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GEOGRAPHICAL VARIATION IN LADY-BEETLES

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THE INTRASPECIFIC AND THE INTERSPECIFIC VARIABILITY

THE coleopterous family Coccinellidae presents very favorable material for studies on variation. The color-pattern of the elytra and of the pronotum is very widely variable in many species. The variations may be arranged in series beginning with entirely light (yellow or red) elytra, ranging through light elytra with a number of dark (black or brown) spots, dark elytra with light spots, and ending with dark, unspotted elytra. The intraspecific variability is not infrequently discontinuous, the intergrades between the different patterns being rare or absent.

Large groups of related species and genera exhibit parallel series of patterns, upholding the rule of homologous series in variation, formulated by Vavilov (1922). Thus, only a few of the more than one hundred patterns that are known to occur in the species of the genera Coccinella, Semiadalia, Adonia and Hippodamia are restricted to a single species. A large majority of these patterns reappear in several or in many species. The similarity of the homologous patterns in different species is often striking (compare Figs. 2 E and 3 H, Figs. 2 L, 4 D and 4 G, Figs. 2 I, 4 J and 5 D). Homologous varieties of different species may appear even more similar to each other than do different varieties of the same species. However, the different varieties of the same species, at least those found in the same locality, intercross freely in nature as well as in experiment, while different species are, as far as known, intersterile (Lus, 1928).

THE GEOGRAPHICAL ELEMENT IN VARIATION

The different patterns known in a given species do not occur equally frequently in every part of the area inhabited by the species. In some sections of the specific area a majority of the population may consist of individuals having a pattern or patterns which are rare or absent in other sections of the same area. The species becomes, thus, differentiated into geographical races (subspecies). Each of the subspecies is characterized

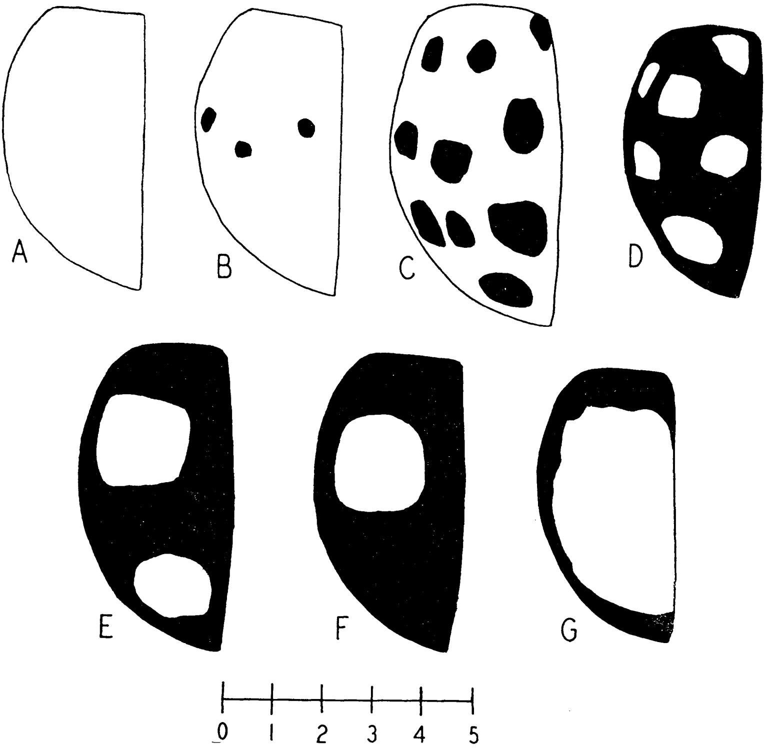

FIG. 1. *Harmonia axyridis* Pall. A—var. *succinea* Hope; B—var. *frigida* Muls.; C—var. *novemdecimsignata* Fald.; D—var. *axyridis* Pall.; E—var. *spectabilis* Fald.; F—var. *conspicua* Muls.; G—var. *aulica* Muls. The scale in this and in the following figures represents five millimeters.

by a definite frequency of the different patterns in the population. This situation may be illustrated by the example of the Asiatic species, *Harmonia axyridis* Pall.

Harmonia axyridis Pall. occurs in the southern stretch of Siberia, from the Altai Mountains to the Pacific, in Manchuria, China and in Japan. The western part of this area, extending from Altai to Lake Baikal, is inhabited by var. *axyridis* (Fig. 1 D, Table 1). Individuals having the pattern of var. 19-*signata* (Fig. 1 C) occur in this region only as an exception. East from Lake Baikal var. *axyridis* loses rapidly its predominance, it is only seldom found in the Maritime Province and in Japan, and is not known to occur in China (Table 1). The variety *19-signata* is the most frequent one in the eastern part of the specific area; var. *spectabilis* (Fig.

TABLE 1

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Harmonia axyridis* (IN PER CENT.)

	succinea	*frigida*	*19-signata*	*axyridis*	*spectabilis*	*conspicua*	*aulica*	n
Altai Mts.	....	....	0.05	99.95	....	....	......	4013
Yeniseisk Province	....	0.9	....	99.1	....	....	......	116
Irkutsk Province	....	....	15.1	84.9	....	....	......	73
Transbaikalia (western part)	....	4.9	45.9	49.2	....	....	......	61
Amur Province	7.3	29.3	41.5	....	....	....	......	41
Maritime Province (Khabarovsk)	18.6	18.1	38.7	0.2	13.4	10.7	0.3	597
Maritime Province (Vladivostok)	16.9	31.1	37.6	0.8	6.0	6.8	0.8	765
Manchuria	12.9	32.8	34.0	....	11.2	8.6	0.5	232
Korea	28.1	26.6	26.6	....	6.2	12.5	......	64
Japan	....	16.4	3.0	4.5	16.4	59.7	......	67
China (Chi-Li, Shan-Si, Shan-Tung)	36.8	12.5	27.0	....	12.5	10.5	0.7	152
China (Kan-Su, Sze-Chuan)	3.7	26.0	40.7	....	11.1	14.8	3.7	54

The column marked "n" in this and in the following tables indicates the number of individuals studied from a given region.

1 E) and var. *conspicua* (Fig. 1 F) are very frequent in Japan, less so in eastern Siberia and in China, and do not occur at all west of Lake Baikal.

The species *Harmonia axyridis* is, thus, segregated into several geographical races. The western race is well differentiated from others, since the population of the western race consists almost exclusively of individuals having the pattern *axyridis* (Table 1), and this pattern occurs in other races only as an exception. The eastern-Siberian, the Japanese and the Chinese races differ from each other only in the average frequencies of the occurrence of the different patterns in the population.[1]

The degree of differentiation of the geographical races may vary greatly. In some species the geographical races are merely indicated, the relative frequency of the various patterns being only slightly different in different parts of the specific area. Other species are subdivided into more or less sharply defined races. In extreme cases nearly 100 per cent. of the population of each race may exhibit a pattern or patterns which are not found at all in individuals belonging to other races. The different degrees of differentiation of the geographical races may be interpreted as different stages of the same process. What we observe in various species at our time level, are the young or slowly differentiating races on one hand, and the old, well-formed races, on the other. A comparative study of the different species may give us an insight into the process of the evolutionary divergence in time and in space.

DIFFERENT STAGES OF THE DIFFERENTIATION OF THE GEOGRAPHICAL RACES

Adonia variegata Goeze inhabits almost the whole Palaearctic region, and, in addition, the eastern part of

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[1] The variability of *Harmonia axyridis* is discussed in more detail in Dobzhansky, 1924. It is worth mentioning here that the varieties of this species differ from each other only or mainly in coloration, and do not differ in the structure of the genitalia.

Africa. The color pattern of this species is very variable. The typical pattern (Fig. 2 E) consists of seven black spots on each elytron. The decrease or the increase of pigmentation leads to the disappearance or to fusion of some or of all of these spots. More than eighty different patterns occur in the species; some of them are represented in Fig. 2. The geographical distribution of the patterns is shown in Table 2

TABLE 2

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Adonia variegata* (IN PER CENT.)

	immaculata	*constellata*	*carpini*	*litigiosa*	Some spots absent	*variegata typica*	Confluent spots	n
Kiev	0.2	39.2	23.3	9.8	9.4	13.2	4.9	1590
Crimea	0.3	33.7	17.7	11.9	13.3	19.6	3.6	362
Uralsk, Turgai and Akmolinsk Provinces	......	28.6	14.3	16.8	13.4	21.8	5.1	119
Transcaucasia	0.5	40.1	26.4	11.6	4.2	11.1	6.4	189
Persia	2.0	53.1	14.3	7.1	14.3	8.2	1.0	98
Transcaspia	2.2	32.6	19.6	10.9	7.6	20.6	6.5	92
Semirechensk Prov.	0.3	27.1	17.2	13.0	11.0	24.8	6.5	354
Pamir and Darwaz	......	1.5	6.0	....	0.8	41.0	50.7	134
Chinese Turkestan	......	4.5	6.4	14.8	3.5	42.6	28.2	202
Ordos and Ala-Shan	......	2.7	21.9	4.1	1.4	27.4	42.5	73
Northern Mongolia	......	15.1	19.1	8.6	1.3	30.2	25.6	152
Transbaikalia	......	5.8	17.4	8.2	....	46.5	22.1	86
Maritime Province	......	....	18.2	....	....	50.0	31.8	22
Yakutsk Province	......	....	....	....	....	18.3	81.7	115
Abyssinia	......	....	....	....	....	3.6	96.4	56

(patterns involving simultaneous disappearance of some of the spots of the typical pattern and fusion of others are included under the heading "confluent spots"). An area extending from Europe to Caucasus, Persia and the plains of Turkestan is inhabited by a lightly pigmented race. In this region varieties *immaculata, constellata, carpini, litigiosa,* and other varieties having some spots missing clearly predominate. Persia seems

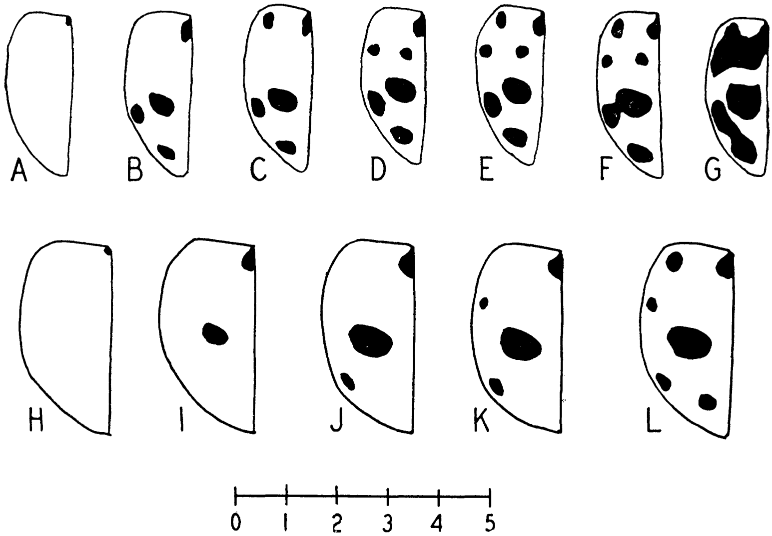

FIG. 2. A–G—*Adonia variegata* Goeze; H–L—*Coccinella quinquepunctata* L.; A—var. *immaculata* Gmel.; B—var. *constellata* Laich.; C—var. *carpini* Geoffr.; D—var. *litigiosa* Wse.; E—the type form; F and G—some of the varieties having confluent spots; H—var. *minckwitzi* Hänel.; I—var. *rossii* Wse.; J—the type form; K—var. *simulatrix* Wse.; L—var. *arthurica* Jacobson.

to be inhabited by an especially light race. Eastward from this area, starting from Pamir and the high mountainous plateaus of eastern Bokhara (Shughnan, Roshan, Darwaz) and up to the northeastern part of Siberia (Yakutsk), there is found a heavily pigmented race in which the var. *typica* and varieties having confluent spots predominate. The process of the accumulation of pigment reaches its peak in Yakutsk Province. Another very dark race is found in the part of the area inhabited by *Adonia variegata* which is furthest removed from Yakutsk Province, namely in Abyssinia and in east-central Africa (Lake Tanganyika).

In spite of the considerable difference between the frequencies of the various patterns in the different regions, *Adonia variegata* may be taken as an example of a species in which the geographical races are merely indicated. Indeed, in no region are one or a few patterns not found elsewhere established to the exclusion of all other patterns. The typical pattern of the species is nowhere very rare, and certain patterns involving a confluence of spots are also found practically in the entire area inhabited by the species. *Hippodamia convergens* Guer. may be referred to as a species which is still less differentiated geographically than *Adonia variegata*. *Hippodamia convergens* is common almost everywhere in North America. The typical pattern of the species, which is very similar to the typical pattern of *Adonia variegata* (Fig. 2 E), is by far the most frequent one in any part of the specific area. However, in the population living in California from 2 per cent. to 10 per cent. of individuals have some of the spots missing. In the eastern states less than 1 per cent. of the population have some of the spots missing.[2]

Anatis ocellata L. is more differentiated geographically than either *Adonia variegata* or *Hippodamia convergens*. The species has twenty (typica) or eighteen (var. *linnaei*) black spots on each elytron. These spots may disappear or may fuse with each other into longitudinal stripes (Fig. 5 E, F, and G). In Europe individuals with all spots fused into stripes (Fig. 5 G) apparently do not appear, but individuals with spotless elytra are frequent. In Siberia the fusion of spots becomes more and more frequent as one proceeds eastward, and east and northeast of Lake Baikal individuals with striped elytra predominate (Table 3). In Maritime Province the population is, however, again less dark on the average.

Coccinella quinquepunctata L. (Fig. 2 H–L) is represented in Europe by the so-called typical form (Fig. 2 J) having five black spots on both elytra (Table 4). The number of spots, as well as the size of the spots, increases as one proceeds northeastward. In Yakutsk Province practically the entire population consists of var. *arthur-*

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[2] The frequency of the different patterns in *Hippodamia convergens* was studied by Johnson (1910). His data are misleading, since he included under the name "convergens" at least three different species.

TABLE 3

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Anatis ocellata* (IN PER CENT.)

	No spots (bicolor)	Some spots absent	*typica* and *linnaei*	Spots confluent (*hebraea*)	n
Ukrainia	26.6	20.0	53.4	....	15
Vyatka Province	3.4	20.7	75.1	0.8	1009
Altai Mts.	3.1	7.8	64.1	25.0	64
Yeniseisk Province	1.4	10.0	71.4	17.2	70
Irkutsk Province	2.5	6.8	60.1	30.5	118
Transbaikalia	1.8	3.6	34.6	60.0	55
Amur Province	....	....	35.0	65.0	20
Maritime Province	8.3	8.3	50.0	33.3	24
Yakutsk Province	....	....	51.1	48.9	47

ica, having eleven large spots. Conversely, the Caucasian race is lighter than the European race: Caucasian individuals have only three spots or no spots (Table 4). Recently *Coccinella quinquepunctata* was found in the northeastern part of Turkestan (in Sungarian Ala-Tau). The few specimens known from there are all spotless.

TABLE 4

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Coccinella quinquepunctata* (IN PER CENT.)

	No spots (*minckwitzi*)	3 spots (*rossii*)	5 spots (*typica*)	7 spots (*simulatrix*)	9 spots	11 spots (*arthurica*)	n
Caucasus	4.7	95.3	....	......	....	....	64
Kiev	......	0.09	98.2	1.7	0.1	....	1100
Vyatka Province	......	....	97.9	2.1	....	....	325
Tomsk Province	......	....	7.1	......	51.8	41.1	56
Yenisseisk Province	......	....	36.6	9.7	19.5	34.2	41
Irkutsk Province	......	....	....	......	....	100.0	31
Transbaikalia	......	....	....	......	10.5	89.5	19
Yakutsk Province	......	....	....	......	1.1	98.9	88

This fact is interesting because the region lying between Caucasus and the northeastern Turkestan (Kirghiz Steppe) is inhabited by a race similar to that living in Europe. It is not unlikely that the similarity between the Caucasian and the Turkestanic races is a result of a process of parallel development.

Hippodamia tredecimpunctata L. (Fig. 3 G, H and I) inhabits nearly the entire Holarctic region. In Europe the spotted var. *typica* predominates (Table 5) but individuals having a few spots missing or confluent are also found. The entirely spotless var. *signata* is not known to occur in Europe, except a few specimens found in southern Russia (Kiev, Askania-Nova, Astrakhan, see Table 5). The situation is reversed in Transcaucasia, Persia and the southern part of Turkestan. In these countries the var. *typica* is not found at all, or is found only as an exception; it is replaced by the variety *signata*. In northern Turkestan and in Siberia the population consists of var. *typica* and of varieties having confluent spots. The frequency of the latter varieties consistently

TABLE 5

Relative Frequency of the Different Patterns in *Hippodamia tredecimpunctata* (in Per Cent.)

	No spots (*signata*)	3 to 11 spots	13 spots (*typica*)	Some spots confluent	n
Kiev	0.2	0.2	91.6	8.0	585
Askania-Nova	2.9	......	94.2	2.9	102
Astrakhan	3.0	......	97.0	....	33
Transcaucasia	87.7	4.1	8.2	....	73
Tashkent	99.3	......	0.7	....	153
Ferghana	100.0	......	....	....	111
Semirechensk Province	....	......	100.0	....	10
Ordos	16.7	5.6	77.7	....	18
Lower Amur	....	......	70.0	30.0	177
Yakutsk Province	....	......	85.5	14.5	55
Kamchatka	....	......	12.5	87.5	8

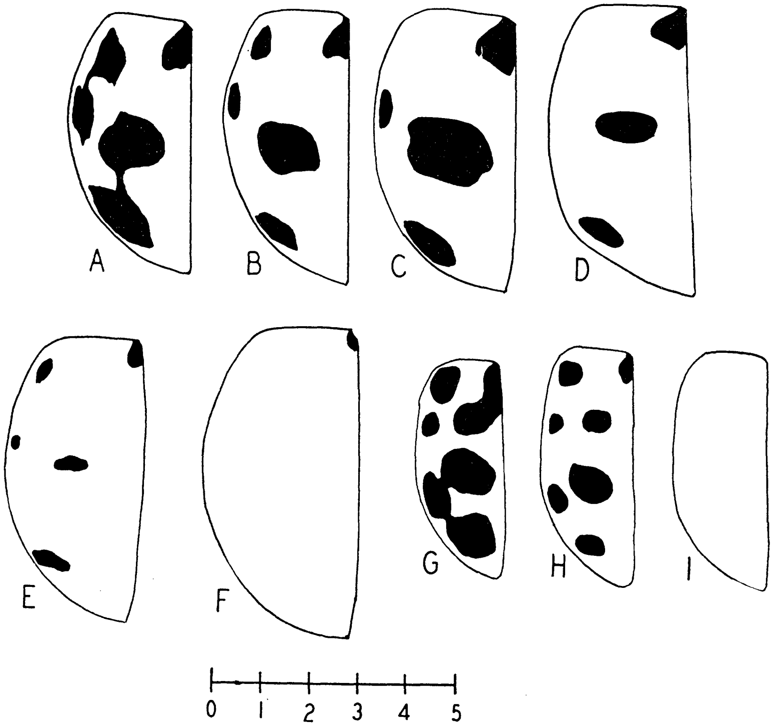

FIG. 3. A and B—*Coccinella novemnotata* Hbst.; E—*Coccinella novemnotata* Hbst. var. *degener* Csy.; F—*Coccinella novemnotata* Hbst. var. *franciscana* Muls. C—*Coccinella divaricata* Ol. var. *typica;* D—*Coccinella divaricata* Ol. var. *distincta* Fald. G—*Hippodamia tredecimpunctata* L. var. *contorta* Wse.; H—*Hippodamia tredecimpunctata* L. var. *typica;* I—*Hippodamia tredecimpunctata* L. var. *signata* Fald.

increases as one proceeds in the northeastern direction, and reaches its peak in Kamchatka. In Canada and United States the var. *typica,* similar to that found in Europe, is again met with.

In *Hippodamia tredecimpunctata* one may speak, consequently, of the existence of two subspecies. One of them, *signata,* occupies Transcaucasia, Iran and Turkestan, and the other, *typica,* inhabits the rest of the specific area. Within the region of each subspecies individuals having the color-pattern of the other subspecies are practically absent. There exists, however, a broad intermediate zone in which *signata* and *typica* occur together.

The intermediate zone includes the southern part of Russia, a part of China (Ordos) and, perhaps, Transcaucasia. A step further from the condition found in *Hippodamia tredecimpunctata* leads to the formation of two races entirely restricted to their respective geographical regions. This condition is approached by *Synharmonia conglobata* L. The European race of this species has pinkish elytra with eighteen black spots, which may be separate or fused with each other. The frequency of individuals with fused spots is higher than 50 per cent. in the European race, and only 3.3 per cent. in Transcaucasia (the latter figure is based on 245 specimens from Erivan, Transcaucasia). In the southern part of Turkestan an entirely different race (var. *buphthalmus*) is found. Elytra are yellowish with eighteen light-brown spots, each having a yellow area in the center. More than 200 specimens coming from various localities in Turkestan (mainly the environs of Tashkent and Fergana) were studied, and all showed the characteristics of var. *buphthalmus*. Chinese Turkestan, Songaria, and the deserts lying between Mongolia and Tibet are also inhabited by var. *buphthalmus* (Kashgar, Kilian, Sanju, Khotan, Keria, Kurla, Aksu, Manas, Barkul, Khami, Sadjou, western Kan-su, central Mongolia, 524 specimens of var. *buphthalmus* and no specimen of var. *typica* examined). The only region in which var. *typica* and var. *buphthalmus* occur simultaneously is the Semirechensk Province (northeastern Turkestan). In the southern part of this province (south of the river Ili, mainly environs of Verny) 89 per cent. of specimens found belong to var. *buphthalmus* and 11 per cent. of the black-spotted varieties (54 specimens examined). In the northern part of the same province (environs of Lepsinsk) only 26 per cent. of individuals are var. *buphthalmus* (23 specimens examined). In Siberia the species under consideration is rare, but all the specimens known from there have black spots.

THE "CENTRA" OF LIGHT AND OF DARK FORMS

As stated above, there is observed a parallelism in the variability of the related species and genera. Homologous varieties of different species may be more similar to each other in appearance than the different varieties of the same species. This parallelism is, probably, due to the essential similarity of the germ-plasms of the related species. This is the genotypical parallelism. A thorough discussion of the genotypical parallelism lies beyond the scope of the present article. A different kind of parallelism is observed if one takes into account the geographical distribution of the various color-patterns. One may call it the geographical parallelism. It manifests itself in that the various species inhabiting a given region usually have more similar patterns than each of these species has in regions widely distant from each other. In some regions most species are represented by light, scarcely pigmented varieties. Such regions may be called centers of light forms. In other regions most species show an extensive development of dark pigmentation. These regions are centers of dark forms.

Two centers of light forms are apparent in the Northern Hemisphere. One of them lies on the Eurasiatic continent, in the southern part of Turkestan and in Persia. The second is found in North America, in California, Arizona, and, probably, in northern Mexico. The center of the dark forms lies in northeastern Asia (Yakutsk Province, Kamchatka). As shown above, the populations of *Adonia variegata, Anatis ocellata, Coccinella quinquepunctata* and *Hippodamia tredecimpunctata* in which dark patterns are most abundant are found invariably in northeastern Siberia. Turkestan is inhabited by the least pigmented varieties of the species just mentioned (except *Anatis ocellata,* which does not occur in Turkestan) and of *Synharmonia conglobata.*

Species inhabiting both Eurasia and North America are most important from the standpoint of the problem of the centers of light and dark forms. One such species is *Coccinella transversoguttata* Fald. The race of this species inhabiting Siberia and Mongolia is the most extensively pigmented. Within the confines of this race the so-called typical form (Fig. 4 A) is decidedly predominant (Table 6). Alaska, Canada, the northern, central and the eastern parts of the United States are occupied by a race the elytral pattern of which differs from that of var. *typica* by the absence of the spot lying near the external border of the elytron (Fig. 4 B). Individuals having the pattern represented in Fig. 4 B occur, however, also in the southern part of Siberia and in Mongolia. Likewise, the pattern shown in Fig. 4 A is not rare in Canada and in northern United States. In the western United States a progressive reduction of pigmentation is observed as one proceeds in the southwesterly direction. The transverse bands forming the pattern of var. *typica* disintegrate into separate spots;

TABLE 6

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Coccinella transversoguttata* (IN PER CENT.)

	Darker than *typica*	*typica*	Bands partly broken into separate spots	11 separate spots	0 to 9 separate spots	n
Tomsk Province	......	100.0	....	....	....	102
Yenisseisk Province	......	100.0	....	....	....	17
Irkutsk Province	1.5	97.0	1.5	....	....	65
Transbaikalia	3.1	93.8	3.1	....	....	96
Amur Province	2.0	93.9	4.1	....	....	46
Tannu-Tuva (Urjanch Prov.)	......	94.7	5.3	....	....	38
Northern Mongolia	0.6	91.8	7.0	0.6	....	172
Central China (Ala-Shan, Kan-Su Provinces)	......	33.4	13.0	50.7	2.9	69
Sungaria	......	8.1	6.1	78.7	7.1	99
Semirechensk Province	......	....	....	89.0	11.0	45
Chinese Turkestan	......	....	....	92.6	7.4	190
Tibet	......	....	....	90.0	10.0	10

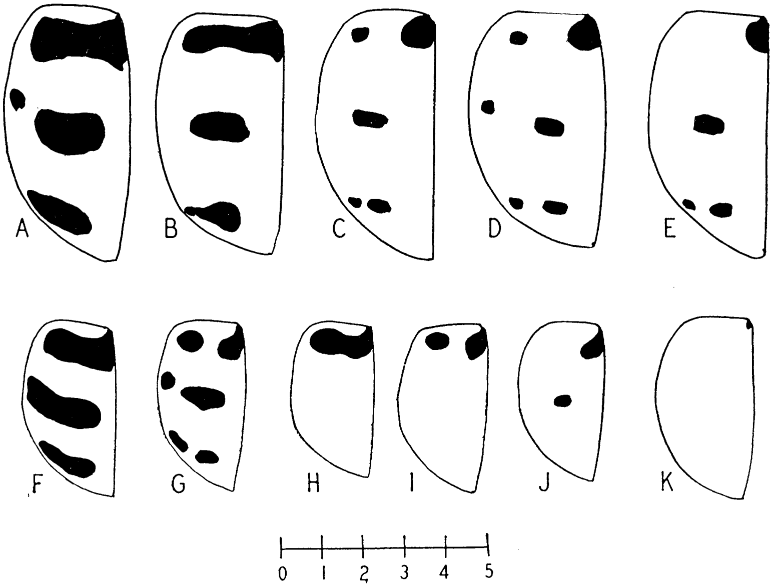

FIG. 4. A–E—various patterns of *Coccinella transversoguttata* Fald.; F–K—*Coccinella trifasciata* L.

the resulting pattern is shown in Fig. 4 C (var. *nugatoria*). Var. *nugatoria* is as frequent, or more frequent, than the typical form in Utah, New Mexico, Arizona and California. In Mexico var. *nugatoria* seems to be decidedly predominant.

The process of depigmentation takes place also in Asia as one proceeds from eastern Siberia in the southwesterly direction (Table 6). A pattern rather similar to that of var. *nugatoria* (eleven widely separated black spots, Fig. 4 D) is found in some specimens from Mongolia, and becomes the predominant pattern in central China, Sungaria and the adjacent mountain ranges. The depigmentation progresses still further in the Tyan-Shan mountains, Chinese Turkestan and in Tibet. Some individuals found in these countries have less than eleven black spots. Races living in Central Asia and in southwestern United States are, thus, more similar to each other than either of them is to the Siberian and the Canadian races.

Similar phenomena are observed in *Coccinella trifasciata* L. and *Coccinella nivicola* Men. (Fig. 4 F–K and Fig. 5 A–D, respectively). The typical form of *Coccinella trifasciata* (Fig. 4 F) constitutes nearly 100 per cent. of the population in Siberia, most of Canada (except British Columbia) and most of the United States (except the Pacific Coast). In the southern parts of Siberia and Mongolia the transverse bands forming the typical pattern become narrower, and show a tendency to disintegrate into separate spots. The same tendency finds a much stronger expression on the Pacific Coast of America, west of the Cascades and Sierra Nevada. In British Columbia, Washington and northern Oregon the patterns shown in Fig. 4 J and K predominate. In southern Oregon and northern California the pattern 4 G is the most frequent one. In the San Francisco region the patterns 4 H and I are the commonest.

Coccinella nivicola Men. is represented in Siberia by the variety having broad black bands (Fig. 5 A). In Canada and northern United States lives a race (var. *monticola*) having narrower bands (Fig. 5 B). A similar narrow-banded race is found, however, also along the southern boundary of the area occupied by the species under consideration in Asia (western Mongolia, Sungaria, northern Tyan-Shan). In America, between the Rocky Mountains and the Pacific Coast the depigmentation progresses still further. The bands become narrow and disintegrate into spots (var. *alutacea,* Fig. 5 C). In the deserts of Utah and Nevada the lightest race (Fig. 5 D) is found.

The behavior of the two closely related species, the American *Coccinella novemnotata* Herbst. and the Eurasiatic *Coccinella divaricata* Ol., is remarkable. In southern California (Los Angeles region) lives the unspotted *Coccinella novemnotata* var. *franciscana* (Fig. 3 F). In central California (San Joaquin valley), Arizona and New Mexico the unspotted form occurs together with individuals having from one to nine small black

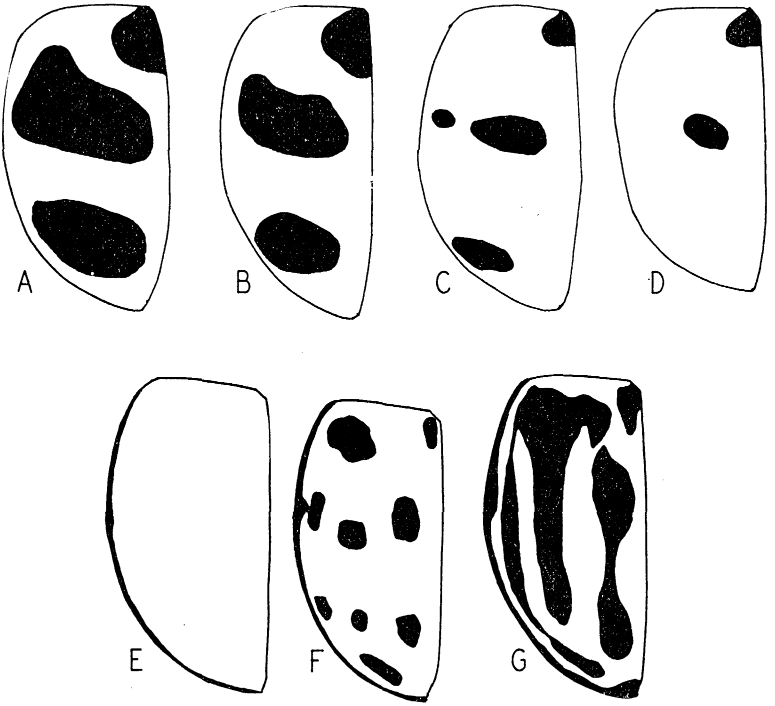

Fig. 5. A–D—*Coccinella nivicola* Men. A—*Coccinella nivicola* Men. type form; B—*Coccinella nivicola* Men. var. *monticola* Muls.; C and D—*Coccinella nivicola* Men. var. *alutacea* Csy.; E—*Anatis ocellata* L. var. *bicolor* Ws.; F—*Anatis ocellata* L. var. *typica;* G—*Anatis ocellata* L. var. *hebraea* L.

spots. Oregon, Washington, British Columbia and the states lying between the Sierra Nevada and Rocky Mountains are inhabited mainly by var. *degener* (Fig. 3 E, nine small spots). In Canada and in states lying east of the Rockies lives the typical form of the species (Fig. 3 B, nine large spots). In the eastern and southern states individuals with some of the spots fused are rather common (Fig. 3 A).

In eastern Siberia a variety of *Coccinella divaricata* is found (Table 7) which is similar in appearance to the typical form of *Coccinella novemnotata* (Fig. 3 B). In Transbaikalia about 20 per cent. of individuals have some of the spots fused together. West and southwest of

TABLE 7

RELATIVE FREQUENCY OF THE DIFFERENT PATTERNS IN *Coccinella divaricata* (IN PER CENT.)

	5 spots (*distincta*)	7 spots (*typica*)	9 spots (*donidua*)	Some of the spots confluent (*intertexta*)	n
Kiev	....	91.9	8.1	....	344
Transcaucasia	90.0	10.0	....	....	10
Semirechensk Province	....	100.0	....	....	35
Tomsk Province	....	93.6	6.4	....	47
Irkutsk Province	....	56.1	43.9	....	57
Transbaikalia	....	1.8	76.0	22.2	113
Northern Mongolia	....	34.7	56.5	8.7	23

Lake Baikal specimens with fused spots become less frequent, and there appear specimens having the typical pattern of *Coccinella divaricata* (Fig. 3 C, seven instead of nine spots). The typical pattern predominates in western Siberia and in Europe (Table 7). The material available from Transcaucasia is very small; it shows, nevertheless, conclusively that in the region just named lives a very light race of *Coccinella divaricata.* Most of the individuals coming from Transcaucasia have only five rather small spots (Fig. 3 D). In southern Turkestan, where one might expect to find the least pigmented race of the species, *Coccinella divaricata* does not occur, or at least has not been found there.

ALLEN'S RULE

There is observed a marked concentration of the scarcely pigmented varieties in Turkestan, Iran, California, Arizona and Mexico. These countries can be described as centers of light forms. The further a region is removed from these centers the darker is the average type of the population found therein. The pigmentation in most species increases roughly proportionally to the distance between a given region and the centers of light forms. In eastern Siberia, which is very far removed from both the Eurasiatic and the American centers of light forms, a center of darkly pigmented forms is found.

These are the facts. The causation of these facts is, at present, a matter of speculation. Attention is naturally drawn toward the analysis of the geographical, and primarily climatical, conditions encountered in the countries in question. The pigmentation of the Coccinellidae seems to be related to the degree of humidity, and, possibly, to the temperature, prevailing in a given region. The depigmentation takes place in the arid, hot, and desert regions of both Eurasia and America. The humid and cold climate of northeastern Asia produces an increase of the pigmentation. The rôle of humidity seems to be more important than that of temperature since the increase of pigmentation is observed in some species (*Coccinella septempunctata,* see Dobzhansky and Sivertzev-Dobzhansky 1927, also in *Adonia variegata*) in humid but otherwise so different countries as northeastern Siberia, Japan, northern Europe, Abyssinia and Himalaya.

The rule of the depigmentation in arid regions, and of the accumulation of pigment in humid regions, is well known under the name of Allen's rule (or Gloger's rule, see Rensch 1929, or even the erroneous name of Allen's law). This rule holds true in many groups of terrestrial Vertebrata and Invertebrata. The results of Sumner (1920, 1924, 1925) in mice, Görnitz (1923) in birds, Zimmermann (1931) in Vespidae, and Netolitzky (1931) in Carabidae may be quoted here as examples. Together with a series of other rules describing the relations between various characteristics of the organisms and the environmental conditions predominant in their habitat (Rensch 1929, Turesson 1922, 1928, 1930, Alpatov 1925, Netolitzky 1931), Allen's rule represents one of the broad generalizations brought to light by the comparative studies on variation.

It must be, however, emphasized that Allen's rule is nothing more than a statistical rule which holds true only as far as the majority of the species and the major subdivisions of the continents are concerned, and which can not be stretched to cover all known cases of variation. Thus, the region of the predominance of the light races of Coccinellidae in America includes the entire Pacific Coast from Mexico to British Columbia, although the northern part of this region (from British Columbia to Oregon) can not be classed as arid. The "centers" of light forms in different species include different regions. Thus, the population of *Adonia variegata* inhabiting Chinese Turkestan (the Tarim depression) is nearly as dark as the Siberian population and distinctly darker than the race living in Iran and Russian Turkestan. In *Synharmonia conglobata, Coccinella transversoguttata* and many other species the races inhabiting Chinese Turkestan are the lightest known in these species, there being no difference in this respect between the Tarim depression and Russian Turkestan, but a striking difference between the former and Siberia.

Are the Variations in the Color-Pattern Inherited?

The question as to whether the color-patterns are inherited is obviously important for any attempt to evaluate the facts presented above. There exist some experimental data bearing on this question. Johnson (1910) studied the inheritance of the variations in the color-pattern of *Hippodamia glacialis, Hippodamia convergens, Hippodamia spuria, Coccinella novemnotata, Adalia frigida* and *Epilachna borealis.* Though his data are unsatisfactory from the standpoint of modern genetics, they leave no doubt that even minor variations in the color-pattern of these species are hereditary. Timberlake (1922) studied the inheritance of three patterns in *Coelophora inaequalis* and of three patterns in *Cheilomenes sexmaculata.* It is clear from the data presented by Timberlake that in the first of these species triple allelomorphs are involved. In the Cheilomenes case Mendelian inheritance is also at hand, although the author does not think so.

Lus (1928) made a careful and extensive study on the inheritance of the numerous color-patterns found in the populations of *Adalia bipunctata* and *Adalia decempunctata* inhabiting northern Russia and Turkestan. The existence of at least three loci concerned with the coloration is established in the former of these species. A series of at least eight multiple allelomorphs determines the color-pattern of the elytra and, partly, of the pronotum. Another gene determines the pattern of the pronotum only. A third factor, encountered only in the population living in Turkestan, transforms the black pigment into a brown one. In *Adalia decempunctata* triple allelomorphs for the pattern of the elytra and the pronotum, and an independent gene for the black *versus* the brown pigment were found.

Timoféeff-Ressovsky (Proceed. VI Internat. Congress of Genetics, 2, pp. 230–232, 1932) has published a preliminary account on his work on the geographical races of *Epilachna chrysomelina F.* He concludes that the geographical races in this species differ from each other in complexes of genes; that these genes may be geographically distributed independently from each other; that the races may be characterized by the different frequencies of the different genes in the population; and that not single genes but rather some "harmonic" gene combinations have selective values under a given set of geographical conditions. The results of Timoféeff-Ressovsky are, thus, in a perfect agreement with the views expressed in the present paper.

The hereditary nature of some of the variations of the color-pattern in Coccinellidae may be sometimes proven by indirect evidence. In a multitude of species individuals having very different patterns occur together, in the same locality, and at the same season. There is no indication that the relative frequency of the different patterns in the population undergoes pronounced changes with seasons, though many species have more than one generation per year, and the different generations develop under dissimilar external conditions. As mentioned above, the variability in many species is discontinuous, so that the population is frequently divided into a number of distinct forms, the intergradations being few or absent. These facts taken alone would not afford an entirely conclusive proof of the hereditary nature of variability. Cases are known (in Forficula, Diakonov 1926) in which a sharply bimodal variability is due entirely to external influences coupled with a complex norm of reaction. In Coccinellidae such phenomena are, however, not known, and, on the contrary, in every case tested experimentally the variations proved to have a genetic basis.

It is, of course, impossible to deny that some of the minor variations in the color pattern may be purely phenotypical. This is especially true for varieties which are never or only seldom found in the same locality. But all the data available argue against the assumption that the phenotypical variation is an important component of either the geographical variability or the variability in populations living in the same region. It is interesting in this connection that the temperature influences applied to pupae and prepupae of various Coccinellidae mostly fail to produce appreciable changes in the patterns (Johnson 1910, and unpublished results of the writer).

Continuous and Discontinuous Variability

As mentioned above, the variability in many species of Coccinellidae is nearly or completely discontinuous, that is to say, the intergradations between different color-patterns encountered within a single species are few or absent (see also Dobzhansky 1924). This fact makes it not only convenient but even necessary to consider the geographical variability in terms of the relative frequencies of the various patterns in the different parts of the specific area. Instances of discontinuous variability are met with not uncommonly in different groups of animals and plants (one may mention here only the classical work of Bateson, 1894). It is, however, known to every one who is sufficiently acquainted with the taxonomy of any group, that cases of continuous geographical variability are also frequent, and in most groups probably even more so than cases of the opposite kind. Races inhabiting remote parts of the specific area may be sharply distinct from each other, and no individuals with the characteristics of the other race may ever occur within the confines of each race. These races may be, however, connected with each other by a series of intermediate races living in geographically intermediate regions, and forming a "sliding passage" ("gleitende Ubergänge") between the two extremes (Rensch 1929).

Within the family Coccinellidae both types of geographical races, and also types intermediate between them, are abundantly represented. In *Coccinella sep-*

TABLE 8

SIZE OF THE DISCAL SPOT IN *Coccinella septempunctata*

Region	Mean value	Lim	n
Italy	39.18 ± 1.23	26 – 50	35
Algeria	38.82 ± 0.73	25 – 52	50
Archangel	40.62 ± 0.72	30 – 60	71
Kiev	38.85 ± 0.54	24 – 50	100
Crimea	37.77 ± 0.67	25 – 52	100
Transcaucasia	35.55 ± 0.97	0 – 53	100
North Persia	33.12 ± 0.95	0 – 45	56
Transcaspia	35.64 ± 0.74	16 – 50	83
East Bokhara	32.64 ± 0.70	12 – 51	82
Samarkand	32.43 ± 0.76	12 – 49	83
East Ferghana	33.06 ± 0.73	15 – 49	100
Kuldja Province	35.76 ± 0.64	20 – 50	95
Yenisseisk Province	39.57 ± 0.76	15 – 58	84
Irkutsk Province	38.97 ± 0.68	25 – 54	100
Amur Province	45.09 ± 1.01	34 – 59	34
Maritime Province	43.44 ± 0.61	30 – 61	100
Korea	47.49 ± 1.32	34 – 56	29
Ordos	41.31 ± 1.10	26 – 57	30
Kamchatka	56.13 ± 0.72	41 – 70	79
Sakhalin	55.92 ± 1.19	37 – 74	53
Japan	66.22 ± 1.67	48 – 82	27

tempunctata L. the size of the black spots on the elytra is different in various regions inhabited by the species. Some of the data bearing on the question are presented in Table 8 (according to Dobzhansky and Sivertzev-Dobzhansky 1926). For each region the mean diameter of one of the spots (expressed in units of the eyepiece-micrometer, one unit being equal to 26.3 micra), the amplitude of variation (Lim), and the number of individuals measured (n) are indicated.

The spots are smallest in the populations inhabiting Persia and the southern part of Turkestan. As shown above, this region is one of the centers of light forms. The further a region is removed in any direction from this center, the larger becomes the average size of the spots in the population inhabiting this region. The maximum size of the spots is observed in Japan and the Pacific Coast of Siberia. This, as we know, is the center of the dark forms. It is noteworthy that the discontinuous geographical variation is also observed in *Coccinella septempunctata.* The confluence of the spots is frequently observed in Himalaya and in India, less frequently in Japan, and very seldom in any other region. The disappearance of spots is encountered mainly in Persia and Turkestan.

In *Coccinella novemnotata* (Fig. 3 A, B, E, F) the spots are largest in the population inhabiting the southeastern United States. The size of the spots becomes progressively smaller as one proceeds in the westerly direction; between the Rockies and Sierra Nevada, and also in Oregon, races are found (var. *degener,* Fig. 3 E, and var. *oregona*) having small spots. In middle California (San Joaquin Valley) a race is found in which most individuals have no spots (see the discussion of this point above); a few individuals still possess spots, but the size of these spots is very small.

Some taxonomists are inclined to see a sharp contrast between the continuous and the discontinuous types of the geographical variability, and to consider these two types as the manifestations of two separate principles, namely the environmental and the germinal variability. A simple analysis may show this contrasting to be entirely fallacious. Provided the racial traits are hereditary (and this is amply proven in a series of cases), the only distinction between the two types under consideration is that between hereditary factors producing minor changes or, else, easily classifiable differences in the external characteristics of an organism. The practice of the geneticists shows that the so-called qualitative differences, especially differences in colors and patterns, are usually inherited on a monofactorial or a simple polyfactorial basis. On the other hand, the so-called quantitative characters, especially those involving the size or the shape of the body or of its parts, are more frequently determined by the interaction of numerous factors. Each of these numerous factors taken alone produces only a small effect, sometimes discoverable only by statistical methods (Sumner, 1930). Here, again, no two distinct types of inheritance are involved. The number of genes concerned in the production of size- and shape-differences may be very small, and color-differences may depend upon the interaction of numerous factors. The distinction between the continuous and the discontinuous types of variation is, then, analogous to that between the simple mendelian inheritance on one hand and the so-called "blending" inheritance on the other. Most geneticists agree nowadays that the latter distinction is entirely spurious.

In cases of discontinuous variability the differences between the geographical races may be expressed in terms of the relative frequencies of genes responsible for the production of various patterns in the different localities. What we are studying is essentially the geography of the genes responsible for the different patterns, and not the geography of the patterns themselves (the "geno-geography," Serebrovsky, 1927). Bernstein (1925a, 1925b, 1930) studied in these terms the geographical distribution of certain hereditary characteristics in man, mainly that of the blood-groups. It is quite possible to visualize also the continuous geographical variation being represented in exactly the same way (the contrary opinion was expressed among others by Rensch, 1929).

Let us suppose that each of the genes A, B and C increases the size of the spots in *Coccinella septempunctata* by a certain small value. The entire population of this species living in Japan may have the genetic structure AA BB CC; hence, the spots are very large. In Kamchatka only a part of the population may be AA BB CC, and the other part AA BB Cc and AA BB cc; the average size of the spots in the Kamchatkan population must be, then, smaller than in the Japanese population. In Maritime Province individuals of the structure AA Bb cc and AA bb cc may also occur; the average size of the spots must be still smaller. Finally, in Persia and southern Turkestan the majority of the population, or even the entire population, may be aa bb cc, and hence, have very small spots. It is obvious that if a character distinguishing geographical races has a genetic basis similar to that just outlined, the intergradations between these races may be as gradual and "sliding" as the absence of the natural barriers separating these races from each other may allow.

GEOGRAPHICAL AND NON-GEOGRAPHICAL VARIABILITY

Many taxonomists place a considerable emphasis on the distinction between the geographical and the non-geographical variability. The geographical forms are those which predominate in a definite part of the area inhabited by the species, and never or only seldom occur outside of the confines of this part. Such forms are termed subspecies, races, natio, varieties, or "local" forms. The non-geographical forms, termed aberratio, phases, mutants or simply "forms," occur more or less regularly in the entire area of the species, or in a part thereof, but their occurrence does not constitute a clear distinction between populations inhabiting different regions (Semenov-Tian-Shansky, 1910).

No less importance is ascribed to another distinction between the geographical and the non-geographical forms. The former are characterized by complexes of differences permeating the whole body. The latter differ from each other by often striking but single characters (Rensch, 1929). Jordan (1905) has given an especially concise analysis of the situation as applied to insects. According to him, the geographical forms differ from each other usually, or at least frequently, in the structure of the genitalia as well as in external characteristics, these two kinds of differences being correlated with each other. The non-geographical forms do not possess such correlative alterations in the genitalia.

As far as these ideas represent merely generalized statements of the facts accumulated by the prolonged experience of the taxonomists with their material, they are highly valuable. Indeed, they describe accurately the situation encountered in most groups. The geographical races in Coccinellidae differ from each other as a rule not only in the relative frequencies of the different patterns encountered in the different regions, but also in the size and the shape of the body, the punctuation of the elytra, and other characters the variability of which is continuous. The structure of the genitalia is not, as a rule, a good racial character in Coccinellidae, but some races do differ from each other in the structure of the genitalia. Thus, the shape of the receptaculum seminis is different in the European and the eastern-Siberian races of *Thea vigintiduopunctata*. It is, however, preposterous to consider on these grounds the geographical and the non-geographical variability to be two separate, independent, and perhaps even conflicting processes.

In spite of the scarcity of exact data on the genetics of geographical variability, some of the main features of this phenomenon are clear enough. The geographical races in man and in the domestic animals and plants differ from each other mostly in more than a single gene, and usually in many genes. The same is true for the geographical races in wild species. Indeed, Sumner (1930) found that the differences between the geographical races of mice are determined by numerous genes. As to the specific differences, which since the time of Darwin have been considered to be merely exaggerated racial ones, the situation is still more clear. Species differ from each other always in many genes.

On the other hand, the differences between the non-geographical forms, however striking they may seem to our eyes, are predominantly monogenic. A change in a single gene may provoke alterations in many characters and in different parts of the body, but one or a few of these alterations are, as a rule, far more conspicuous to our eyes than the rest of them. Hence, the differences between geographical forms involve usually many characteristics, while those between the non-geographical forms are restricted to few characters. This distinction between the geographical and the non-geographical forms seems to follow from the very nature of things. A segregation of a panmictic population into two groups differing from each other in a complex of genes encounters considerable difficulties on its way. As soon as such two groups start to interbreed, the genes concerned will tend to become distributed in the whole population at random, unless some exceptional conditions (found, for instance, in Oenothera) prevent it. The formation of such groups becomes more probable if they are at least partly isolated from each other by geographical, ecological or seasonal factors. The geographical isolation seems to be, at least in most animals, the most important kind of isolation contributing toward the splitting of a Linnean species into minor units.

The present analysis of the geographical variation in Coccinellidae deals with the behavior of a single character, namely that of the color-pattern. This particular character and this particular group seem to be especially favorable for an exact study because the variability in this case happened to be discontinuous. As far as this character is concerned, there is no essential difference between the non-geographical and the geographical variation. In fact, they seem to be merely two stages of the same process. The study of the behavior of the characters the variability of which is continuous is for purely technical reasons more difficult. There is, however, no ground to assume that the behavior of the latter kind of characters is in any respect different from that of the discontinuously variable characters.

An analysis of the mechanism of the formation of the geographical races and species ought to begin with a study of the behavior of the single characters distinguishing the different forms from each other. Only subsequently can one study the interaction of the unit-characters in the complex systems representing the types with which taxonomy is primarily concerned.

It would lead us too far to discuss here the possible causes of the differentiation of the species into races distinguished from each other by the relative frequencies of the different biotypes. Three explanations may be mentioned here. First, an originally homogeneous population extending its geographical distribution may become differentiated in accordance with the environmental conditions prevailing in the different parts of the area. Second, various biotypes may arise by mutation; the mutations may be equally frequent in all parts of the specific area, but some of them may become established and others rejected by the natural selection. Different mutations may be favorized in different regions. Third, the phenomena observed may be partly accounted for by assuming a hybridization of two or more preexisting races each of which, before the hybridization began, was characterized by a definite color-pattern or patterns. In any case, there is no need to assume that the color-pattern itself is the character with which the natural selection is working. The accumulation or the reduction of the amount of pigment produced in the organism may be responsible for an alteration of its physiological characteristics, and make it more or less adapted to the environment encountered in a given region.

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