm of possibility that this character may be selected to predominance in more than one population of the species. Dice (1940) reports the apparent independent origin of populations of the races *Peromyscus maniculatus rufinus* and *P. m. artemisiae* in western North America; these have arisen through the selection of certain coat color alleles best suited to the color of their environmental background. Cazier (in Mayr, Linsley, Usinger, 1953) has found a similar origin for certain color races in the tiger beetle genus *Cicindela*. We have observed the polytopic occurrence of a distinctive racial character involving appendage length in populations of the ant *Lasius niger* (L.) occupying eastern Asia and the eastern Mediterranean and Atlantic Islands region. Mayr (in the work cited) has expressed the opinion that such populations be recognized under a single subspecific name if no other characters vary geo-

graphically to form racial patterns. The extreme taxonomic difficulties arising when the distribution becomes more complex are self-evident and need no further comment here.

The microgeographic race. Even when only one or a few characters are employed by the taxonomist, these often vary so elaborately and extensively that nearly every local population is distinguishable from all the others. The best-known examples of this phenomenon are in the snail genera *Achatinella, Partula, Cepaea, Io, Polymidas, Liguus, Europtis, Orion, Chondrothyra,* etc., the first three of which have been discussed so often in general papers on evolution that they need little additional comment here. The most obvious variation is in shell color patterns, but variation in sculpture, size, coiling, etc., also occurs, and the resultant characters can be used in combination to distinguish endless distinct populations even by the most stringent racial standards.

Microgeographic races are especially prominent in snails because of the sedentary habits of these organisms and their tendency to form isolated local colonies. The same phenomenon is evident in more active animals restricted to habitats of a discontinuous or isolated kind, such as bogs, desert streams, and caves. Examples can be drawn from such diverse groups as butterflies (Higgins, 1950), cave beetles (Valentine, 1945), and *Dendroica* warblers (Hellmayr, 1935; Bond, 1950).

The chief disadvantage inherent in formally recognizing microgeographical races is that regardless of how valid the distinctiveness and internal concordance of their characters may prove them, the list of their trinomials must reach stupendous proportions in time. The result is a top-heavy nomenclature helping little of itself to clarify the nature of the geographical variation, but which instead will certainly obscure it as synonymies are recognized and diagnoses shifted. This is apparently the situation being approached in certain rodent groups. In the pocket gophers *Thomomys bottae* and *T. tal-*

poides a total of thirty-five races has already been recognized from Utah alone (Durrant, 1946), and the area has not been so exhaustively worked as to preclude the possibility that many more races remain undetected.

The microgeographical race as conceived in present evolutionary literature is an unusually well differentiated deme, or local communal population. There is no reason to believe that it is an exceptional phenomenon or anything more than the extreme of the tendency prevalent in all geographically variable species to form local populations of a homogeneous and distinctive genetic constitution. If several independent characters enter into the geographical variation, it is reasonable to assume that many demes can be distinguished by racial standards ordinarily applied in taxonomy if enough of the characters are used in combination. This is in fact the condition described in *Rana pipiens* by Moore, and it is reflected by the many references of geneticists and taxonomists to special "strains" typifying geographical localities.

The arbitrary lower limit of the subspecies. Even when the discrepancies arising from discordant geographical variation are eliminated by the use of one or a very few characters, systematists are faced with the fact that there is no real lower limit to the subspecies category. It has been affirmed repeatedly in a variety of animal groups that racial populations show all degrees of divergence from the lowest level of statistical reliability of mean difference to complete differentiation, with no particular tendency to fall either way. Obviously the only way to resolve this situation taxonomically is to establish an arbitrary lower limit above which populations will be formally recognized as subspecies. This subject has been dealt with thoroughly in the recent text on animal systematics by Mayr, Linsley, and Usinger (1953), and there is no need to treat it in any detail here. The point we wish to emphasize is that no arbitrary lower limit will ever be completely satisfactory, for even if only one character is used, there will always be borderline cases of an extremely vexing nature. Samples defined with vague, untrustworthy characters will often fall above a fixed lower limit, while samples usefully distinguished by striking characters will often fall below it. Furthermore, any hard and fast line will unavoidably produce a condition in which some populations are recognized formally as races while others, essentially of the same constitution but of a slightly lower statistical level, are not recognized.

This difficulty concerning the lower limit of the subspecies is well known to most taxonomists who have devoted much serious attention to the problem. Some have compromised the situation by choosing the level of statistical reliability most nearly conforming to their preconceived notion of what should constitute a valid race in the particular group under study. This appears to have been the procedure followed by Austin (1952), for instance, in his study of Pacific petrels: "A subspecific name designating a geographical population is of no practical use unless at least three-quarters or more of the individuals of that population can be correctly assigned by their morphological characters alone." Austin chooses the "84% from 84%" rule of Simpson and Roe, making the illuminating statement that the "97% from 97%" rule would be too stringent, since "Among the petrels it is rare indeed to find the means of any character separated by two standard deviations, allowing a 97% separation." Austin's method is in no way irregular as modern systematic practice goes, a fact that should signal a general re-examination of the relationship between the "taxonomic intuition" and the choice of hard statistical bases of differentiation.

It is apparent that in their application of the subspecies concept most revisionary workers have misinterpreted the nature of geographical variation as revealed by the more careful analyses in the literature. It is also apparent that taxonomic revisions, using as they do relatively small

samples and usually only one or two independent diagnostic characters, rarely present any valid general information with regard to the nature of geographical variation in its own right. Most formally named subspecies are in effect little more than special cases deduced from the established concept of subspeciation, and their validity is no stronger than the concept itself. For this reason it is important that we do not stop at disclosing the inconsistencies of the concept; rather, we should attempt to revise it to conform as rigorously as possible to fact. From the data supplied in studies such as those by Goldschmidt, Moore, Welch (1938), Crampton (1932), Vanzolini (1951), Brown and Comstock (1952), and others, it is possible to draw several outstanding conclusions having an important bearing on the taxonomic application of the subspecies concept.

1. Where one character varies geographically, other genetically variable characters can be found to vary also.

2. The geographical variation of independent characters tends to be discordant to some degree. The degree of concordance increases with the degree of isolation of populations, but complete concordance from locality to locality is rarely if ever attained. In fact, complete concordance of several known independent characters in an isolated population may (usually?) be a good indication that the population has attained species level. For example, Goldschmidt's *Lymantria dispar hokkaidoensis* shows concordance of at least three characters, more than any other race of this species, but at the same time it appears to be sufficiently cross-sterile with adjacent races to justify recognition as a distinct species.

3. It follows from (2) that the greater the number of characters, the greater will be the total discordance. As a result, the racial lines first drawn from the most prominent "diagnostic" characters will be increasingly obscured or contradicted by the addition of characters, and the situation will be resolved only by either recognizing additional races marked by dif-

ferent combinations of characters, or by recognizing only the major tendencies in concordance. The first of these two solutions, that of recognizing all racial limits by whatever characters can be used to demarcate them by conventional standards, may be the better one in populations that have differentiated *in situ,* i.e., without initial isolation. When this approach is used, the number of distinguishable races has been found in practice to increase at a slightly more than arithmetical progression with the addition of characters used in combination. The second solution, involving the determination of what might be called *peaks of concordance,* seems the more promising where distinguishable populations are totally isolated or are undergoing secondary intergradation. However, since races are then defined according to character peak concordance, nonconforming characters will of necessity have to be omitted, while the extensiveness of the intergrade zones of the species will increase in proportion to the number of characters included in the peaks. The taxonomist will find himself faced with a dilemma: he must either ignore certain poorly conforming characters or else he must incorporate them in his subspecies diagnosis and thereby broaden the zones of intergradation.

4. It would not be too much of a truism to mention that the greater the geographical area encompassed, the less homogeneous will be the population. Conversely, it appears that in geographically very variable species the only thoroughly homogeneous and concordant units, if any exist at all, are the demes (*sensu* Carter, 1951), which tend to be isolated and completely panmictic within themselves. Where clines occur they are marked between but not within these populations.

As noted previously, most taxonomic recognition of subspecies so far has proceeded on the oversimplified "coadaptive system" concept of the race, which assumes that genetically independent characters will tend to be concordant in their geographical variation. We believe that

this assumption has resulted in the establishment of a basic fallacy in the taxonomic method of studying geographical variation. The tendency in this method has been to delimit races on the basis of one or several of the most obvious characters available in preserved material; the remainder of the geographically variable characters are then ignored, or if they are considered at all, they are analyzed only in terms of the subspecific units previously defined. A slight variation of the procedure is to choose several discordant characters, employ them in combinations of two or three to establish racial limits, and then analyze each character individually in terms of these limits.

A case in point is the recent study of the red-eyed towhee *Pipilo erythrophthalmus* by Dickinson (1952). Seven characters are used in various combinations to demarcate four races ranging successively from *alleni* in the south to the typical *erythrophthalmus* in the north. Wing length, plumage and iris color, and tail-spot size vary clinally along the succession of races. Culmen, tarsus, and toe length are greatest in the two intermediate "races" *(rileyi* and *canaster*. The total picture of the variation gleaned from this study gives the strong impression that the intermediate forms are nothing more than segments of a broad, partly clinal intergrade zone connecting two extreme terminal populations. This is the conclusion reached by Huntington (1952, *vide infra*) in his analysis of remarkably similar variation found in the eastern purple grackle (*Quiscalus quiscula*); the same kind of characters vary in the same way in both the towhee and grackle, and the intermediate zones in both are geographically very close. The increase in culmen-tarsus-toe lengths in the intermediate towhee populations seems comparable to the increase in culmen-wing lengths in the grackle intergrade zone. In addition, the variation of independent characters in the towhee is obviously quite discordant, as evidenced by the rather poor correspondence of the iris-color distribution as charted by Dickinson with the racial limits previously decided upon.

From Dickinson's data alone it cannot be proved that the geographical pattern in the towhee is the same as in the grackle, and that it may therefore be best expressed by the recognition of two races; yet the fallacy in Dickinson's method of analysis stands out clearly enough. His entire treatment is predicated on the shaky assumption that the races he has defined represent concrete biological units, and this despite his introductory warning: "In ornithological studies in large part the taxonomist is dealing with continuous variates and with variation that appears graphically as a cline. Under such circumstances lines of demarcation must be vague." Having established the four races, Dickinson thereupon uses them as sample groupings from which to analyze each character individually. Only one character, iris color, is plotted geographically as an independent variate. As a result, the true nature of the clinal trends can be inferred only from gross comparisons of the racial diagnoses. Instead of outlining the geographical variation of each character and then synthesizing from it the overall racial pattern, Dickinson has done just the reverse, thereby closing the door to further analysis and interpretation of the data which he has so laboriously gathered and presented.

Because of its closely similar nature and quite different approach, Huntington's analysis of geographical variation in the purple grackle deserves further attention. Much as in the towhee, four races can be demarcated arbitrarily along a southeast-northwest cline, but Huntington chooses to synonymize the intermediate two, *ridgwayi* and *stonei*, as segments of a clinal intergrade zone between the southern nominate race and the northern *versicolor*. Culmen length and wing length vary independently and discordantly with color, this time along a north-south cline. Huntington analyzes these two characters separately to demonstrate that both increase unexpectedly in size (with respect to their

over-all clinal trends) at the zone of inter-gradation of the color characters. This Huntington suggests may be due to a heterotic effect caused by the secondary intergradation of the two terminal races. By deciding upon the racial units *after* the variation of the genetically independent characters has been analyzed separately, Huntington arrives at what appears to be a more natural classification than that proposed by Dickinson for the towhee. But even more important, his data are presented in such a fashion as to allow ready incorporation into future studies of this species.

Insular Races

The more critical reader may have noted by this time a special condition of the foregoing critique of the subspecies concept: the published analyses of geographical variation that have been considered are in nearly every case concerned with Holarctic continental species. Our review of the literature convinces us that really critical analyses of this sort are virtually lacking for insular populations, and herein rests a point. Much of the background of the modern subspecies concept has been drawn from taxonomic studies of insular and montane groups, all of which are essentially the same in their marked fragmentation into completely isolated populations. Special emphasis in this respect has been laid on birds, and it is not too much to say that the development of the entire theory of geographical speciation has been dominated in large part by ornithological leadership. Yet a survey of ornithological taxonomic literature, including the long series of papers by Mayr, Zimmer, Amadon, Lack, and others (cf. Mayr, 1951), has convinced us that the morphological and distributional data on relevant bird populations leave much to be desired, and in fact offer very little definitive information on the two central topics, independent character variation and the subspecies-species evolutionary transition, as they apply to insular populations.

This literature is characterized by two outstanding shortcomings. First, a very limited number of characters is used; taxonomic revisions are typically based on studies of variation in size, external proportions, and color. Even the detailed analyses of (continental) geographical variation, such as those by Dickinson and Huntington just discussed, are based on these same few characters. To these we may add Miller's well-known *Junco* revision, which is the most thorough of all such studies on birds known to us. We have already stressed the weaknesses of any infraspecific classification based on limited numbers of characters. It would be of the utmost interest to see an ornithological revision employing the same number and kinds of characters studied by Goldschmidt in *Lymantria* and Moore in *Rana;* these might include internal features, egg color and size, morphological and physiological nestling characters, microscopic barbule structure, epidermal sculpture, and many others. This sort of work may well be rendered unduly difficult by the limitations of standard ornithological materials and methods, and it would perhaps be presumptuous to suggest a shift of technique. Nevertheless, it is important to emphasize the little-appreciated point that ornithological studies do not remotely approach in morphological detail those published on some other groups of animals.

The second shortcoming of ornithological revisions is the paucity of data on the subspecific versus specific status of insular and other isolated populations. It is true that sharp character discontinuities are often set from isolate to isolate; this allopatric pattern occurs in so many groups as to create a striking faunal picture, especially in tropical archipelagoes. Again we need to point out that few characters have been determined to participate in the discontinuities, and little information has been obtained on concordance of variation, especially as it occurs between islands and island groups. Furthermore, it is a fact that many of these striking racial differ-

ences are based on limited samples (occasionally consisting of a single specimen) which may have originated from the same immediate locality or even from a single clutch. There is no way of knowing, on the basis of the mass of published taxonomic work, whether or not the study of additional, less obvious, and possibly discordant characters in larger bird samples might reveal alternative racial divisions among island groups, and finer divisions on single islands, such as occur in snails and probably in other animal groups.

A stronger aspect of this shortcoming is seen in the other direction. Where the several characters utilized show marked concordance, there is always the distinct possibility, previously mentioned, that the allopatric populations have already attained species level. A certain amount of evidence is accumulating to indicate that this may be a very common phenomenon. We have already mentioned the example of Goldschmidt's *Lymantria dispar hokkaidoensis*, which, showing a high degree of character concordance, is partially cross-sterile with adjacent populations. Kinsey (1936) describes four pairs of sympatric species of the *Cynips dugèsi* complex in southern Mexico, none of them more strongly differentiated than are the numerous isolated populations to the north; the extreme paucity of hybrids between the northern allopatric populations may be taken as additional support for the contention that they really represent member species of a superspecies, notwithstanding the high degree of isolation. Most edifying, however, are the numerous cases cited in the literature of pairs of closely related species with contiguous or narrowly overlapping ranges. Taxonomists often consider such pairs to be races of a single species until their true relationship is verified by a careful investigation of their interaction in the zone of contact. The significance of this particular kind of taxonomic clarification has been reviewed for ornithology by Mayr (1951), who uses the expression "pseudo-conspe-

cific pairs of allopatric species" to refer to pertinent cases.

Summing up, we must affirm that present knowledge of insular races, including those of birds, is actually too limited to allow close comparison with the patterns elucidated in studies of continental races. While it is true that striking discontinuities often occur between island or other isolated populations, any interpretation of these discontinuities must carry two serious qualifications. First, insular races, like most continental races, have been defined on the basis of limited numbers of characters, often in assorted combinations, without consideration of the possibly discordant variation of other, more cryptic characters. Second, where some degree of concordance is demonstrated, the excellent possibility that the populations have already attained species level has very seldom been ruled out.

Subspecies: the Taxonomic Application

Because the geographical race has a demonstrably flimsy conceptual basis, it is unfortunate that it has become through the years a deeply rooted taxonomic resort. That the race has become so integral a part of our systematics is due largely to the circumstance that, under the more hierarchical-sounding alias "subspecies," it has established itself gradually but ever more firmly as a unit that could and should be dignified with a Latin name. Caught up in the wave of enthusiasm for the new systematics, the International Commission of Zoological Nomenclature, meeting at Paris in 1948, gave its most recent formal sanction to the named subspecies at the same time that it quite rightly consigned the "variety" and other minor categories without geographical connotation to an inferior rank. In effect, the Commission again officially recognized subspecific names on a level of availability with those given to full species insofar as priority is concerned, and again gave formal recognition to the employment of the neo-Linnaean trinomial. The pool of

available trivial names, many of which may never prove assignable to definite species, has been more firmly fixed at discouragingly vast proportions by this action.

If it is now clear that the subspecies trinomial is fast becoming an unquestioned and traditional fixture, it is equally clear, at least to us, that in its assumed function as a formal means of registering geographical variation within the species it tends to be both illusory and superfluous.

Mayr sums up our general philosophy perfectly in his very recent (1953) advice, offered in a different connection to those in attendance at the birth of a struggling taxonomy of viruses:

The history of all classification, whether dealing with inanimate objects or with organisms, shows that early attempts of classification are based on superficial similarities and very often on single characters, while all improvements of classification are due to ever more penetrating analysis and a broadening of the basis of classification by including more and more characters. The soundest classifications are those built on the greatest possible number of clues. Reciprocally, it can be stated that, in sound classifications, there is usually a fair concordance of the various characters.

The application of this logic to our present knowledge of geographical variation cannot fail to stir a feeling that the trinomial has outlived its usefulness in taxonomy. We are encouraged to note that ornithologists have been among the first to apprehend this circumstance. Lack (1946), after grappling with trinomials in the European robin and finding them based uneasily on convergent polyphyletic characters and complex clinal trends, concludes:

The use of subspecific names not only implies discontinuity where none may exist, but also unity where there may, in fact, be discontinuity. . . . Certainly, in the case of *Erithacus rubecula*, it is both simpler and more accurate to describe subspecific variation in terms of geographical trends, and to omit altogether the tyranny of subspecific names.

Mayr (1951), in reviewing twelve years of progress in the study of bird speciation, observes, "Instead of expending their

energy on the describing and naming of trifling subspecies, bird taxonomists might well devote more attention to the evaluation of trends in variation."

We are inclined to feel even more strongly about the situation. We are convinced that unless our own sampling of the taxonomic literature has badly deceived us, we shall soon begin to observe the withering of the trinomial and its cumbersome appurtenances—the types, the tinted labels, the ponderous subspecies lists gravely entered in a thousand catalogues, the awkward labelling of masses of "intergrade" specimens, and all of the other procedural details that so unnecessarily consume the few effective working hours a modern taxonomist has. We anticipate the time when the taxonomist, if he wants to apply a formal Latinized name to his sample, will have first to produce indications that the population represented has the characteristics of a species. The more irresponsible or naive worker will not then be able, after a weak gesture in the direction of systematic study, to retire to the comfortable, safe nebulosity of a subspecies designation under a name having guaranteed availability against the future contingency that someone will perform the labor necessary to define a good species fitting his type. The study of geographic variation may eventually become just what the term implies, and not merely remain the subspecies mill it so largely is today.

The possibility that some International Congress not too far in the future will see fit to relegate unborn subspecific names to the nomenclatural limbo now occupied by the variety, the natio, the aberration, the forma, etc., inevitably brings up the question of the kind of reference shorthand we shall need to aid in the description of geographical variation. Fortunately, all the reference we require for this purpose is contained in (1) the correct determination to species, and (2) the locality and ecological data that will have to accompany any specimen worth studying. Thus, in publications, we can speak

of "*Rana pipiens* Schreber, Montauk Pt., New York"; or "*R. pipiens*, southeastern corner of J. B. Smith farm, 5 miles west of Montauk Pt., in cattail swamp"; or even "*R. pipiens* from Long Island," ". . . from the East Coast," and so on. The precision or breadth of the geographical designation will vary according to the needs of the investigator and with the actual geographical distribution of the character or combination of characters under study. Inevitably, perhaps, repeatedly discussed populations will come to be referred to as "Montauk A," "Reelfoot Lake," "Rock Island," and so forth, but this will no more prove a pitfall than is the geographical vernacular familiarly applied to "strains" of *Drosophila virilis* (Patterson and Stone, 1952), or the locality names by which experienced trappers can often distinguish a series of pelts.

If a character combination of a population remains at all co-ordinate and consistent in its territorial occupancy, there is every reason why we should refer to it merely by mentioning the species concerned and either the locality or full distribution that it occupies. There is no evident advantage in the use of the recommended form "*montaukensis*" over "Long Island race" or "Montauk A." If we find at Lhasa a population of mice of known species that carries a distinctive black cheek stripe, the name "*lhasensis*" conveys this no more readily than does "Lhasa race." If it subsequently be found that the entire Tibetan Plateau is inhabited by mice carrying black cheek stripes, "Lhasa race" is readily expanded, so that we can speak of the "Tibetan race" just as easily as, and interchangeably with, "Lhasa race." The city of Lhasa remains a feature of the Tibetan Plateau, and so do the black-cheeked mice of both places. The very informality and flexibility of a vernacular system are among its most appealing characteristics. A geographical vernacular designation lacks the esoteric authoritarianism surrounding the Latin trinomial, but it is this very quality of trinomials that we consider most mis-

leading, cumbersome, and generally repellent, especially to the uninitiated. The geographical vernacular is more broadly communicable, more frankly expressive, fully as mnemonic, at least as certain in the long run to be precise, and it cuts the taxonomic red tape to practically nothing. Its present unostentatious use in many individual papers in several taxonomic fields reveals no serious operational drawbacks. In short, we feel that the facts we have outlined call for serious, conscious consideration of the desirability of eventual abandonment of the subspecies trinomial and its replacement by a system of reference based on the vernacular employment of relevant geographical names.

Summary

1. Mayr's criterion for the species, that of free interbreeding of populations in nature, when qualified by the conditions of sympatry and synchrony, and extended by morphological analogy to isolated populations, has proved to be objective and practicable for taxonomic work.

2. Roughly, the subspecies has been defined as a genetically distinct geographical fraction of the species. The assumption has been followed, tacitly or otherwise, that when secondary characters vary geographically, this variation tends to follow whatever "diagnostic" characters are chosen to delimit races, and that the subspecies in general can be shown upon further analysis to be a concrete unit. This assumption is demonstrated herein to be contravened by the data available in the literature dealing with geographical variation.

3. Three other prominent features affecting the subspecies concept render it even more subjective and arbitrary in taxonomic practice: the polytopic race, the microgeographic race, and the artificiality of quantitative methods of defining the formal lower limits of the subspecies.

4. Most taxonomic analysis at the intraspecific level has been directed toward the end of naming and characterizing new

subspecies. This tends to be an inefficient and misleading method. It is felt that geographical variation should be analyzed first in terms of genetically independent characters, which would then be employed synthetically to search for possible racial groupings.

5. Although "insular" races (as opposed to contiguous "continental" races) appear at times to be exceptionally clear-cut and have been extensively used in generalizations on raciation, the data in most available analyses are in all respects insufficient to evaluate the intricacies of this process. It is not even certainly known in most such cases whether distinctive isolated populations are races or species.

6. We feel that as the analyses of geographical variation become more complete, the trinomial nomenclatorial system will be revealed as inefficient and superfluous for reference purposes. It is suggested that, for the study of such variation, the use of the simple vernacular locality citation or a brief statement of the range involved is adequate and to be preferred to the formal Latinized trinomial.

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The Cushman Foundation for Foraminiferal Research, Inc., was organized in June 1950 in the District of Columbia for the purpose of continuing work initiated by the late Dr. Joseph Augustine Cushman, who founded the Cushman Laboratory for Foraminiferal Research at Sharon, Massachusetts, in 1923. The Foundation is a private organization, the purposes of which are the promotion of research in the paleontology and biology of the Foraminifera and related organisms and the publication of the results of such researches.

From 1925 to the death of its founder and Director, the Laboratory was operated as a non-profit organization for scientific research in cooperation with the U. S. Geological Survey and the U. S. National Museum and for advanced study in cooperation with Harvard University, Radcliffe College, and Massachusetts Institute of Technology.

For twenty-five years, from 1925 through 1949, the Laboratory published a quarterly journal, the *Contributions from the Cushman Laboratory for Foraminiferal Research*, devoted to papers on Foraminifera written by Dr. Cushman and his many students and collaborators.

Following his death in 1949, the journal was concluded with its 25th volume.

Slightly over a year later in August 1950, the then newly organized Cushman Foundation issued the first number of Volume 1 of the *Contributions from the Cushman Foundation for Foraminiferal Research*, a quarterly established to continue the earlier *Laboratory Contributions*. This new periodical is patterned after the old one, but its size and scope have been enlarged. Its publication facilities are open to all serious students of the Foraminifera and allied organisms.

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