SYSTEMATISTS AND SUBSPECIES

by PAUL R. EHRLICH[1]

When WILSON and BROWN published their well-known paper (1953) attacking the subspecies concept, they caused an uproar which still continues, more than three years later. A number of taxonomists have rushed to the defense of the subspecies, either defending the taxon as it is employed at present, or favoring its retention in a restricted sense. VAN SON (1955) states "The old definition of a subspecies as a 'geographical or host variation' is very vague, because populations of a climatically (and often also seasonally) variable species of wide distribution often present local 'population characters' in accordance with prevailing external conditions, quite independent from the presence or absence of isolation which alone can maintain distinctions of a genetic (mutational) nature." In many cases these local "population characters" that VAN SON feels are phenotypic responses to "external conditions" actually have a genetic basis. An excellent illustration of this is provided by the extensive work of CLAUSEN, KECK, and HEISEY (see 1948 for summary), who demonstrated, among other things, that altitudinal dwarfs of the Composite plant *Achillea lanulosa* were genetically dwarfed. A reasonable explanation of this phenomenon (a phenotypic reaction of an organism under some circumstances having a genetic basis in other circumstances) supported by experimental evidence has been advanced by WADDINGTON (1953, 1956) under the name "genetic assimilation of acquired characters." This phenomenon has long been known to paleontologists as the "Baldwin Effect."

VAN SON also oversimplifies isolation, since the macrogeographic gaps in distribution to which he is referring are not necessary for the maintenance of genetic distinctions. VAN SON supports the thesis that the only populations deserving recognition as subspecies are those which are separated by geographical barriers and whose members can be separated with certainty from members of other populations of the same species. As GILLHAM (1956) points out, however, the group of entities classed by VAN SON as subspecies of *Papilio ophidicephalus* may well have attained specific status. Considering the phenomenon of character displacement to which BROWN and WILSON have recently drawn attention (1956), and the extreme constancy claimed for the so-called subspecies, it seems quite possible that this is the case.

It is interesting to note that VAN SON, GILLHAM, and several other contributors to the literature on the subspecies question seem to believe that breeding experiments can prove whether or not two allopatric entities are conspecific. While in certain circumstances laboratory studies can give rather definitive answers, in other situations (especially those involving such phenomena as rings of races, psychological barriers which break down in restricted laboratory surroundings, etc.) they merely provide supplemental information.

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[1]Contribution no. 953 from Department of Entomology, University of Kansas, Lawrence.

DURRANT, whose subspecies of pocket gophers have been repeatedly employed as examples of abuse of the taxon, presents what is probably the weakest defense of the subspecies, as an example of his exposition will demonstrate: "In the syngameon of the species are demonstrated all characters to be found in the subspecies. At the level of the subspecies, it appears to be but a reshuffling of the gene pool and the appearance of certain combinations of characters that are already present in the syngameon. When these combinations appear in a frequency which is statistically significant, it indicates that the animals have attained certain genetic stability — and gene frequency for the distinguishing characters — and they can be distinguished from other geographic populations. They are then recognized as subspecies. Between species, however, the situation is quite different. At the level of the species, cumulative changes of such magnitude as to cause the obliteration of certain foramina in the skull, the total shifting of positions of foramina, and the different arrangement of bones, must certainly be the result of the expression of the cumulative mutations and therefore constitute new additions to the gene pool." LOTSY, who coined the term, defined *syngameon* as "an habitually interbreeding community of individuals." DURRANT apparently has a different definition. Statistical differences in gene frequencies give no information on genetic stability and are to be expected between any two populations. It is an axiom of neo-Darwinian evolutionary thought that there is no qualitative distinction between specific differences and the differences between infraspecific segregates.

On the other hand, in my opinion, the arguments of WILSON and BROWN also contain flaws. They admit the utility of having a handle for certain populations within a species and suggest that we might designate such populations with vernacular names. Obviously the same reasons for having latinized names for species can be given for having latinized subspecific names. The rituals involved in formally naming subspecies seem only slightly more onerous than those involved in describing species. WILSON and BROWN also heavily stress abuse of the subspecies as a reason for discarding it. Following this line of reasoning we would be obliged to eliminate families and subfamilies in the butterflies and genera in the birds. These authors also have not answered MAYR'S argument (1954) that handling geographic variation by vernacular locality designation gives no clue to the degree of difference between the populations discussed. However, the information conveyed by a latinized name is usually slight, because of the varied usage of the subspecific taxon.

From the above one can see that the conclusions which can be drawn at present are few considering the volume of material published. In my opinion the most significant paper to appear in the course of the controversy was that of HUBBELL (1954) in the symposium on subspecies and clines in *Systematic Zoology.* He claims that the variety of situations encountered in infraspecific variation is too great to be covered by a set of rules, and that while the subspecies may be a suitable tool for handling geographic variation in some cases, it is inadvisable to employ it in others. He further emphasizes the often neglected point that a cline cannot be a taxonomic unit since it deals with variation in a character over a geographic area, not with the variation of populations.

While I agree in general with HUBBELL, I feel that the root of the whole matter lies in the verification of the contention by WILSON and BROWN that discordant geographic character variation is much more common than concordant variation. Is this only apparently true because in many cases discordant variation has been intentionally or unintentionally publicized, while concordance, where it occurred, has been taken for granted? The answer will only be found in further studies, not in further writing about the relatively few organisms which have been thoroughly investigated. Discordance and concordance themselves will have to be more critically defined, and more objective methods of delimiting subspecific entities (if they exist) will have to be developed.

Should discordance prove to be the rule, then we will have to reevaluate critically the situation in the light of recent thought on the integrated genotype, gene action, and selection. If discordance indeed predominates, then most subspecies would not be biological entities and the trinomen will lose much of its validity. In this case systematists, such as myself, who have used the subspecies as an approach to variation, should be prepared to discard it or restrict its application.

In conclusion it is important that we remember a principle the disregard of which has brought adverse criticism of lepidopterists in the past. This is the principle that a scientific name is a tool, not an end in itself. A person's name after a scientific name is in no way an honor; it is there to fix the *responsibility* for that name on the individual proposing it. Because of the nature of their material, lepidopterists, especially those working on butterflies, have unique opportunities to contribute to our knowledge of organic evolution. Let us be sure, when studying geographic variation, that we present a thorough study of as many characters as possible, regardless of whether or not we employ the trinomen. Let's not waste time and effort haggling over names.

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Chicago Academy of Sciences, Chicago 14, Ill., U. S. A.