

CONSIDERATIONS CONCERNING THE VARIABILITY OF AMPHIBIANS  
AND REPTILES

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Almost forty years ago, in 1928, Robert MERTENS and Lorenz MÜLLER published their first check list of European amphibians and reptiles. Thanks to this work the concept of geographical races (subspecies), and the corresponding trinomial nomenclature, became commonplace in herpetological literature published in Europe. This process paralleled the development of herpetology in the United States, where STEJNEGER and BARBOUR, and then Karl P. SCHMIDT, introduced the concept of geographical races into the study of amphibians and reptiles. The trend of herpetological research toward the study of geographical races was greatly stimulated by Bernhard RENSCH's synthesis of views on the subject (1929). Finally, the second edition of MERTENS and MÜLLER's check list (1940), and the comprehensive works of TERENTJEV and CHERNOV (1940, 1949) on the amphibians and reptiles from the U.S.S.R., were events in European herpetology which definitely established the concept of geographical race instead of the old Linnean expression "variety," which lacked precision.

The utilization of the theory of geographical races in the systematics of amphibians and reptiles (and of vertebrates generally) was valuable. Being methodologically efficient, this theory contributed to a better understanding and to a more realistic view of the species of amphibians and reptiles, got rid of a chaotic situation which then existed in taxonomy, and freed systematics from a lot of names without content. But soon this theory itself became a source of extreme formalization in taxonomy. The old systematics, with its typological theories, pressed living things into the procrustian bed of the species concept metaphysically interpreted. The theory of geographical races, although free from that viewpoint, led often to unjustified description of new geographical races, which were very doubtfully real. In addition, the variability of species was implicitly restricted to the process of genesis of new geographical races.

I do not contest a priori the background of the subspecies concept in reality. But I intend to discuss some facts which cannot be explained by the theory of geographical variability in the sense given by RENSCH.

With some species, students were unable to discover geographical races by means of old classical methods based on the observation and detailed description of a few specimens. A new hope arose when mathematical methods were applied to the study of large samples of specimens. But often even the most detailed statistical analysis did not substantiate geographical races. So it was clear that there were species with intense population and individual variability; but this variability did not always permit the definition of geographical races. This was established, for instance, in the case of the Eurasiatic viviparous lizard (Lacerta vivipara JACQ), by TARENTJEV (1948) and WERMUTH (1955). WERMUTH established that geographical variation of some morphological features was independent of other characters. The theory of geographical races includes an implicit correlation between the trends in the geographical variation of the species characters. STUGREN and VANCEA (1961) established similar evidence for the viviparous lizard from Rumania, in a study of populations from the Eastern and Southeastern Carpathian Chains and from the Western Mountains (Apuseni Mountains in Rumanian). Even in this last massif where the populations of L. vivipara have been entirely isolated from the main area of the species since the warmer postglacial period, no geographical race has developed. The authors noticed that morphological differences between males and females in a population are (statistically considered) more significant than those between individuals belonging to the same sex but living in different areas. With regard to the correlation between the variation of morphological characters, STUGREN and VANCEA observed three groups of traits, using the Chi square - test:

1. Characters which vary independently (density of squamae temporalia versus constellation of squamae praefrontalia, and versus the index of density of squamae dorsalia (Schuppendichte-Index).

2. Characters which apparently vary independently from each other, but the hypothesis of an independent distribution has a low probability (constellation of squamae praefrontalia versus the index of density of squamae dorsalia).

3. Characters which are correlated (density of squamae temporalia versus the conformation of the scutellum massetericum<sup>1)</sup>

1). As defined by SCHREIBER in the second edition of his work "Herpetologia europaea" (1912), the scutellum massetericum is a larger central scale in the temporal region of the head of some lizards.

These observations, together with other details discussed by STUGREN and VANCEA, confirm the peculiar nature of the variability in the viviparous lizard. It may be designed as clinal variability in the sense of J. HUXLEY.

In a second example, Eremias arguta PALL. did not evolve in Rumania by the way of allopatric speciation. The species reaches its westernmost point of distribution in Rumania where it occurs in small isolated populations only. The isolated colonies in the Danube Delta and in the typical steppe habitat of southeastern Moldavia, at Hanu Conachi, do not present any differences of subspecific, taxonomic value (BACESCU, 1937). Utilization of statistical methods (FUHN and VANCEA, 1961; STUGREN, 1961a), did not show significant differences between populations. It is obvious that geographical and genetical segregation between the populations of E. arguta did not lead to evolution by means of allopatric speciation. Despite the favourable conditions for the evolution of separate geographical races, the event did not take place. Therefore I suggest that the mechanisms of natural selection have a reduced action in the isolated colonies of E. arguta, from Rumania. The populations are small, their variability is uniform. It seems that non-selective forces (such as the Sewall Wright effect) are directing the evolution of those populations. I consider these facts contradictory to the theory of geographical races and to the theory of allopatric speciation also. An objection might be raised that the isolation of populations of E. arguta in Rumania is a recent one, dating probably only from the holocene age. But according to the theory of geographical races, 8,000 years - and the isolation is probably not more recent than this - are quite enough for the development of subspecies.

In my opinion, in other species of Lacertidae, there are also some characteristics which show a clinal variability. The color pattern of Lacerta agilis exigua EICHW., a subspecies inhabiting a large area east of the Dnieper, gradually fades towards the west. But some specimens of L. agilis from the Danube Delta still present a distinct color pattern. Since this opinion is based on the examination of only a few specimens from the Danube Delta and the Southern Ukraine, it was not possible to use statistical methods. I consider also the variation in the pholidosis of the temporal region of the head in Lacerta viridis (LAUR.) to be clinal. For instance, a big scutellum

massetericum, which reaches the supratemporalia and the supralabialia, is generally considered as a differential characteristic of L. viridis meridionalis CYRÉN. There are no available data on the frequency of this feature in the Balkan Peninsula. Among populations of L. viridis from the Dobrugea region of Southeastern Rumania, there are some individuals which present this feature. I found few such individuals in the northern parts of the Dobrugea, in the Măcin Mountains. But in the Southern Ukraine and, much more in the north, in Bassarabia, there are some lizards which present the typical massetericum of L. viridis meridionalis. These facts were not tested by statistical methods, and we cannot be sure that there is a real cline. But these data lead us to the hypothesis that the massetericum changes in a clinal fashion from larger in the south to smaller in the north.

A distinctive mode of variability is to be found in Lacerta praticola EVERSM. This species is found in the Caucasus, in the Balkan Peninsula and in the south of Rumania, being absent from Asia Minor (MERTENS, 1952). The species has been split into geographical races: L. praticola praticola EVERSM. in the Caspian basin of the Caucasus, and L. praticola pontica LANTZ and CYRÉN in the pontic basin of the Caucasus and in the Balkan Peninsula. In an earlier paper (STUGREN, 1961), I suggested that the populations from the Banat province in south-western Rumania, belong to a peculiar geographical race, described by SOBOLLEWSKY (1930) as L. praticola hungarica, and I suggested the revalidation of the name hungarica. To my mind, the populations in the neighborhood of Bucharest represent an intermediate form between hungarica and pontica. Other Rumanian herpetologists (FUHN and VANCEA, 1961), do not recognize the validity of the hungarica race, and neither did MERTENS and WERMUTH (1960). But the taxonomic status of the population from south-western Rumania is not the main problem to be discussed here. Whether we accept the validity of the hungarica race or not, we must recognize the fact that the populations from south-western Rumania have a distinctive pholidosis, which closely resembles that of the remote L. praticola praticola. In this case, two population-groups, situated at the geographical extremities of the species range (Eastern Caucasus and Banat), present common traits. L. praticola hungarica and L. praticola praticola are much closer to each other than to L. praticola pontica. According to the "rules" of clinal variability, and according to the theory of RENSCH as well, populations situated at the geographical extremes of the species-range are usually very differentiated from each other. The variability of L. praticola follows an opposite trend. I suggested the term anticlinal for this pattern of variability.

Facts concerning amphibians not in conformity with the theory of geographical races have been reported by many investigators. TERENTJEV (1949, 1960) discussed an independent variability of measurable features in Bombina variegata (L.), B. bombina (L.), and B. orientalis (BLGR.), as well as a typical clinal variability with Hyla arborea arborea L. The same trends of variability were observed by KAURI (1959) in Rana esculenta L. CURRY-LINDAHL (1956) has shown that the distribution of the so-called varieties "maculata" and "striata" of the moor frog (Rana arvalis NILSS.) is not in agreement with that expected of geographical races. Investigations made by LAC (1956) on moor frogs from eastern Slovakia have shown that there are intermediate populations between R. arvalis arvalis and R. arvalis wolterstorffi FEJ. The same author (LAC, 1957), also noticed intermediate populations between Triturus cristatus cristatus (LAUR.) and T. cristatus dobrogicus (KIR.). This intermediacy was earlier noted by FUHN (1953), in populations in the neighborhood of Bucharest.

My investigations have confirmed such statements. I have especially studied the variability of the European species of Bombina. Examining large samples of individuals, I stated (STUGREN, 1959, STUGREN and POPVICI, 1961), that in the area where the red bellied toad (B. bombina (L.)) and the yellow bellied toad (B. variegata (L.)) live together, heterogeneous populations, with some characteristics of both species, are often to be found. The distribution of these characteristics in the populations studied follows the rule of POISSON. But no intermediate subspecies between the two European species of Bombina have developed. Every population can be determined as belonging to B. bombina or to B. variegata. I suggested that the "mixture of traits" is not a consequence of a mass-hybridization, because the populations are ecologically segregated. But no mechanism able to explain these facts are so far available. These phenomena being at the limit between two clines, I suggest the term of interclinal variability.

Rana arvalis is represented in Rumania by isolated populations. Some of them are reported as belonging to R. arvalis arvalis, while the others to R. arvalis wolterstorffi. But no clear morphological differences have been found between them. STUGREN and POPOVICI (1960), described an intermediate population between the two races. Yet unpublished data (manuscript in print), lead to the conclusion that R. arvalis cannot be split into geographical races.

Some striking phenomena were noticed in Triturus vulgaris (L.). FUHN (1951) described an endemic race from Transylvania - T. vulgaris ampelensis. But intermediate populations between this and the nominate race were found as well (STUGREN and POPOVICI, 1961a). In addition T. vulgaris borealis from Sweden, based on the description given by GISLÉN and KAURI (1959), closely resemble ampelensis. I have examined a few specimens from the Central Ukraine which also have some traits of ampelensis. No definite statement can be given as yet, because of the lack of sufficient information for statistical tests. In Triturus cristatus (LAUR.), STUGREN and POPOVICI (1960) have found an intermediate population between the nominate race and T. cristatus dobrigicus (KIR.).

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It is apparent that our data do not contradict the theory of geographical races. This theory does not exclude such phenomena as gradual transitions between geographical races, intermediate populations, and the existence of species that do not split into geographical races. The theory does emphasize that geographical races are the main forms in which variability appears. But, I believe, the very numerous facts concerning the existence of intermediate populations allow us to have certain doubts on the validity of geographical races within some species. Some races are described and differentiated only by means of statistical methods, by average values (averages of certain measurable characteristics). But are statistical criteria sufficient to form the basis for differentiation of geographical races? Some distinguished zoologists, like CAIN (1958) and MAYR (1957), consider as valid both races and species differentiated only by average values or statistical indexes. Other zoologists, for instance PFAFF (1935) and WERMUTH (1955), feel that a race, like a species, must be distinctive enough to be recognized by the eye ("nach dem Augenschein"). I think that populations which differ from one another only by typical biometrical values should not be considered as geographical races. Only when a population bears certain qualitative characteristics, not subjected to intense variability, would I regard it as a valid subspecies. My opinion is that only such features are useful to be differential ones between races which are not expressed by statistical values, but by classical morphological diagnoses.



Some years ago, TERENTJEV (1957), proposed the hypothesis that the concept of geographical races does not express a biological reality, and he regarded it as methodologically out of date. The above published data are not sufficient as arguments to support his hypothesis. They do it only in part. In conclusion, study of the amphibians and reptiles of Rumania indicates that there are four kinds of variability: geographical (sensu RENSCH), clinal, anticlinal, and interclinal. It seems that geographical races are not frequent in nature. On the contrary, they are restricted, because many traits characteristically vary independently of each other.

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