

Мы не ссылаемся, но  
своим экспансивным типом  
нарастаем ввиду резкого  
неэкономного экспансивного поведения

# Population Structure, Geographic Variation, and Microphylogenesis of the Sand Lizard (*Lacerta agilis*)

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## INTRODUCTION

Evolutionists are becoming increasingly aware of the need for comprehensive studies on the microevolution of individual species. The variations occurring throughout the entire ranges or most of the ranges of *Cepea nemoralis* (Jones *et al.*, 1977) and *Mus musculus* (Selander, 1970; Berry, 1963, 1977) have been the subject of intensive study; there are numerous reports on the microevolution of several closely related *Drosophila* species (e.g., Dobzhansky, 1937, 1971; Carson, 1970; Ayala, 1975); and some interesting studies concerned with the microevolution of perhaps a score of other species have been published. That the number of species involved in special microevolutionary research is relatively small is explained by the fact that a species selected for such research must meet certain rigid requirements, including at least the following: the species must (1) be wide ranging so that the impact of evolutionary factors could be assessed from data on geographic variation; (2) be present in reasonably high numbers; (3) be readily accessible; (4) possess a large set of genetically determined characters and properties that are easy to record and that lend

themselves to large-scale investigations in the field and laboratory; and (5) be a member of a well-studied taxonomic group.

In the process of selecting species that would meet these requirements, since 1961 the Laboratory of Postnatal Ontogeny of the N. K. Koltzov Institute of Developmental Biology has studied several animal groups, including some species from the suborder Pinnipedia (Yablokov, 1974), two species of *Larus* (Yablokov and Valetzky, 1970, 1972), one species from the order Bradibaena (Yablokov and Valetzky, 1971), four species from the order Odonata (Yablokov *et al.*, 1970), and *Clethrionomys glareolus* (Krylov and Yablokov, 1972). For various reasons none of these species has been found suitable for an extensive microevolutionary study. Finally we chose the sand lizard (*Lacerta agilis*), a species which ranges more than 5000 km from west to east and in some areas over 2000 km from north to south, is reasonably abundant even in regions completely dominated by man, is readily accessible so that sufficiently large population samples can be collected (a single person can capture as many as several dozens of lizards daily), and possesses, in common with all other reptilians, very many characters (mainly those associated with coloration and scaling) that are easy to record. The taxonomy of this reptilian group has been studied in a reasonably comprehensive manner (Sukhov, 1948; Peters, 1958, 1960; Fuhn, 1967; Fuhn and Vancea, 1964). Moreover, its biology has been thoroughly investigated (which is another important consideration in selecting a species for special microevolutionary studies) in an extensive program of general biologic research that was part of the international program "Man and the Biosphere" which culminated in the publication in 1976 of a review entitled *Prytkaya yashcheritsa: Monograficheskoye opisaniye vida* [The sand lizard: A monographic description of the species] (Yablokov, 1976).

The purpose of this chapter is to describe the population structure, variation, and phenogeography of *Lacerta agilis* L., the most numerous and most widely distributed reptilian species in Eurasia.

## MATERIALS AND METHODS

The materials used in the present work included 7165 specimens from various Eurasian regions maintained in collections of the Institute of Developmental Biology and 2679 specimens that form parts of the collections available in the Museum of Zoology at the Moscow State University, Moscow, the Museum of Zoology under the Academy of Sciences of the Ukrainian SSR, Kiev, and the Zoological Institute under the USSR Academy of Sciences, Leningrad, as well as (small series of lizards) in museums in Vienna, London, Stockholm, Basel, and Bonn.

Furthermore, field studies were conducted in some areas of the *L. agilis* range (Gorky and Kaluga regions, Dagestan and western Altai) to collect samples from the same populations over several successive generations. This material, which comprised 3824 specimens, served as the basis for elucidating the population structure and determining the mean radii of individual activity.

All in all, the material on which this work is based comprises 13,668 specimens from 135 sampling sites within the *L. agilis* range.

Essentially, the method used in the present study involved the recording of discrete, nonmetrical phenotypic variations (i.e., of phenes and their groups) considered as marker characters for the genotypic constitutions of the populations investigated. Altogether, 5 phenes of color, 20 phenes of pattern, and 197 phenes of scaling (pholidosis) were studied:

**Color.** The presence or absence of brown, green, red (var. *rubra*), or platinum (var. *platinumus*) color on the dorsum and the occurrence of melanistic forms.

**Pattern.** The dorsal pattern in sand lizards is determined by central and lateral striping and by spots between the stripes. A total of 17 dorsal and lateral body pattern phenes (Fig 1A) and 3 auricular region phenes (Fig. 1B) were used.

**Pholidosis.** Because of the large number of pholidosis phenes used in this study, only the names of phene groups are listed below. The figures in parentheses after the respective phene groups indicate the total number of phenes in the group. The arrangement of the main scales is shown in Fig. 2.

**Scale number and arrangement:** postnasalia (3); frenalia (2); nasolalia (2); praeocularia (2); lateriocollaria (5); ventralia relative to praeanalina in the last horizontal row (2); accessory scales along thoracic midline (6) and along ventral midline as well as between the rows of pori femoralis and between praeanalina (12); granulae between supraciliaria and supraocularia, rostrale, lobonasale, and frontale (7); between the last row of ventralia and the upper row of praeanalina (2).

**Arrangement of scales relative to adjacent scales:** nasalia-supralabialia (3); accessorius (2); postnasalia (5); interparietale-occipitale (3).

**Scale division pattern:** loreale (2); supralabialia (5); subocularia (1); subtemporalia and orbitotemporalia (2); nasale (2); praefrontale (5); supraocularia (5); parietalia (3); sternalia (7); the first and second rows of praeanalina (11); rostrale, frontonasale, frontale, and interparietale (12); occipitale (7).

**Relative size of adjacent scales:** subtemporalia (3); subocularia (3); orbitotemporalia (2); ventralia-squamae lateralia (3).

**Shape of whole scale or of part thereof:** fronto-parietalia (3); mediacollare (9); anale (5).

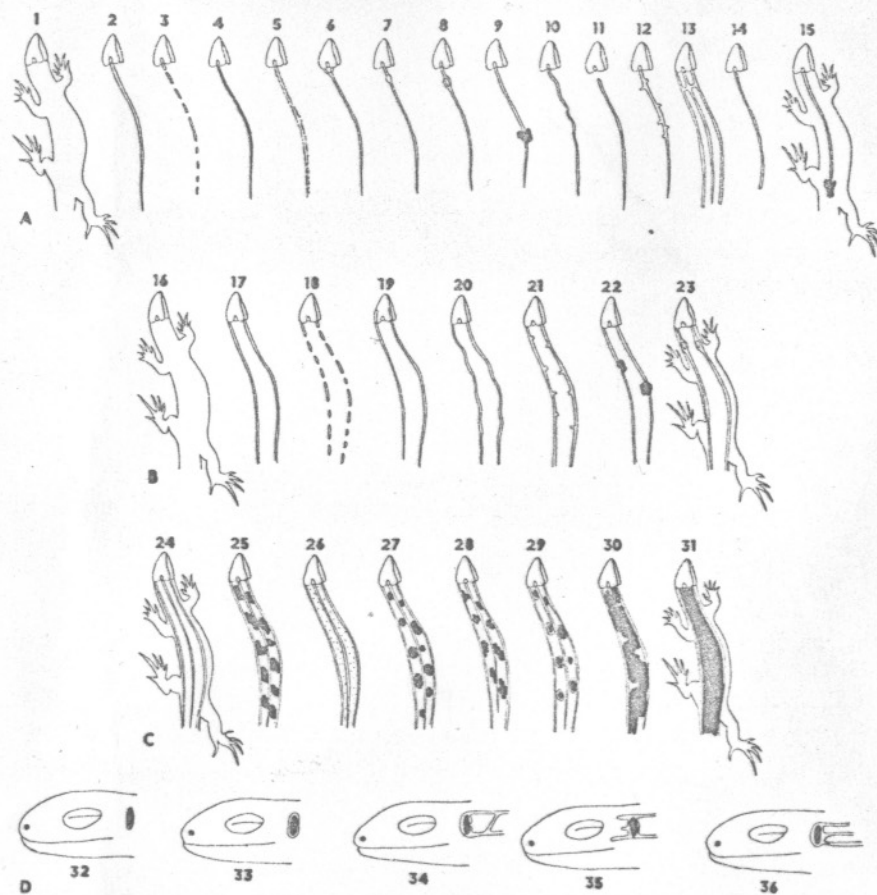


FIG. 1. Discrete variations (phenes) of dorsal and auricular patterns in *Lacerta agilis*. A. Phenies of central stripe: (1) no stripe; (2) unbroken stripe; (3) broken stripe; (4) dark stripe; (5) blurred stripe; (6) stripe forming a "fork" at head; (7) stripe thickening at head; (8) stripe forming a loop at head; (9) stripe broken by spot; (10) zigzag stripe; (11) stripe not reaching head; (12) stripe with processes; (13) stripe fusing with lateral stripes; (14) stripe terminating abruptly in caudal region; (15) stripe interrupted by spot. B. Phenies of lateral stripes: (16) no lateral striping; (17) unbroken stripes; (18) broken stripes; (19) stripes continuing on head; (20) zigzag stripes; (21) stripes with processes; (22) stripes interrupted by spots; (23) stripes forming loops. C. Phenies of dorsal spots: (24) no spots; (25) large spots; (26) punctate spots; (27) roundish spots; (28) angular spots; (29) spots with light rims; (30) partially fused spots; (31) completely fused spots. D. Auricular phenies: (32) no pattern around ear opening; (33) light ring; (34) two light bands with crosspiece; (35) light outgrowths toward eye; (36) three parallel stripes running backward.

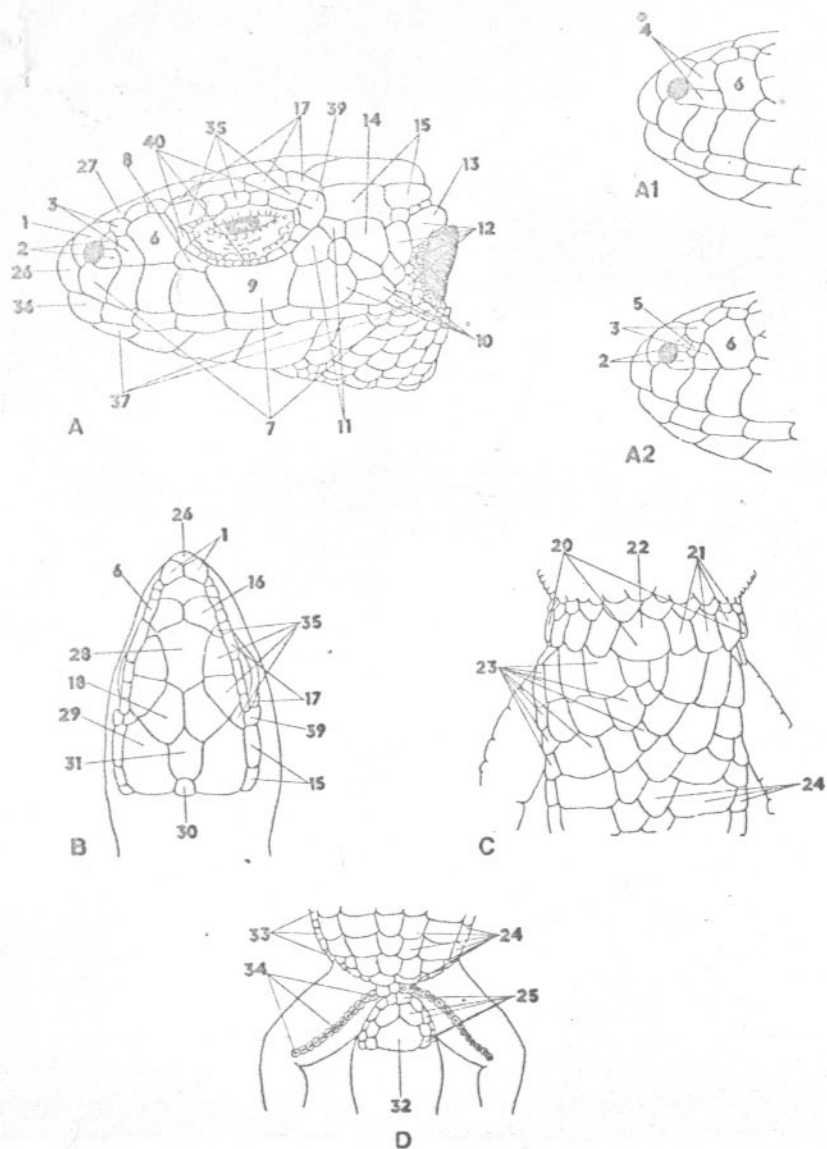


FIG. 2. Arrangement of main scales in different body areas of *Lacerta agilis*. A. lateral view of head; B. superior view of head; C. thoracic region; D. anal region: (1) nasalia; (2) postnasalia; (3) frenale; (4) nasoloreale; (5) accessorius; (6) loreale; (7) supralabialia; (8) praeocularia; (9) subocularia; (10) subtemporale; (11) orbitotemporale; (12) auriculare; (13) tympanale; (14) massetericum; (15) supratemporalia; (16) praefrontalia; (17) supraocularia; (18) frontoparietalia; (19) collare; (20-21) latericollaria; (22) mediacollare; (23) sternalia; (24) ventralia; (25) praeanal; (26) rostrale; (27) frontonasale; (28) frontale; (29) parietalia; (30) occipitale; (31) interparietale; (32) anale; (33) squamae lateralis; (34) perifemorales; (35) supraciliaria; (36) mentale; (37) submaxillaria; (38) sublabialia; (39) suprapostoculare.

Presence of accessory scales: between massetericum and subtemporalia, orbitotemporalia, supratemporalia, or auricularia (13); between the rows underlying supratemporalia and surrounding massetericum, subtemporalia, or auricularia (4); between tympanale and supratemporalia (2); behind occipitale (4); presence of a third praeanal row (1).

## POPULATION STRUCTURE

Of particular relevance from a microevolutionary point of view are such populational characteristics as the biochorologic distribution of individuals and the mean radii of individual activity. These characteristics make it possible to understand the possible system of crossing, to identify the different levels of intraspecific hierarchy, and to solve the problem of defining the boundaries and abundances of populations and intrapopulational groups characteristic for the species under study.

### Chorologic Distribution of Individuals within a Population

Data on the distribution of lizards within populations are available for a number of natural zones and biotopes (Yablokov, 1976). Individual small groups within a population tend to be distributed nonuniformly, forming a mosaic pattern (Fig. 3).

The minimal number of individuals in a primary (i.e., the smallest) group ranges from four to six, to several dozens.

The hierarchy of chorologic distribution can be conveniently considered with reference to a locality 10 × 10 km in area in a piedmont forest-steppe zone of the western Altai (48° 10' N, 85° 15' E, 800 m above sea level), for this locality has been better studied than any other.

As is shown on a small scale in Fig. 4, the small primary assemblages of lizards are united into larger assemblages consisting of hundreds of thousands of individuals, with well-defined density "nuclei." The nonuniform distribution of lizards over this territory (see Fig. 4) is partly due to the lack of uniformity in environmental conditions; thus the stony tops of hills that become frozen in winter are completely devoid of lizards. Such areas, however, make up less than 5% of the total area, and population densities are much different even in different places of an apparently homogeneous steppe characterized by mixed grass vegetation. For example, at station A [60 hectares (ha)] lizards tend to inhabit only an area of 371,000 m<sup>2</sup> whereas on the remaining area of 229,000 m<sup>2</sup> only 14 individuals were collected over a period of 2 years; at station B (9.75 ha) not a single lizard was captured on an area of 4.61 ha for the same period.

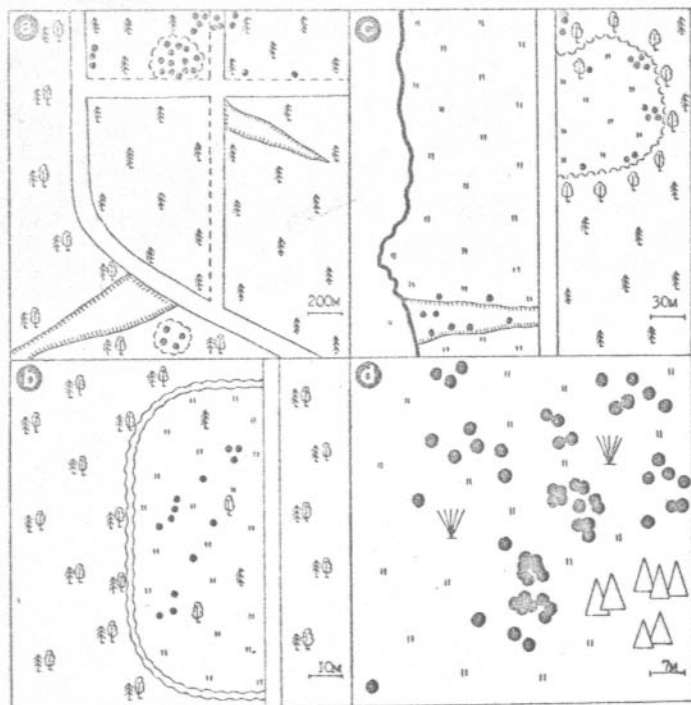


FIG. 3. Examples to illustrate the distribution of lizards in different habitats. (From Yablokov, 1976a, with addenda.)

On a still smaller scale (Fig. 5), there are seen larger zones having high population densities and coinciding in distribution with biotopes particularly favorable for lizards (in this case, small valleys of streamlets). Some of these zones overlap in places of streamlet junction while others are relatively isolated. The total estimated number of lizards in such a valley varies from several thousands to tens of thousands.

Therefore, if a group of from several lizards to a few dozens of lizards is taken as the primary territorial group, then groups of two higher levels can be distinguished on a chorologic basis: those consisting of several hundred thousand individuals occupying an area of several thousand square meters, and those consisting of tens of thousands of individuals forming high-density zones in favorable biotopes.

In some cases, four or five levels of chorologic groupings have been identified in studying areas populated by sand lizards.

If the evolutionary importance of all these groups is to be assessed, their identity and stability over a number of generations must be traced.

The identity of a group can be ascertained either directly, i.e., through a long-term field observation of marked individuals, or indirectly, by calcu-

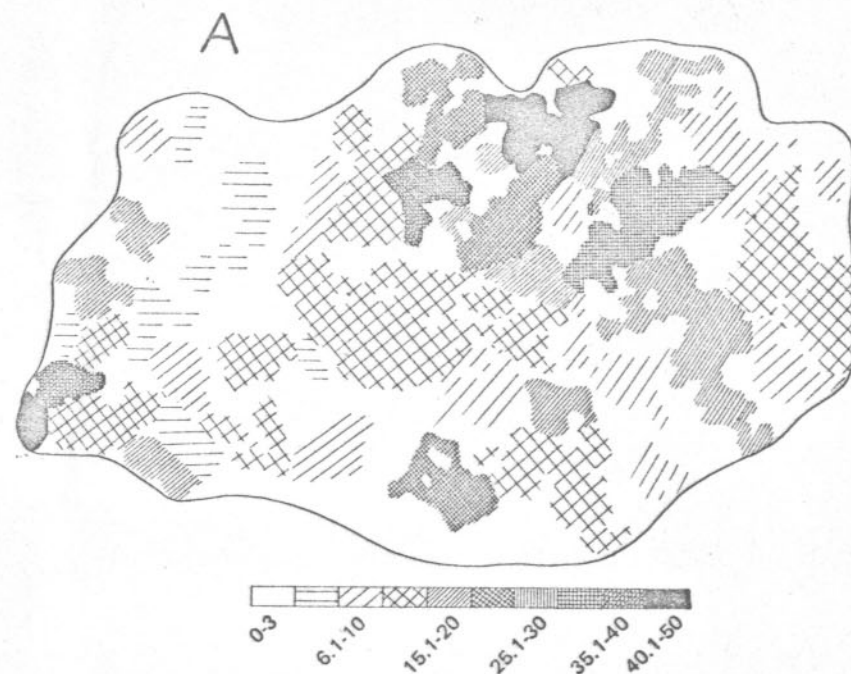


FIG. 4. Population density of lizards at stations A and B (western Altai) in marked lizards per 1000 m<sup>2</sup>.



FIG. 5. Population density of lizards in a 10- by 10-km area in the middle course of Kaldzhir River (western Altai). A and B indicate the respective stations shown in Fig. 4.

lating the mean radii of individual activity. Direct observations during several seasons in the steppe zone referred to above have shown that primary, first-order groups usually retain their identity during one season only: in the fall, during the reproductive period, nearly the entire territory becomes populated by lizards, and the next year groups of adults are formed that differ somewhat in distribution from those that existed the previous year (Fig. 6).

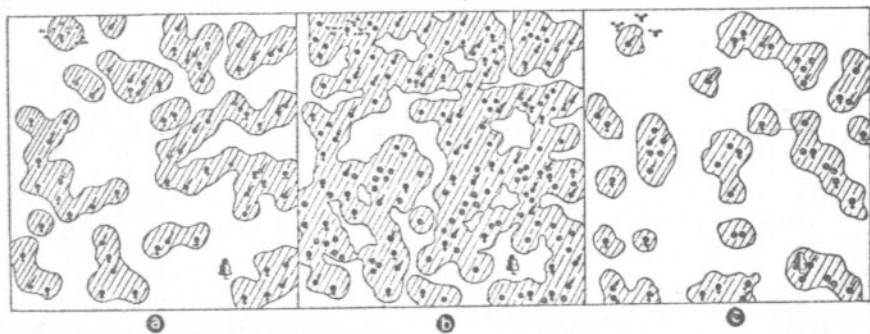


FIG. 6. Variations in the distributive pattern of small groups of lizards in different years in the same area. (a) in 1969; (b) in 1971; (c) in 1973. [From Yablokov *et al.*, 1976, based on M. F. Tertshnikov's data; with modifications.]

To sum up, at least three hierarchical levels of groups are distinguishable chorologically on the territory under consideration.

#### Radii of Individual Activity

Consideration of chorologically identified groups in relation to genetic and evolutionary factors is of particular interest when it is possible to ascertain the number of generations during which such groups exist while retaining their genetic individuality, i.e., when one can assess the gene flow between these groups. The degree of isolation is determined by the gene flow from one group to another. A direct determination of the magnitude of this flow between groups is hardly feasible under natural conditions. However, it is possible to determine, in nature, the radii of individual activity, i.e., the distances from a specified place covered by individual lizards during their lifetimes. One can speak of minimal, maximal, and mean radii of activity, as well as of diurnal, seasonal, and annual radii. When one is concerned with the degree of isolation of chorologic groups, the mean annual radii of individual activity are of particular relevance (Timofeeff-Ressovsky *et al.*, 1977). By considering these latter radii in relation, on the one hand, to the distributions of particular groups and, on the other, to their numerical sizes, it is possible to assess both the gene flow between these different groups and how long the groups of particular rank tend to survive.

Accordingly, we considered the distribution of young individuals (from the time of hatching), the movements of adults during the mating season, and the overall annual movements of all lizards together. For this purpose, in 1975-1976, 1560 lizards were marked in the 10-km<sup>2</sup> study site; 572 of these lizards were then recaptured over a period of several weeks to 1 year. The recaptured lizards were used to determine the mean radii of individual activity defined as the mean arithmetic distance between the place of marking and the place of recapture (Table I).

TABLE I. Mean Radii of Individual Activity by Different Sex and Age Groups of *Lacerta agilis* in the Western Altai from June 1975 to September 1976<sup>a</sup>

Group	Mean radius of activity (m)	Number of recaptured marked lizards
Adult males	34.8	197
Adult females	25.0	295
Young individuals of both sexes	40.6	80
All lizards	30.6	572

<sup>a</sup> Source: Rozanov *et al.*, 1977.

For a more accurate determination of the magnitude of the possible intergroup gene flow, one can calculate the relative frequency of runs over different distances (Table II) from the formula

$$P = \frac{n_j}{a_j \cdot \sum_{i=1}^m \frac{n_i}{a_i}}$$

where  $P$  is the relative frequency of runs,  $m$  is the number of class intervals,  $a$  is the class interval,  $n$  is the number of returns in a class interval, and  $i$  and  $j$  are the class interval numbers.

It can be seen from Table II that 70% of the adult lizards traveled not farther than 30 m from the marking place and that only 25% of the young lizards advanced farther than 60 m from the hatching site, while 55% did not move farther than 30 m. On the average, less than 7% of the lizards moved more than 100 m from the marking site.

The available data indicate some other features of locomotor activity by adult and young lizards. Thus, during the mating season the distances covered by most lizards near their burrows somewhat decrease (apparently being limited to 5–7 m) while the number of individuals covering relatively long distances increases. Also, although the number of captured young lizards was comparatively small (80), it has been possible to establish that where the population density on the border of an inhabited area is low, young lizards tend to occur rather frequently in places uninhabited by adults (up to 30 m from the border); on the other hand, where a densely populated area is contiguous with an unpopulated one, not a single juvenile was found outside the limits of the populated area. In other words, young lizards show a clear preference for already-occupied areas.

The data we obtained point to a strikingly low mobility of lizards and, consequently, a low level of genetic exchange within a generation. Indeed, 70% of the lizards did not advance farther than 30 m from the site of birth. These data also suggest that a majority of the chorologically defined population density centers corresponding to second- and third-order groups are quite isolated one from another, as are a number of first-order groups. However, confirmation of these inferences requires a phenetic analysis which enables one to judge the genotypic characteristics of various groups.

#### Phenetics of Intrapopulational Groups

As already stated, a special feature of the present study was the use of discrete, nonmetric variations (phenes) as markers of genotypic constitutions of individual groups. These phenes were employed to analyze the chorologically defined groups on the territory studied.

TABLE II. Relative Frequencies of Runs ( $P$ , in percent) over Various Distances by Sand Lizards of Different Sex and Age Groups in the Western Altai during 1 Year after Marking\*

Group	Class interval (m)							
	0-5	6-10	11-30	31-60	61-100	101-200	201-400	401-700
Males	61.2	19.7	13.7	3.3	1.1	0.7	0.2	0.1
Females	75.5	10.4	8.3	3.3	1.7	0.5	0.2	0.04
Young individuals of both sexes	35.7	28.6	17.9	9.7	4.7	3.2	0.2	0.0
Mean values	60.1	25.9	10.0	2.5	1.0	0.4	0.07	0.03
Number of lizards	99	22	64	34	21	23	10	5

\* Source: Rozanov *et al.*, 1977.

Even a straightforward comparison of the occurrences of individual rare phenes over the territory investigated makes it possible to delineate those areas where such phenes occur in appreciably higher concentrations than elsewhere. There may be two different situations.

First, certain rare phenes are found in some areas but not in others (Fig. 7). As a rule, such rare or extremely rare phenes occur in individuals living in close proximity to one another, sometimes at a distance of only a few meters. A good example is the phene of anal scale division found in only 3 individuals among nearly 3000 examined throughout the study area. The places where those three lizards were captured were separated by distances of less than 10 m.

Second, if one estimates the frequencies of occurrence of particular phenes in the total population of lizards inhabiting the territory under study (i.e., if one determines, in fact, the frequencies of individual phenes in the chorologically defined groups), one will almost certainly find that different areas of the territory differ appreciably as regards the concentrations of these phenes. The boundaries between such areas may be rather clear-cut or quite indistinct (Fig. 8). In both situations just described, phenetically (and, in all probability, genetically) distinct groups of individuals can be recognized within the population.

For our phenetic study of intrapopulational heterogeneity, we employed a modification of cluster analysis in which a generalized Euclidean distance was used as the metric of distance and the distances between clusters consisting of several objects each were calculated as those between



FIG. 7. Occurrences of rare phenes at station A. Thin lines designate microrelief. ●, phene no. 8; ▲, phene no. 3; ■, forking anal scale. (See Fig. 1 for designations of phenes.)

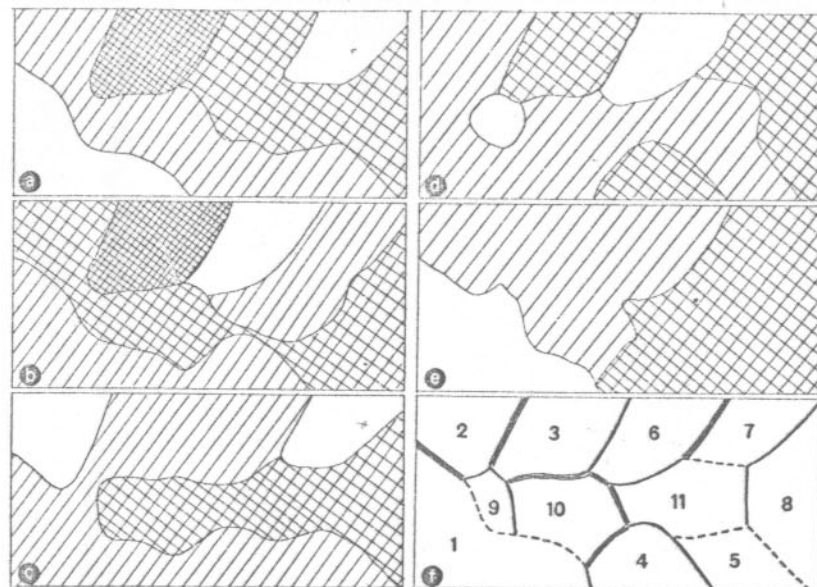


FIG. 8. Steep frequency gradients of some phenes at station A: (a) phene no. 6; (b) phene no. 8; (c) phene no. 20; (d) phene no. 35; (e) phene no. 10; (f) overall limits of frequency gradients for all five phenes (1 to 11, phenetically homogeneous areas).

the centers of the clusters. The calculations were done on an EC-1020 computer.

As was mentioned above, at stations A and B spatially isolated groups were identified on the basis of chorologic data, such as groups made up of several dozens of individuals each and larger groups of several hundred individuals. These different size intrapopulational groups were compared in terms of color phenes and pholidosis phenes by calculating the generalized Euclidean distances from the frequencies of the phenes used (15-187 phenes in different cases), with determination of the significance of differences between the groups. It can be seen from Fig. 9 that the chorologic groups can also be defined on the criterion of phenetic similarity. Moreover, it has been found that the groups made up of several dozens of individuals are rather uniform phenetically and that the neighboring groups are as a rule significantly different in the frequency of at least one phene. Groups consisting of several hundred individuals are much more different from one another than are smaller groups. Small groups within a single large group show smaller differences than such groups from different large groups. Collation of the chorologic and phenetic groups has shown that what we call the first-order chorologic groups correspond to those "smallest" phenetic groups that were recognized by cluster analysis while the second-order chorologic groups correspond to the "larger" phenetic groups.

In the larger area shown in Fig. 9, there are two second-order groups, 1 + 2 + 6 and 4 + 5 + 7 + 8 + 10 + 11, which strongly differ one from another and which, at the same time, are rather homogeneous. However, at the junction of these two groups there arise phenetically unique groups (9 and 3), quite dissimilar from their neighbors; possibly these latter groups are transitional between the others.

On chorologic analysis, second-order groups were combined into third-order groups that encompassed zones of high population density distributed over favorable biotopes (see Fig. 5) and consisted of tens of thousands of individuals each. On phenetic analysis (both cluster and purely phenomenologic analyses; see Fig. 8), some second-order groups are found to have common phenes and similar phene frequencies. Therefore the population of even a rather uniform habitat occupying an area of several hectares to several dozens of hectares can be separated into a number of groups in terms of phenetic complexes. These phenetically defined groups will not

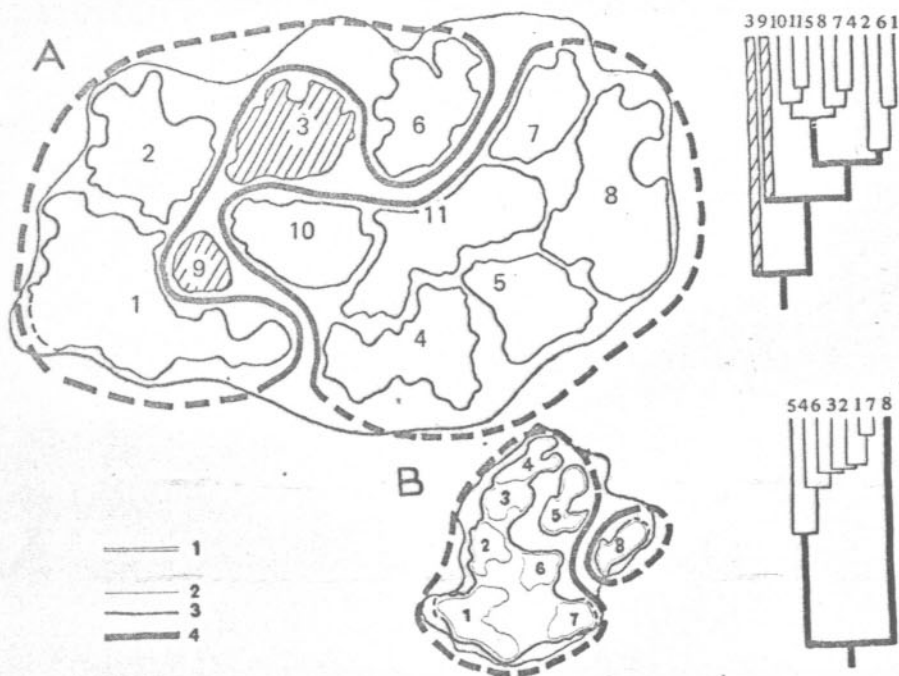


FIG. 9. Generalized similarity of phenetically homogeneous areas (1 to 11 and 1 to B) at stations A and B, respectively, as determined by cluster analysis from the frequencies of 16 (station A) and 15 (station B) phenes. Groups of demes at station A form two sets (1 + 6 + 2 and 4 + 7 + 8 + 5 + 11 + 10) with possible intermediate ("hybrid") zone (9 + 3). Demes at locality B form a single large set (7 + 1 + 2 + 3 + 6 + 4). The differences between any demes in this set are more or less proportional to distances between them. Borders: (1) stations, (2) dems, (3) groups of dems, (4) populations.

necessarily be definable chorologically since the boundaries between them will be drawn on the basis of changes in phene frequency rather than on the basis of zones of reduced population density. Conversely, it is not always possible to define chorologically those very small groups of several individuals each carrying rare phenes, for such individuals may occur side by side with others and may not be isolated spatially.

Comparison of samples from different parts of the 10- by 10-km study site (Fig. 10) indicates that the samples that are closest phenetically are those taken from the bottomlands of the same streamlet and that samples taken from the bottomlands of different streamlets are strongly different even in cases where they were collected in places separated by smaller distances than samples from the bottomlands of the same streamlet.

In summary, within the territory studied (10 by 10 km), there exists an enormous number of biochorologic first-order groups (up to several dozens of individuals each) that form biochorologic second-order groups (up to several thousand individuals), and these in turn form biochorologic third-order groups (up to tens of thousands of individuals comprising the population of valleys of an intermittent streamlet). Within a second-order biochorologic group, phenetic complexes of various complexities may be singled out from first-order biochorologic groups (Fig. 11), while within a first-order biochorologic group it is possible in some cases to distinguish (by the presence of unique phenes) phenetic groups of several individuals each.

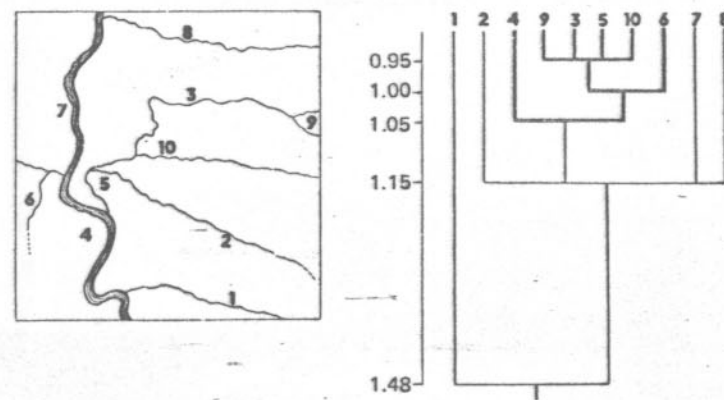


FIG. 10. Generalized similarity of various *Lacerta agilis* populations in the middle course of Kaldzhir River (western Altai) as determined by cluster analysis from frequencies of 187 pholidosis phenes. Populations occurring in the bottom land of the same streamlet (5, 10, 3, 9) show closer resemblance one to another, which may be explained by their common origin. Similar results were obtained by cluster analysis of pattern phenes.



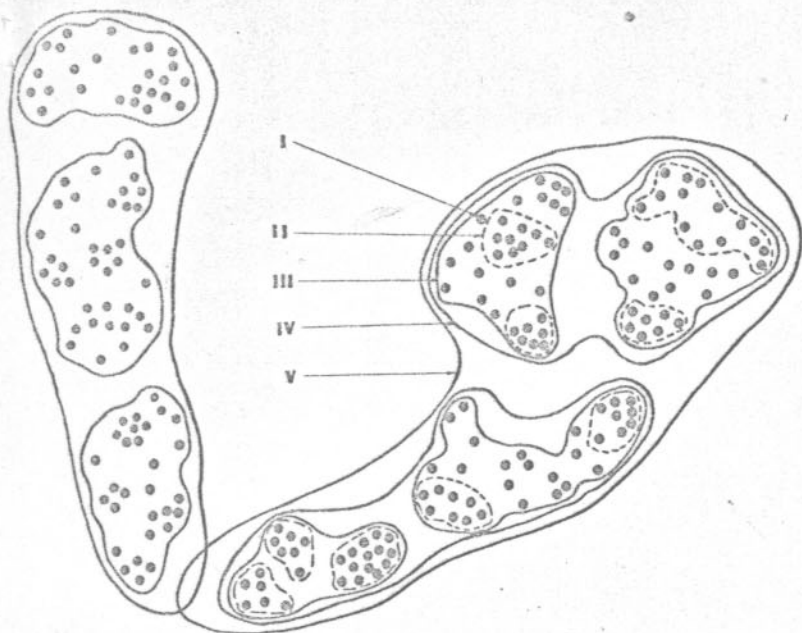


FIG. 11. Scheme showing the separation of a population into several biochorologic groups: (I) family; (II) deme; (III) group of first-order demes; (IV) group of second-order demes (population); (V) group of populations. See Table III for further details.

### Intrapopulation Hierarchy of Groups and Population Size

Collation of chorologic and phenetic data on population structure and of data on individual activity radii can give a general concept of the intrapopulation hierarchy of *L. agilis* groups and offer a tentative solution to the problem of defining a population for the species under consideration.

Such a collation has made it possible to characterize individual groups of lizards as shown in Table III.

The information we have obtained on the levels of integration of the lizard population inhabiting the 10- by 10-km territory in that part of the *L. agilis* range studied in detail (a steppe zone in the western Altai) is not at variance with a number of previously reported data from other habitats of this species. Thus, family groupings of lizards were recognized by Darevsky (1946), and small biochorologic groups consisting of several dozens of individuals (demes) were recognized by many researchers (see Baranov *et al.*, 1976, for a review). In a number of instances approximate estimates were made of the size of a population defined as a stable and isolated group existing over many generations (Baranov *et al.*, 1976). The estimated sizes of

TABLE III. Distinctive Features of the Main Levels of Integration of the *Lacerta agilis* Population in the Western Altai

Level of integration	Basis on which the level was identified	Number of individuals	Occupied area	Level of gene exchange with neighboring groups per generation	Survival time	Proposed name
1	Rare phenes	Several	0.1 ha	50%	1-2 generations	Family
2	Chorologic data and specific phene frequency	Several dozens	1 to several hectares	Approx. 20%	Several generations	Deme
3	Specific phene frequency	Several hundreds	Several to several dozens of hectares	Approx. 3-4%	Tens of generations	Group of demes
4	Chorologic data and specific phene frequency	Several thousands	Several to several dozens of hectares	Approx. 0.01%	Hundreds of generations	Combination of groups of demes (population)
5	Chorologic data and specific phene frequency	Tens to hundreds of thousands	Hundreds of thousands of hectares	Undetectably small	Thousands of generations	Group of related populations

nine such groups from different parts of the range vary from 300 to 4000 adults. These data were mainly obtained for regions where lizard populations are fairly isolated and probably characterize the lower limit of the population size for this species, and so they do not contradict those reported here for a territory which is virtually entirely populated by *L. agilis*.

## GEOGRAPHIC VARIATION

By studying the distribution of discrete characters (phenes) within the *L. agilis* range it is possible to gain a better (as compared to the study of quantitative characters) insight into the geographic heterogeneity of the range, to define zones inhabited by phenotypically (and genetically) more similar populations as well as boundary zones between the various groups of populations, and to recognize unique populations and population groups. All this can provide a basis for further microevolutionary studies aimed at reconstructing the microphylogenesis of the species.

### Phenogeography of Patterning

Figure 12 shows the geographic distribution of frequencies of nine phenes, four of which are related to the central stripe, two to dorsolateral striping, and three to dorsal spots. Each of these patterning characters shows a specific frequency distribution. Zones of high frequencies (concentrations) of a character may occur both in eastern and western parts of the range as well as in its southern and northern parts. This conclusion, drawn from data on males, is supported by those on females (these latter data are not given because of space limitations).

By drawing all the boundaries of phene concentrations on a single map we can obtain a web of lines covering the entire range. It appears that almost every population differs from the neighboring populations in the concentration of at least one phene. On the other hand, some of the zones of steep frequency gradients of different phenes show a good coincidence with one another, forming boundary zones between population groups having more similar phene constitutions.

It should be noted that the accuracy with which the boundaries of phene frequency gradients were drawn is different for different parts of the range. It is high for those parts represented by many samples and rather low for Western Europe (from which only a few small samples were analyzed) as well as for the northern and the extreme eastern parts of the range (especially the Yenisei-Angara interfluvial area and the eastern Altai).

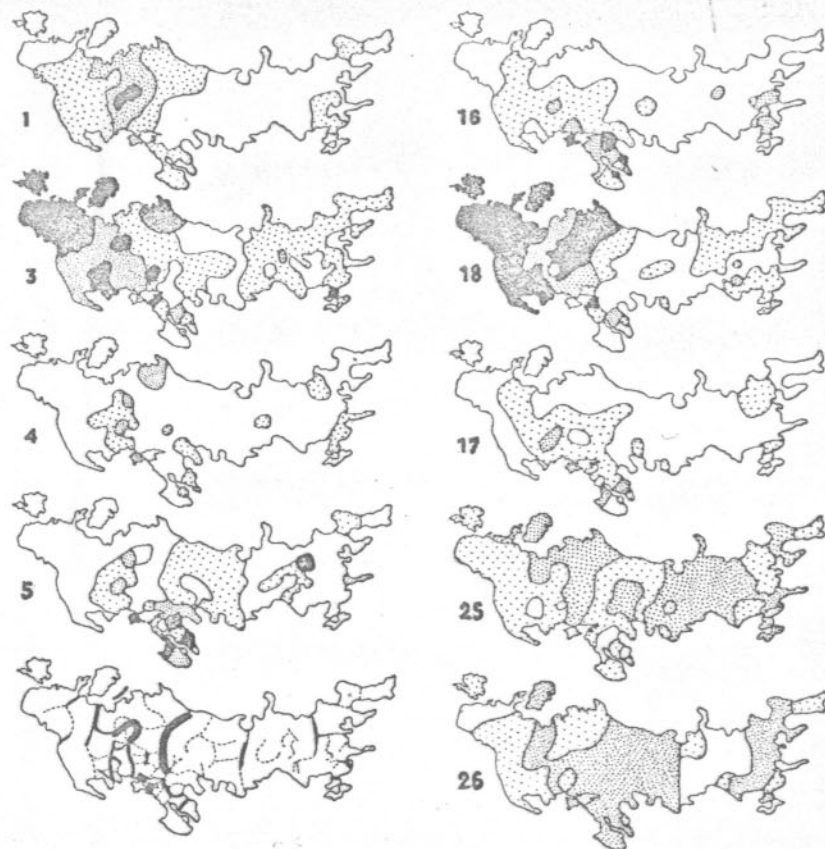


FIG. 12. Phenogeography of patterns in *Lacerta agilis*, showing zones having similar concentrations of phenes 1, 3, 4, 5, 16, 17, 18, 25, and 26 (See Fig. 1 for designations of phenes.) Bottom left: combined data on frequency gradients for all nine phenes; thickness of the lines is proportional to the number of boundaries passing in this area.

Viewing the range from west to east, it is possible to identify a number of boundary zones of steep phene frequency gradients (Fig. 12). The Western European populations are relatively uniform. Here the largest boundary zone appears to pass in the northwestern part of the German lowland. Another large zone begins on the Baltic Sea coast in the Polish lake region and extends southward, apparently to the Sudete Mountains and farther east. From it there arises a smaller boundary zone that extends through the Czecho-Moravian highland toward the upper Danubian lowland.

One of the largest boundary zones begins in the lower course of the Danube and Prut rivers and extends northwesterly along the eastern slopes

of the eastern Carpathian Mountains. It crosses the Volhynia highland and then curves around the Polesye from the west to pass, in places, along the Byelorussian ridge. At 30° E this zone makes a sharp turn southward to cross the Byelorussian ridge and then extends along the right bank of the upper Dnieper River to pass in the western part of the Dnieper lowland and to end in the Dnieper highland. A small boundary zone passes in the southern Carpathian Mountains.

In the north, this complex of western boundary zones (shown in detail in Fig. 12) is connected along the Moscow-Smolensk highland with a large Eastern European boundary zone. This extends almost meridianally from the north (from the Vologda region) along 40° E in the western part of the Meshchera lowland and the eastern slopes of the middle Russian highland. In the region of the Donets chain, this zone divides into two zones, one of which curves around the Donets chain from the east to run along the lower course of the Volga and the other extends to the Sea of Azov in the Azov highland.

The Crimea is populated by phenetically quite peculiar lizards, as a result of which the Crimean Peninsula stands out phenetically from both the Black Sea lowland and the northern Caucasus.

In the Caucasian part of the range, a powerful boundary zone passes in the region of the Kumo-Manychskaya depression between the Azov and Caspian Seas and partly extends to the northern part of the Stavropol highland. Moreover, each of the studied eastern populations of the northern Caucasus has quite distinct phene frequencies.

A considerable boundary zone is apparent in the middle and southern Ural Mountains. The next boundary zone toward the east is small and partly coincides with the Turaiskaya trough. The largest boundary zone in the eastern part of the range passes in the southern part of the Barabinskaya steppe (80° E) and divides into two zones in the south: an eastern zone passing along the foothills of the Altai, and a southwestern zone which extends to the Caucasian hillocky area in the region of the Tengizskoye depression.

Two powerful, although small in extent, zones are seen in the southeastern part of the range: one of these coincides with the Dzhungarsky Alatau ridge and the other passes along the Tarbagatai ridge.

Figure 12 also shows several other smaller boundary zones in the eastern part of the range.

The foregoing data show that in a number of instances groups of phenetic boundaries closely follow relatively small changes in relief (lowlands, depressions). Interestingly, in many cases the phenetic boundaries pass across large rivers (e.g., Neman, Volga, Irtysh). Generally, the impression is produced that the phenogeographic boundaries follow orographic boundaries more closely than hydrographic ones.

## Phenogeography of Color

Although there exist a series of variations of yellow, brown, gray, and green dorsal colors, it was not feasible to make a reasonably objective assessment of these; the only consistent results were obtained in the case of brown and green hues in the dorsal coloration of males. The evidence obtained indicates that all males from northern populations have no green hues whereas those from many southern populations do have green on the dorsum. In some southern populations all males are green, the only exception among them being a group of populations found on the southern border of the range around Lake Issyk Kul in the Tien Shan Mountains, where males are devoid of green hues.

In contrast, the distribution of those phene complexes that mark such rare types of coloration as the var. *rubra* and var. *platinumus*, as well as complete melanistic forms, can serve, within limits, as markers of geographic regions as a whole. Thus, the var. *rubra* occurs mainly in elevated regions of Middle and Eastern Europe, between 15° and 35° E (Borcea, 1975; and our findings) while the var. *platinumus* invariably occurs more easterly, in the basins of the rivers Don, Volga, and Kura, as well as in the Maly Caucasus region (between 36° and 50° E). Complete melanists were encountered only in the eastern part of the range, in the Altai region.

Generally, it seems that the color phenes can be used only to define relatively large groups of populations covering entire geographic regions.

## MICROPHYLOGENESIS OF THE SPECIES

After describing the main phenogeographic features of the species, an attempt can be made to reconstruct its microphylogenesis, namely the history of establishment of its range from data relating to Quaternary paleogeography on the one hand and to modern phenogeography and systematics on the other.

### History of the Range

Today the sand lizard is a eurytopic species within the steppe and forest-steppe zones. Most of its range is in forest-steppe zones, but the northern part of the range extends into the forest zone where sand lizards are found in conjunction with *L. vivipara*, a typically forest form; in the south its range extends virtually throughout the steppe zone as well as to some high-altitude (up to 2000-2200 m above sea level) regions of the Alps,

Caucasus, and Tien Shan. Many areas in the southern part of the range are coinhabited by sand lizards and some other species belonging to this extensive genus (*L. viridis*, *L. strigata*, *L. saxicola*, *L. taurica*, *L. trilineata*, *L. derjugini*), although *L. agilis* is characterized by a tendency to occur in particular biotopes.

In general, the present-day sand lizard is an inhabitant of steppe and forest-steppe zones and is the most numerous and the most widely distributed reptilian species in Eurasia. This suggests that during most of its history the sand lizard as a species must have been associated with mesophytic biotopes of moderate climates.

Paleontologic finds of the genus *Lacerta* from the northern Caucasus and southern Ural (Belaya River) regions date back to the upper Pliocene and those from Western Europe to the Eocene (Darevsky *et al.*, 1976). The paleogeography of the Eocene and Miocene in Eurasia has been studied inadequately, as have the systematics of extinct forms from this group of lizards. For this reason one can only state that the territory of modern Europe was already inhabited by this genus about 30 million years ago. In subsequent epochs, and particularly in the Quaternary period, large expanses of land were covered by glaciers on several occasions, and the boundaries of seas and internal water bodies underwent repeated changes, as did the climate of large regions. We proceed from the hypothesis that the sand lizard as a species had its origin in the northern Caucasus (Peters, 1958; Darevsky *et al.*, 1976). In the later Miocene and early Pliocene (ca. 10 million years ago) it appeared in Transcaucasia, which is a major center of speciation for palearctic forms (Fig. 13). It is possible that this species owes its origin to the grandiose process of steppe formation in Eurasia whereby tropical forests were replaced by steppes and forest-steppes over vast areas stretching from Mongolia to Central Europe.

In the upper Pliocene, the Caucasus gained extensive links with the Russian platform so that the sand lizard could begin dispersing westward and eastward from the Caspian lowland (Darevsky *et al.*, 1976). Alternatively, it could spread in the south. By way of low mountains covered by mesophytic vegetation along the Black Sea and Caspian Sea coasts, it could reach the Balkan Peninsula and spread farther to the Carpathian Mountains through the Bosphorus isthmus, which formed several times in the past. Along the Crimean uplands it could well reach the then less elevated foothills of the Pamir-Altai and Tien Shan mountains. In this way the Balkan-Carpathian and Central Asian centers of this species distribution could form, respectively, with the Caucasian and Asia Minor centers in between (see Fig. 13). In the Riss, during the period of maximal glacier advancement (ca. 200,000 years ago), these centers could well serve as refugia whence secondary dispersion of the species into the limits of its modern range could subsequently begin. Advancing and retreating glaciers

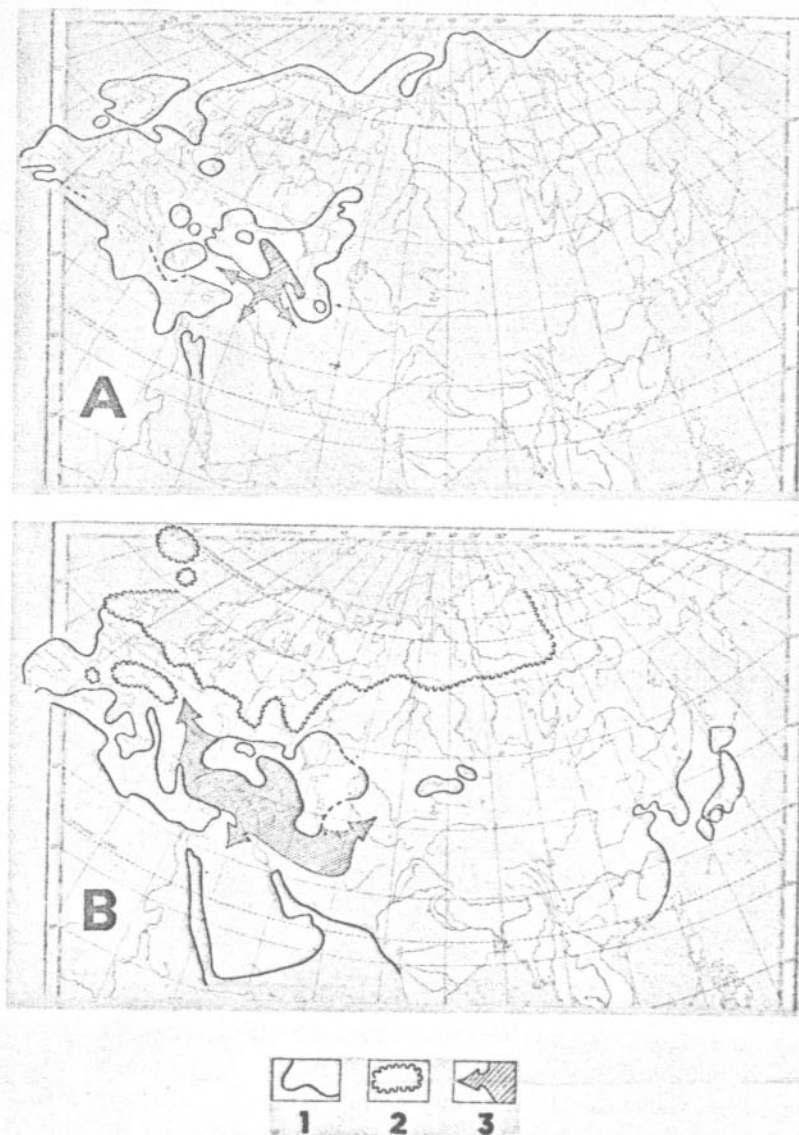


FIG. 13. Paleogeography of Eurasia and possible stages in the formation of the *Lacerta agilis* range. A. Outline of land in Pliocene (5-7 million years ago). B. Outline of land and boundaries of continuous ice sheet ca. 200,000-230,000 years ago (Riss I, Middle Quaternary glaciation). (1) boundary between land and sea; (2) glacier boundaries; (3) presumed direction of *L. agilis* distribution.

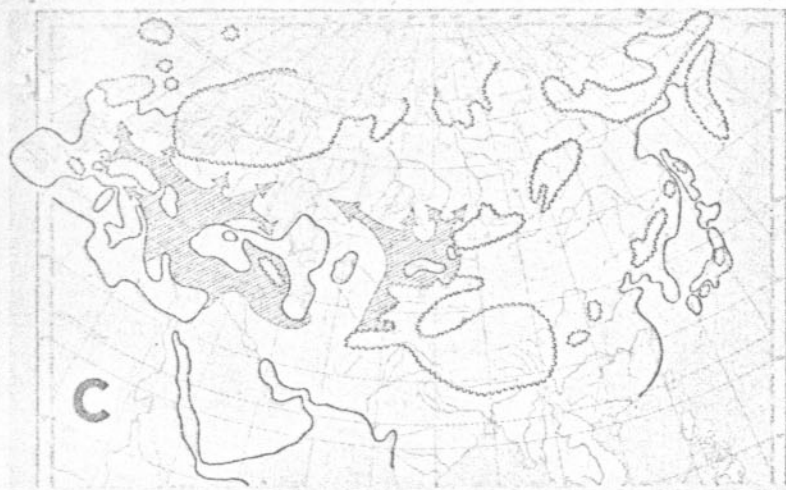


FIG. 13. (cont.) C. Outline of land and boundaries of continuous ice sheet ca. 50,000–65,000 years ago (Würm). (From Sinitsin, 1962; Gerasimov, 1964; Tchebotareva, 1977.)

(at least seven in Eurasia over the last 200,000–250,000 years) must have played an enormous role in this, as well as transgressions and regressions of the sea, which were of a fairly large magnitude, the sea level being dozens of meters higher or lower than the currently existing ocean level (Zubakov, 1975).

While many details of the development of Quaternary landscapes in Eurasia still remain obscure, some events may be singled out which did take place with certainty. Thus there repeatedly occurred periods of cooling and of glacier advancement from the north (during the Dnieper glaciation, the southern edge of the glacier reached the lower courses of the Dnieper and Don rivers; see Fig. 13). During the periods of maximal glaciation the ice caps in the Caucasus, Alps, Pyrenees, and Central Asian mountains all increased appreciably while the level of the world ocean became lower.

The connection between the Mediterranean Sea basin and the world ocean remained disrupted for very prolonged periods (hundreds of thousands of years). During such periods, as a result of internal tectonic movements, the level of the Mediterranean Sea rose and fell dozens of meters and, it appears, not necessarily concurrently with the world ocean level.

The Black Sea and the Caspian Sea became interconnected more than once, and for a long time the Caspian Sea itself occupied the entire Caspian lowland, spreading as far as Kamyshin in the north and possibly merging with the Aral Sea in the east.

It follows, then, that in the region of the Eastern European plain conditions suitable for *L. agilis* existed for only relatively short periods, so its

range must have been repeatedly disrupted; therefore the final settlement of the species in this region is a rather recent event—not more than 30,000–50,000 years old. Still more recent must have been the colonization by *L. agilis* of the Baltic part of its range which finally became free from glaciers as recently as 10,000–12,000 years ago (Tchebotareva, 1977).

Comparison of these two hypotheses regarding the pathways of the original dispersion of the species (i.e., in the south or in the north) indicates that both postulate the existence of Quaternary glacier refugia for this species in the Balkan and Caucasian regions. These parts of the present range may be considered to be the oldest—at least several hundred thousand years old (see Fig. 14). The middle European part of the range, extending from southern England to the Donets steppes, may be regarded as one of medium age (no more than 100,000 years old) and the northern part within Europe as the youngest (10,000–15,000 years old). As regards the Asian part of the range, there are at least two alternatives: if the hypothesis postulating the southern dispersion of lizards is confirmed, then the Balkan–Zaiskanansk refugium may be taken to be approximately 200,000–300,000 years old; if, on the other hand, the northern Caspian dispersion hypothesis proves valid, then the southeastern part of the range should be considered as being very young (several thousand years old). In the eastern part of the range, all high-altitude areas of the range in Tien Shan (in the environs of Lake Issyk Kul), Dzhungarskoye Alatau, Tarbagatad, and Altai should undoubtedly be regarded as relatively young, as

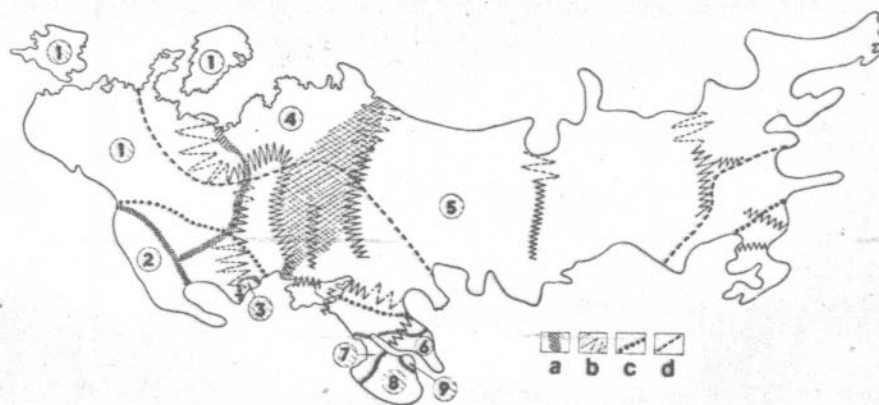


FIG. 14. Structure of the *Lacerta agilis* range: (a) zones of intergradation between subspecies; (b) zones of concentration of phenetic boundaries; (c) presumed boundary between three oldest parts (over 100,000 years old) of the present day range; (d) presumed boundary between old (ca. 50,000 years) and young (ca. 10,000 years) parts of the range. Subspecies: (1) *Lacerta agilis agilis*; (2) *L. a. bosnica*; (3) *L. a. euxinica*; (4) *L. a. chersonensis*; (5) *L. a. exigua*; (6) *L. a. boemica*; (7) *L. a. grusinica*; (8) *L. a. brevicaudata*; (9) *L. a. iorensis*.

should groups of Uralian populations and of populations inhabiting the north of western Siberia.

#### Relationship between the Phenogeography, Systematics, and History of the Range

The current state of paleogeographic and paleoclimatological knowledge does not make it possible to decide unequivocally which hypothesis regarding the establishment of the *L. agilis* range is most plausible and, on this basis, to account for the phenogeographic boundaries that have been detected. The question arises as to whether phenogeography can be drawn upon to shed light on the problem of range formation.

The first step in solving this problem is to consider the discovered phenetic boundary zones in relation to the available data relating to the establishment of the range (Fig. 15). Both ancient parts of the range prove to be partially separated by phenetic boundary zones: the Carpathian-Balkan part is delimited from the northeast (no comparative population data for the western part of this zone are available) while the Caucasian part is separated from the rest of the range by a powerful zone passing along the Kumo-Manycharskaya depression. The boundary zones passing along the Baltic ridge, the middle Russian highland, and the Vyatka spur possibly coincide with the margins of the ice sheets that existed during the periods of great glaciations and so may mark zones of different ages within the range. Therefore, some of the phenetic boundaries may well coincide with regions of different ages within the range that have been defined independently.

Collation of our phenogeographic data with data on the distribution of *L. agilis* subspecies (see Fig. 15) shows, on the one hand, that some phenetic boundary zones coincide with zones of subspecies boundaries (e.g., with the boundaries between *L. agilis agilis* and *L. agilis chersonensis* in Central Europe and, more important, a broad intergradation zone between *L. agilis chersonensis* and *L. agilis exigua* in the Eastern European plain), and on the other, that the phenetic subdivision of the range is much more complicated than the currently recognized "subspecific" subdivision, since the ranges of all major subspecies prove to be highly nonuniform phenetically. At this stage, when not all of the pertinent material relating to many characters has been analyzed, we do not intend to attempt revision of the intraspecific taxonomy, although the need for such revision is evident.

In particular, a noteworthy feature of the phenogeographic maps referred to above (see Fig. 12) is that in some parts of the range all individuals within populations share some phene whereas in other parts such a common

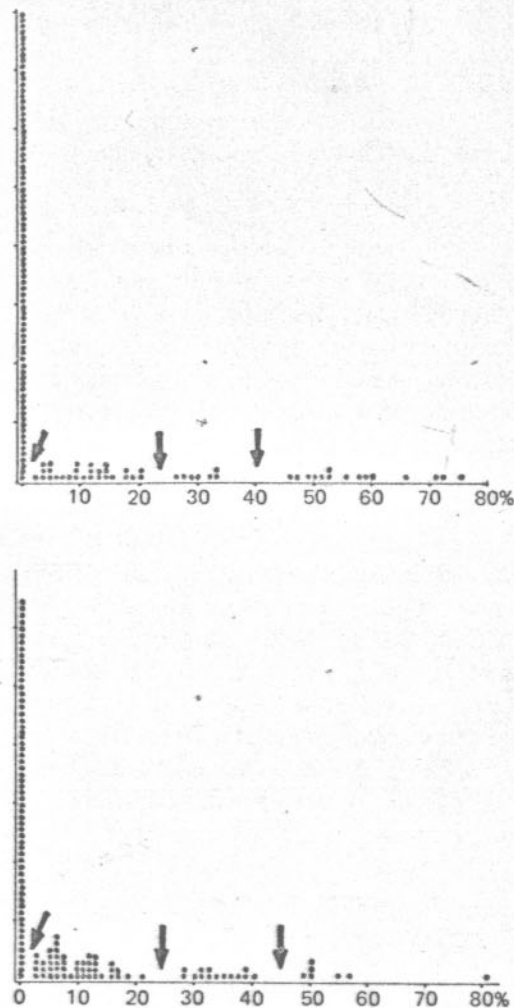


FIG. 15. Discreteness in the frequency distribution of phenes 1 (top) and 7 (bottom) within the *Lacerta agilis* range. Each dot represents the frequency of a given phene in a population. Arrows indicate the breaks in frequency distribution (grouping) that served as a basis for identifying phene frequency gradients and for drawing phenetic boundaries on the map of these phenes (see Fig. 12).

phene is lacking in all individuals. Formally, on comparing these two sets of populations in pairs (and disregarding the transitional zones), they may even be assigned to different species. Certain groups of *L. agilis* populations would seem to deserve being accorded a rank higher than the subspecies, not only in terms of color phenes but also in terms of a number of classic

systematic characters. The situation is made more complicated by the fact that in Dagestan, and possibly in Armenia, there exist forms of an obviously hybrid origin transitional between *L. agilis* and *L. strigata*. The possibility of hybridization of *L. agilis* and *L. trilineata* has been demonstrated in experiment (Bischoff, 1969, 1973). Nor can one rule out the possibility of hybridization of *L. agilis* and *L. viridis*.

All this taken together—that is, on the one hand the considerable intraspecific differentiation of the sand lizard and on the other the existence of forms transitional to certain closely related neighboring species from the *Lacerta* genus—again warrants the statement that, in this case, the formal taxonomy does not adequately reflect the situation existing in nature. Within the species *L. agilis* as it is recognized by taxonomists there may well exist some forms approximating the species rank (such forms may tentatively be called “potential species”). *L. agilis* as a whole, together with some other species from the extensive genus *Lacerta*, probably constitute a kind of rassenkreis which are more closely associated with one another than the remaining species in the genus. It should be reiterated that so far the question of the taxonomic position of *L. agilis* population groups has been formulated in a highly preliminary form, pending the complete analysis of all available material relating to hundreds of characters shown by all the populations studied within the range of the species. Therefore, no final taxonomic conclusions will be attempted here.

## GENERAL DISCUSSION

The first results of our studies on the microevolution of the sand lizard have been reported above. As already stated, the main purpose of these studies is to attempt a detailed reconstruction of both the past microevolution of the species and the currently operating evolutionary factors.

A major achievement of evolutionary thought in this century was the formulation of the concept of microevolution (Dobzhansky, 1937; Timofeeff-Ressovsky, 1939; Huxley, 1942). Today it is clear that the elementary evolutionary unit is the population (see Mayr, 1965, 1970, for reviews) and that the elementary evolutionary factors are natural selection, isolation, population waves, and mutation.

Although the theory of microevolution has been developed to a rather high degree, there is not nearly enough precise information about naturally occurring microevolutionary processes to permit recognition of typical evolutionary situations (Yablokov, 1968; Lewontin, 1974) and thus to pass gradually from mere descriptions of evolutionary processes to their regulation. Even though the problem of “controlled evolution” (Vavilov, 1922) is

now seen to be much more complicated than was formerly believed, the only acceptable strategy to be adopted in the face of catastrophically rapid changes that occur in the earth's biosphere is one that envisages control of the evolutionary process.

To be able to effect control over evolution it is necessary to have adequate data on intrapopulational and interpopulational structures, on the operation of various evolutionary factors in different species, and on the overall patterns of microphylogenesis of a multitude of species from various groups. One of the most promising avenues for obtaining such data is analysis of intraspecific (both within and between populations) variability of individual species.

It should be noted that lizards have already been the objects of such research, namely the side-blotched lizard *Uta stansburiana* (Soulé, 1966, 1967, 1972; Soulé and Yang, 1973; Ballinger and McKinney, 1967; Ballinger and Tinkle, 1972), *Lacerta melissellensis* and *Lacerta sicula* (Radovanović, 1960), *Sceloporus woodi* (Jackson, 1973), and the iguanid genus *Anolis* (Schwartz, 1968). As a result, many interesting data have been obtained on the rates of microevolutionary processes, origins of isolation, and intra- and interpopulations variations in various characters. The data reported in the present study both supplement those on reptilian variability and call attention to some of the aspects that so far have not been specifically dealt with in studies devoted to reptilians, in particular, problems of intrapopulational structure and phenogeography.

At this stage of research on *L. agilis* it is already possible to speak of two groups of encouraging results. It has been shown, first, that biochorologic groups at the population level are fairly complex and, second, that the range of this species is extremely heterogeneous phenogeographically. These two facts in turn raise a number of questions, both of theoretical and of methodological nature. Some of these are briefly discussed below.

The multilevel biochorologic hierarchy revealed in naturally occurring *L. agilis* populations complicates, rather than clarifies, the problem of defining boundaries between populations. In our view such a boundary should be drawn between groups of the fourth level (see Table III) inhabiting an area of several hectares to several hundred hectares, consisting, as a rule, of several thousand individuals, and having a level of gene exchange with neighboring populations of about 0.01% per generation. However, one cannot rule out the hypothesis that populations proper are those groups comprising the third or fifth, rather than the fourth, level in the hierarchy.

That all the groups from the third level upward represent reasonably balanced gene systems is suggested by the fact that intermediate, “hybrid” zones have been detected at the boundaries between such groups. These

"hybrid zones" may prove to be represented by groups 9 and 3 mentioned above (see Fig. 9a).

The interaction between these peculiarly balanced gene systems upsets the genetic equilibrium, and this is reflected in the unusual phenetic diversity of such "hybrid" assemblages.

Whatever the case may be, an answer to the question as to which of the actually existing groups is to be regarded as the population proper requires that the magnitude of gene exchange between adjacent populations be referred to in the genetic-evolutionary definition of the population concept.

The evidence obtained for *L. agilis* indicates that the population structure of this species is many times more complex than the often-used scheme in which the population of a species is considered as consisting of a set of elementary (so-called Mendelian) populations that exchange genetic material to roughly equal degrees. Even within a limited *L. agilis*-populated area millions of times smaller than the total range there were found to exist groups of at least five ranks. Even if one excludes from consideration the small and extremely small groups (demes) that survive not more than a couple of generations, one will still have three ranks of groups that may exist over many generations. There can be no doubt that this hierarchy is bound to make the microevolutionary processes far more complex so that certain calculations, such as those to elucidate the fate of alleles in systems of Mendelian populations, would appear oversimplified and biologically meaningless. At the same time the species-specific population hierarchy must be taken into consideration in solving any particular problem of population control (e.g., in searching for ways of preserving the gene pool).

One of the problems concerns the methods of placing phenetic boundaries both at the intrapopulation level and at the level of the range as a whole. Which frequency gradients of particular phenes are to be regarded as essential for defining boundaries and boundary zones on the territory under study? To answer this question as objectively as possible, we used the method in which all real values of phene frequencies in the different groups being compared are plotted on the abscissa; if the number of variates is sufficiently large, a natural discreteness in the distribution of data points will be apparent in a vast majority of cases (Fig. 15), and this discreteness will show the more important (for each particular case) phene frequency gradients which should be taken into account.

A group of problems is associated with estimating the "weight" of individual phenes. In the examples given above it was tacitly assumed that all phenes being compared are equivalent. Generally this does not seem to be the case. We know that there are phenes of "different scopes": those that mark by their presence groups of some particular rank while failing to mark groups of other ranks, as well as those marking more or less distinctly by

their frequencies the groups being compared. In other words there are phenes of different "weights." The concept of weight as applied to phenes is highly relative: a phene that fails to show differences in frequency on comparing groups of the same rank may prove highly indicative when groups of some other (more or less large) level are compared. The problem of phene weights should be given proper consideration in cluster analysis where all characters are usually equated.

Turning now to the possible reasons for the appearance of phenetic boundaries (and boundary zones), the following three main assumptions appear plausible. First, by its specific concentration each phene can mark a given adaptive boundary (i.e., each phene is associated, as far as its distribution is concerned, with a particular direction and pressure of natural selection; e.g., a brown coloration is protective against a brown background and a green one against a green background). Second, phene frequency gradients can mark places inhabited by populations with differing gene pools, i.e., places where different gene pools meet. For example, when lizard populations were moving toward one another from different refugia in postglacial times and when a single range was being reconstructed, these gene flows must have met in some region or other. Such a process should involve the introgression of genes (phenes and whole gene complexes which is manifested phenetically in sharply defined boundaries of phene frequency gradients.

As yet there do not exist criteria for demarcating these two possibilities; in any event they must be closely associated biologically. But these possibilities suggest that there existed a much larger number of refugia (or of some other gene flows which, when they met, could give rise to phenetic boundary zones). Alternatively, there may have existed within the *L. agilis* range much more diverse environmental conditions (and hence many more directions of natural selection) than would seem on first sight. The second assumption is more amenable to verification than the first. This verification would include detailed consideration of the distributions of various phenes in relation to the distributions of climatic boundaries, soils, temperatures, moisture levels, and plant and animal species.

The third assumption is that the appearance of phenetic boundaries is due to the effects of isolation. It is known that the gene pool (and consequently the phene pool) may change as a result of chance processes (population waves, mutations)—even under similar conditions of natural selection in isolated populations. One example possibly supporting this assumption are considerable phenetic distinctions between some of the highly isolated parts of the *L. agilis* range such as the Crimean Peninsula, certain mountain populations in the Caucasus, and populations of the Zailiisky Alatau and Dzhungarsky Alatau. It is interesting to note that if the colonization of southern Scandinavia by lizards took place in postglacial times by way of



the terrestrial bridge that arose across the sound, the Swedish populations should be more similar to Western European populations than to Eastern European ones. This is just the case.

To conclude this brief discussion it seems desirable to dwell at some length on the approach to the identification and recording of phenes in naturally occurring populations. As is known, the concept of "phene," together with that of "gene," was introduced by Johanssen in 1909. Long before, however, Knight (1824), Bateson (1894), and others spoke about "unit characters," "mutation characters," "single characters," and other phenotype characters.

More recently Osborn (1916) again drew the attention of zoologists to the study of discrete, discontinuous phenotype characters. Vavilov (1922) clearly showed that nonmetrical, discontinuous variations, if considered in accordance with his rule of homologous series in hereditary variation, may serve as an important tool of what is in effect genetic research in naturally occurring assemblages of individuals. Using the same principle, Serebrovsky (1929), considered data on discrete variations in relation to biogeography and substantiated a new line of research in "genogeography" (in fact, "phenogeography"). After the 1950s, nonmetrical variations in animals have been studied most successfully by the British school of Gruneberg (Gruneberg, 1952; Berry and Searle, 1963; Berry, 1963, 1977).

There is only one publication concerned with the genetics of *L. agilis* (Drzewicki, 1926). In it the Mendelian nature of inheritance of main variations in dorsal coloration was demonstrated. There can be no doubt, however, that the coloration patterning, down to its minutest details, is also hereditarily determined to a high degree. This is attested, in particular, by direct genetic experiments on the closely related lizard species *L. melisellensis* (Gorman *et al.*, 1975).

The genetically determined coloration patterns have often been used in intraspecific taxonomy and microevolutionary research on reptilians (White, 1975; Beatson, 1976; Schneider, 1972; Erkinaro, 1974; Radovanović, 1960; Walker and Taylor, 1966; and others), including *L. agilis* (Fuhn, 1967; Borcea, 1974). Also used as genetic markers in *L. agilis* were subtle variations in scaling (Fuhn, 1967). In several studies on the intraspecific taxonomy and population biology of reptilians, pholidosis characteristics have been used as reliable indicators of the genotypic constitution of populations (Soulé, 1967, 1972; Soulé and Yang, 1973). Thus there seem to be good grounds for using the discrete characters of coloration (patterning and color) and pholidosis as marker characters for the genotypic constitutions of *L. agilis* populations.

The present results attest to a high effectiveness of phenes as used at the various levels of research on *L. agilis*—all the way from the identification of its families and demes to making phenogeographic generalizations

for its range as a whole. There is increasing evidence to suggest that the phenetic approach holds much promise for the solution of a wide variety of microevolutionary problems (for reviews, see Berry, 1977; Timofeeff-Ressovsky and Yablokov, 1973; Timofeeff-Ressovsky *et al.*, 1977). The present study has confirmed this. The phenetic approach may well prove the main method for obtaining large quantities of information on population genetics which is so necessary today in solving many problems of evolutionary genetics (Lewontin, 1974). Further development of this approach will certainly require studying discrete variations in an increasingly larger number of species, expanding the range of the variations studied by considering most diverse organ systems, and recording not only morphologic characters in the broad sense (including the biochemical phenotype), but also physiological and ecological ones.

## SUMMARY

Analysis of the frequencies of occurrence of 222 discrete, nonmetrical phenotype characters (phenes) relating to coloration, color patterning, and scaling in 13,688 *L. agilis* specimens from 135 sampling sites of the range has shown that phenes, by the frequency of their presence, can mark intraspecific groups of different ranks—from families and demes to geographic groups of populations. Study of the population structure on a 10- by 10-km area populated throughout by this species has revealed five levels of biochorologic groups: the family (in which the gene exchange between adjacent groups is about 50% per generation and whose survival time is 1–2 generations); the deme (gene exchange, ca. 20%; survival time is several generations); the deme group (gene exchange, 3–4%; survival time is dozens of generations); the combined deme group, or the population (gene exchange ca. 0.01%; survival time is hundreds of generations); and the population group comprising several closely related populations (gene exchange is undetectably small; survival time is thousands of generations).

Study of the geographic distribution of phenes within the *L. agilis* range has revealed a number of boundary zones where the boundaries of frequency gradients of certain phenes coincide. These boundaries are possibly of an adaptive nature and may coincide with orographic boundaries as well as mark some events in the microphylogenesis of the species (zones of glacier refugia, gene flow in periods of active postglacial dispersion of the species, effects of long-term isolation).

The existence of several population groups within the species that represent "potential species" is briefly discussed, as is the need for modifying the current concept of population by specifying the possible magnitude

of gene exchange with adjacent populations. Also discussed is the methodology for defining phenetic boundaries on the basis of sharp variations in phene frequency.

The use of the method whereby the frequencies of phene occurrence are recorded for the purpose of studying microevolutionary processes is considered to hold much promise for research on naturally occurring populations.

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