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The relations between local Lepidoptera-faunas as the basis of the zoogeographical regionalization of the Palaearctic

[11 text-figs.]

Wzajemne związki pomiędzy lokalnymi faunami motyli, jako podstawa zoogeograficznej regionalizacji Palearktyki

Взаимосвязь между местными фаунами чешуекрылых как основа зоогеографического районирования Палеарктики

GENERAL

One of the main aims of biogeography is to obtain knowledge of the spatial differentiation of phenomena occurring in the biosphere and thus to work out their regional distribution. Although the object of biogeographic studies includes only living organisms (and the role they play in an environment), there are different approaches to regionalistic problems, and these approaches depend, above all, on the purposes which they are designed to serve.

There are many types of regionalistic studies based on the material of living organisms. They not only come within the scope of biogeography but also constitute the subject of medical geography, chemical geography, geography of soils, etc. The greater part of biogeographic studies on regionalization, however, belong to four essential groups.

1. Formal regionalization. The purpose of this type of studies is to present the spatial differentiation of living beings or their chosen characters (e.g., size or coloration) against the background of arbitrarily selected environmental elements and according to arbitrary criteria, without attempting to find the causes determining this very differentiation. An example of this are attempts to establish regions on the basis of the mean size of specimens of particular

species or a chosen group of species, the predominating type of coloration, the mean number of species within a spatial unit (e.g., 1 sq. km) or of those occurring in intervals between definite contour-lines, etc. This trend, fairly popular in the past, especially in the mid 19th century, has been almost quite given up nowadays. It is obvious that mechanical association of particular elements, unrelated or very loosely related, contributes nothing to the general knowledge of the problem. The results obtained from this type of investigations serve as a basis for scientific generalizations only in very rare cases. They are usually nothing but worthless curiosities.

2. Utilitarian regionalization. The aim of the utilitarian regionalization is to get to know the spatial differentiation of the role which its object, living organisms, plays or is potentially capable of playing in human economy. This type of studies includes all the regionalizations of vermins, parasites, weeds, but also those of economically important supplies of seas, potentialities of introduction, etc. Here I must also mention the regionalization of potential fertility and that of possibilities of cultures, which stand on the border-line between biogeography and geography of agriculture or that of soils. In the recent years more and more attention has been given to the so-called bioindicative regionalization, which makes the detection of accumulations of chemical compounds, ores, petroleum, etc. possible and comparatively easy on the basis of the distribution of bioindicators. The utilitarian regionalization constitutes a branch of now so intensely developing applied biogeography. A particularly intense development of this branch of science took place after World War II in connexion with researches for pitch ores, of which some animals and plants are very sensitive indicators.

3. Ecological regionalization. The studies of this group aim at uniting ecologically similar areas, areas resembling each other in their systems of utilization of the creative powers of environment. Such areas need not be genetically related, they may have entirely distinct floras and faunas, but are bound by similar ways of existence. This is exemplified by ecologically related prairies, pampas and steppes or deciduous forests of Europe, North America and Tasmania. In this case the object of studies is not particular species or other systematic units but biocenoses, formations or biomes. This trend is widely adopted in botany, within which it constitutes a separate branch of science, geobotany. In zoology its progress is retarded mainly because of the vast richness and ecological differentiation of the animal kingdom.

4. Genetic regionalization. The purpose of the regionalistic studies of this type is to gather information on the differentiation of the faunas and floras of various sections of the Earth surface, their interconnexions, history, developmental tendencies, etc. The genetic and ecological regionalizations are often confused and considered to be synonymous. This opinion seems to be quite wrong, for the aim of the genetic regionalization is not the knowledge of the system of distribution of plants and animals in an environment but that of connexions, similarities, or affinities, and thereby the history of particular

faunas and floras dwelling in a definite environment. Naturally, both these trends are connected and complement each other, but the aims as well as the methods are in either case quite different. The mixed forests of the central part of the U. S. A. and the analogous forests in Europe are very similar from the ecological point of view. They also belong to the same geobotanic region. However, the specific compositions of these forests are completely different. They have not a common tree species (except those artificially introduced) and so they are not related genetically. On the other hand, both the fauna and the flora of the European woods and meadows of low-lying overflooded areas are very closely related, though both these communities belong to different vegetative formations varying in their ecological nature. The mechanical association of both these types resulted in many wrong generalizations in numerous regionalistic studies. According to the principle pars pro toto the results of detailed studies carried out in a definite place of a given zone or plant formation were frequently generalized over the whole zone. If, for example, two steppe areas possess the same fauna, it does not mean that all the steppes have the same fauna. This gave rise, among other things, to the tendency observed in some zoogeographers and phytogeographers (KOZHANCHIKOV, 1937; LAVRENKO, 1962) to combine the whole plant zones into one faunal or floral unit.

After this necesserily short characterization of the types of regionalistic studies met with in biogeography I shall dwell somewhat longer on the essential problem of criteria and methods so far used in this type of investigations. Even a cursory glance at the present achievements in this field shows a great variety of results obtained. The differences, being of great importance in some cases, have undermined the trust in this sort of investigations and have even caused the questioning of their purposefulness. Some zoogeographers, e.g., DARLINGTON (1957) and HESSE (1924, 1951) and phytogeographers (DANSEREAU, 1957; PACZOSKI, 1933), without inquiring into the causes of these differences, declared the problems concerning the spatial differentiation of faunas and floras to be marginal and of rather descriptive historical significance. These opinions can only partly be justified by the so characteristic of our age underestimation of general studies, by the predominance of analysis over synthesis. It is the zoo- and phytogeographers themselves who are in fault. The use of unproper, sometimes greatly subjective, methods and the desire to satisfy the demands of numerous biologists, especially systematicians, for the only and ultimate regionalization falling in with all the groups of living beings, became one of the factors responsible for this wide range of results. It seems obvious that the working out of the only and „ultimate“ regionalization is impossible at present and will still be impossible for a long time. Each systematic group of animals and plants has its own distinctive history, different adaptive possibilities, and, above all, its own specific ways of living in the environment and utilization of its supplies. For this reason the attempts to work out regionalistic systems based on the whole of the living world or on representatives chosen from different groups have failed in most cases as yet. The principal condition of the correctness of any regionalistic studies is the homogeneity of the material on which they are based, irrespective of its being systematic (e.g., one family or order) or ecological (phytophages, carnivores) in nature. The use of heterogeneous material, in which particular elements are alien to each other and only slightly act on each other, cannot lead to correct results. For example, it is impossible to carry out a sensible faunistic regionalization on the basis of reptiles and insects taken together or a physico-geographic regionalization on the basis of rainfalls and volcanic activity treated together, and yet many studies have been published in which, as, for example, in SCHMARDA (1853), one region is marked out on the basis of the *Insectivora*, *Staphylinidae* and *Carabidae* and the other is characterized by the occurrence of pheasants. It is plain that the application of other groups may result in a quite different division into regions. Taking, besides, into consideration the uncommon rashness of some zoo- and phytogeographers in forming land bridges between continents and islands, often in spite of the geological data, one cannot be surprised that the confidence in the regionalistic studies in biogeography has been shaken.

The differences between particular studies based on different animal groups (e.g., mammals, birds, butterflies) are natural and it would be rather strange if they did not exist, but there should be no differences, if the same groups of animals are used as a basis for division. Unfortunately, they are sometimes very remarkable (e.g., divisions based on the *Lepidoptera* made by PAGENSTECHER (1909), AMSEL (1933) and KOZHANCHIKOV (1937). This is caused by the adoption of different methods and criteria of division. As far as criteria of division are concerned, the regionalistic studies so far carried out can be classified in 5 groups.

1. Differential criterion is historically the oldest. It was applied by ILLIGER (1815) and WAGNER (1845) and is also used by most of contemporary zoo- and phytogeographers. The fundamental criterion of division of any area into smaller faunal or floral units is the lack or the presence of strictly defined guiding groups (edificators). The guiding group may be either a systematic unit (genus, family) or an ecological unit (species from various groups with special adaptations for life under definite conditions) or, finally, a chorological unit (defined type of range). The boundaries of lower regional units are generally marked out on the basis of guiding species, those of the higher units on the basis of genera, families, or even orders. The main defect of this criterion is the arbitrariness of choice of the guiding group. The opinions of the author sometimes play the decisive role and the edificators are used only to support them. Thus a vicious circle arises. The distinctness of a fauna is evidenced by definite edificators, which again are edificators, because the fauna amidst which they inhabit is distinct. A choice of some other species as guiding species may lead to completely opposite results. It is undisputable that the zoogeographic autonomy of a fauna depends to a great extent upon the species existing exclusively within it, but they must be sufficiently numerous to change its structure in

an essential manner. One, two or even ten endemic species cannot constitute a basis for the distinction of a fauna numbering, say, thousand species, especially its distinction as a unit of a higher order. Similarly, ten or somewhat more species which a few faunas have in common are not sufficient to combine these faunas into one unit. Nevertheless, out of a large number of species a few or some dozen were selected, and though they may have been interesting in some respects, they did not represent the whole fauna of the given area on any account. Often a single species is the edificator marking out the boundary of the area. In the initial period of the development of biogeography, when the knowledge of particular faunas was very poor, the demarcation of regions on the basis of single species was in a sense natural. Now that the fauna and flora are sufficiently well known, the basing of regionalization on single species is incompetent, even if the range of these species is the generalization, the „symbol" of differences between the regions. At the time when ILLIGER (1815) marked out the boundary between the so-called northern and southern hemispheres on the basis of the ranges of the lion and tiger, the animal kingdom of Eurasia was practically unknown. Nowadays, however, the marking of boundaries between particular regions should be carried out on the basis of detailed studies. None the less, in most textbooks of phytogeography the boundary of the Mediterranean region in Eurasia is defined by the range of the olive tree and the boundary of, for example, the Altantic region by the range of *Ilex aquifolium* L. (D. C.).

The differential criterion, in its classical form, cannot be accepted now as the basis of regionalistic divisions chiefly because of the subjectivism and arbitrariness of choice of the guiding groups. The results obtained (even in the case of the same preliminary group) are often quite different, and the possibility of comparative studies on the spatial differentiation of the fauna of various systematic groups is point-blank insignificant. The variety of results leads in consequence to the loss of confidence in the problems of regionalization at all and causes trivial controversies like that on the so-called „Wallace line".

Only in some cases the application of the differential criterion may prove useful. This is true chiefly of working divisions into the largest units, as it allows the rough demarcation of their boundaries in a relatively short time. Such boundaries are naturally approximate and after close studies may be modified.

In the last decades attempts have been made to render the differential methods more objective either by increasing the number of edificators (e.g., KUCHERUK, 1959) or by basing them on chorological analyses of as many numbers of species as possible.

2. Criterion of substitute species. The supporters of this trend, such as REINIG (1937, 1950) or RENSCH (1950), assume that the faunal distinctness of any area is best evidenced by the existence of species replacing each other. The boundaries between the ranges of substitute species are also the boundaries of distinct types of environments and thereby of distinct faunas.

Thus, for example, the boundary between the Central and the East European regions is marked out both by RENSCH (1950) and by PETERSON (1954) along the contact-line of two substitute species of nightingales, *Luscinia luscinia* (L.) and *L. megarhynchos* BR. Also the adherents of this method do not take into account the whole fauna of a given group, but only a selection of species, which, though objective, cannot make a satisfactory basis for regionalization, for the notion of substitute species has not been defined clearly enough as yet. Are they only species which playing an analogous role in an environment exclude each other, such as the green lizard *Lacerta viridis* (LAUR.) and the sand lizard *L. agilis* L., or also those which having gone away from the common stem a comparatively short time ago live together at the contact of their ranges, often giving fertile hybrids (e. g., *Dendrolimus pini* L. and *Dendrolimus sibiricus* Ev.)? Besides, the determination which of the numerous related species are actually substitutes also encounters many difficulties. A list of the so-called „double“ species (Dualspezies) replacing each other in the Lepidoteran fauna of Germany was published in the period between World War I and II. Further studies showed that many species mentioned in the list are only loosely related with each other or even belong to quite different genera. A selection of a few substitute species does not seem to constitute a satisfactory basis for making any regionalistic conclusions, the more so, because the factors governing the ranges of one pair of substitute species may be different from those acting on the other pairs. Perhaps the application of the method of overlapping of ranges, used by KULCZYŃSKI (1940) in phytogeography, would give a better picture for these species, but even then the crowded limit-lines of ranges would rather present material for considerations on the history of formation of the given fauna and not on its spatial differentiation.

3. Ecological criterion. This is chiefly used in regionalistic studies of ecological type (geobotany and geography of biocenoses); however, it is often employed to distinguish spatial units in sensu stricto zoo- and phytogeographic investigations. The application of theoretical presuppositions and methods used in ecological regionalization in regionalistic genetic studies many a time caused fairly significant errors. The more so, because the supporters of application of the ecological criterion, concentrating all their attention on the environment and its characters, lost sight of their study object (ranges). A striking example of this is the paper of SUSHKIN (1925), who based his zoogeographic division of the Palaearctic, above all, on the specific characteristics of environment, nearly entirely neglecting both the chorology and the origin of animals. For example, he established a faunal steppe region extending from the Pannonian Lowlands to Zabaykal on the basis of the similarity of the plant cover only and ascribed all the animal species living there to it, regardless of their ranges or origin. As KUCHERUK has shown, among the mammals there is a group of species closely associated with steppes, but it is neither chorologically nor historically uniform, nor does it predominate numerically over the other species occurring there. SHTEGMAN (1936), who has analysed the origin of the birds

of the steppe zone, claims that a vast majority of these birds come from the forest zone. The *Macrolepidoptera* of the steppe zone, which will be discussed in a further part of this study, are also related with the forest ones in an evident manner. In the light of the foregoing facts the distinction of the European steppes as a separate faunal province seems to be incorrect. Similarly, the work of KURENTSOV (1961) on the faunistic regionalization of the Far East, based on the differentiation of environments, though interesting as an attempt to work out the theory and methods of ecological regionalization, practically has no bearing on the knowledge of the regional nature of the faunas inhabiting there, which was its end in view.

Another manner of application of the ecological criterion in zoogeographic regionalization is represented by the works in which the division is based on selected autecological characters, such as fenology, number of generations, periods of emergence of imagines, etc. These studies are for the most part connected with utilitarian regionalization and they are exemplified by respective chapters of the works of UVAROV (1931) and KOZHANCHIKOV (1961).

4. Historical criterion. Advocates of this criterion lay emphasis, above all, on the origin both of particular components of faunas and of faunas as such, on the historical centres of evolution, the history of formation of the faunal population of a given area, and the changes taking place in particular faunas in the past and at present. On the basis of the origin and the time of arrival of animals in an area they establish spatial units characterized by historically homogeneous faunas. This trend, connected both with palaeogeography and with palaeoecology, is one of the most interesting and fertile branches of biogeography. None the less, the historical factor, though very important, does not play the main role in the regionalization of contemporary faunas. There are only very few faunas which are historically homogeneous; the majority of them are conglomerates of species differing in their origin and time of arrival in given areas. An inquiry into historical factors is indispensable in the monographic elaboration of particular faunas, and then after their regionalization has been completed. The historical criterion was used in regionalistic studies, among other authors, by PAGENSTECHER (1909), CARADJA (1935), REINIG (1937, 1950), de LATTIN (1957), and GROSS (1960), 1961).

5. Criterion of affinity. This criterion has been applied rarely as yet, and even then rather intuitionally than consciously. It is grounded on the assumption that the regional division of the faunas and floras of an area is determined by the affinity between these faunas or floras. The larger the share of common species, the more closely these faunas/floras approach each other. The basic object of studies is the ranges of all the species or genera of a group. This group should be abundant and well known. In the result of an analysis of the faunas, territories are combined into spatial units of various classes. Thus, both the course of studies and their results are based on the same material. The significance of all secondary factors (ecological, environmental, historical) is not defined a priori, but is shown up only by the results of studies. This criterion is the most

objective, because it is based on the whole material of a systematic group (or a random sample) and the result depends not on the hypotheses accepted beforehand but on the precision of the analysis alone. However, the application of this criterion demands the use of statistical methods, which a great majority of zoogeographers, unlike phytogeographers, avoided in practice, preferring qualitative studies to quantitative ones. Some zoogeographers, e.g., FRANZ (1950) and KOZHANCHIKOV (1937), questioned the need of application of statistical methods in zoogeography at all, restricting their use to ecological studies on the spatial differentiation of associations or biocenoses. It seems that there is no need to argue the fallacy of this opinion, as only the quantitative approach may provide a fully objective picture of the faunal differentiation of an area. Unfortunately, the application of statistical methods in zoogeographic investigations is rare and, besides modest attempts of AMSEL (1933) and PETERSEN (1947), they were adopted, though not very luckily, by SCHILDER (1952, 1956).

To sum up, it may be stated that the variety of results in the present regionalistic studies in biogeography has been brought about by the following factors:

a. the application of different criteria in regionalistic studies,

b. the application of different methods characterized by various degrees of subjectivism, and

c. the nearly exclusive basing oneself on arbitrarily chosen guiding groups (edificators) for particular spatial units.

METHODICAL

In regionalistic studies it is important to choose the right group, which is to become a basis for division. This group should satisfy the following conditions:

1. It should be well known in respect of systematics and chorology so that it shall be possible to delineate the ranges of all its constituents correctly.
2. It should be comparatively abundant so that it shall be possible to carry out statistical studies.
3. It should be as homogeneous as possible from the viewpoint of the role its constituents play in the environment, that is to say, it should include phytophages or predatory animals or geophages or coprophages, but not all these groups together.
4. It should be a compact systematic unit consolidated by the ties of common origin and phylogenetic relationship.

All these conditions are fulfilled to a high degree by the *Lepidoptera*. Besides vertebrates, they are the best-known group of animals, the number of their species in the area under study is very large, they are all phytophagous and constitute a systematic whole. Some difficulties and restrictions are caused by only two factors:

1. All the families of the order *Lepidoptera* are not equally well known. There is a distinct difference in the degree of knowledge (both of their systematics and distribution) between the families of the so-called *Macrolepidoptera* and the *Microlepidoptera*. The species belonging to the *Macrolepidoptera*, forming about two-thirds of the total of the *Lepidoptera* in the Palaearctic, were given over 90% of all the publications: faunistic, systematic, monographic, etc. For this reason, the division into the two groups, though quite incorrect from the point of view of systematics, must be maintained in zoogeographic works concerning regionalization. The consideration of both these groups together might result in quite a number of obscurities and would greatly influenced the value of results obtained. This is the cause of the omission of the *Microlepidoptera* in the present study, which omission as a matter of fact does not diminish the value of the remaining group, the *Macrolepidoptera*, as the basic material for regionalistic investigations.

2. The second factor is a specific situation in the systematics of the *Lepidoptera* consisting in the lack of accurate criteria allowing the distinction of particular units whose position in the system is between species and families. Genera, supergenera, or subfamilies, which in other groups of animals are generally easy to distinguish, in the systematics of *Lepidoptera* are fluid notions of the type of vague taxons, and the range of these units has so far been determined rather by the authority of the investigator than the real affinity between particular species. These specific conditions present rather significant difficulties, because they prevent the carrying out of hierarchic regionalization in which the first division would be based on family relationships, whereas the smaller units would be established on the basis of the generic and the smallest ones on the basis of the specific relationships. However, besides individuals and populations there exist only species in nature. All the higher systematic units are, above all, systematizing notions. Would the regionalization based on these units be a picture of actual affinities or would it again introduce a subjective element into what is designed to reach the maximum objectivism? It is difficult to answer this question unambiguously. The adoption of genus as the basic unit for regionalization seems most reasonable; the more so, because the position of particular regions in the hierarchic system may be defined also on the basis of the magnitude of the coefficient of affinity.

In this study the so-called *Macrolepidoptera* have been chosen as the initial group. The main object of study is the range of species in the wide comprehension of this word, that is, including also these places where the given species occurs periodically, producing at least one generation. All the localities of migration, however, in which this species appears only occasionally, or visits now and again but does not breed there, are omitted. As far as possible the analysis has covered all the species of the *Macrolepidoptera* found in the territory of the Palaearctic and a few adjacent areas for comparison, up to 1958.

It may be supposed that part of these species are in fact subspecies or forms wrongly raised to the rank of species. On the other hand, some of the forms described as subspecies may turn out to be true species. Nevertheless, the number of these changes seems to be small. The *Macrolepidoptera* are so well-known a group that such changes may concern only a few or some score species, and then a very low percentage of nearly 14 000 species recorded from the Palaearctic.

Another problem is presented by the fact that not all the parts of the Palaearctic are equally well known. While the fauna of Europe or Japan is known so well that the discovery of a new species in these territories is a rare event, the faunas of Tibet and south-eastern Siberia are poorly known and sure enough many species will still be found there. Are the available data then sufficient to carry on any more generalized considerations? It seems that they are, because

1° According to the opinion of the specialists dealing with this subject even in the least explored areas the estimative degree of the knowledge of the *Macrolepidoptera* approximates to 70%.

2° Seeing that the methods used to collect material in the field, especially in areas poorly explored, are rather casual, it is improbable that just the species connected with one fauna should be picked up and those approaching another fauna omitted. Since collection of materials in the field is generally made at random, even if the number of the species found in an area is doubled, the relations between this fauna and some other faunas will not undergo any far-reaching changes.

The ranges of particular species were determined on the basis of the data gathered from numerous faunistic papers, monographs, descriptions of local faunas, atlases, etc. I used the catalogues and monographs of the faunas of these countries for which such publications were available, completing them with more recent data. Where however no such publications were available, or there were some but incomplete such as, for example, „The Fauna of the USSR“, I based myself on numerous, often small, faunistic papers and monographs of particular families or genera. The materials thus collected were used to complete or correct the primary data comprised in the work of A. Seitz „Die Grossschmetterlinge der Erde“. Much information was also drawn from the „Zoological Record“ and „Biological Abstracts“ or obtained through the kindness of foreign lepidopterologists.

As the plotting of the ranges of all the species on maps would be useless both because of technical difficulties (14 000 maps) and on account of ensuing calculations, they have been worked out in the form of tables, in which the ranges of particular species are assigned to the previously established working spatial units.

The establishing of these working spatial units, in other words, the preliminary division of the area under study, presented a rather great difficulty. The cutting of the Palaearctic into quadrants of appropriate size seemed to be the most objective method, and then the first attempts were made in this direction. In practice, however, it appeared that the method of quadrants could not be applied, because of the considerable differentiation of environments, the irregular courses of mountain ranges and coast lines, etc. Particular mountain ranges or their fragments could be enclosed within very small quadrants,

e. g., those having areas of 10 000 sq. km each. The number of such quadrants would be enormous and the territories of uniform scenery chequered quite needlessly. Large quadrants, e. g., those 1 million sq. km in area, would include territories as different as the Alps, Italy, Corsica and Croatia. It is obvious that the picture obtained on the basis of such a division would be fundamentally false. Another method often used to establish the working spatial units consists in enclosing them within the boundaries of administrative districts or countries. Neither could this method be accepted, because the administrative boundaries are artificial and only very seldom coincide with the natural boundaries. The adoption of this method, more often than not, leads to false generalizations and empty notions, like those in the papers of KUNTZE and NOSKIEWICZ (1938) or FORD (1945, 1955). Having analysed different alternatives I resolved to base the preliminary division of the Palaearctic on geobotany. The application of the geobotanic division as a basis seems reasonable, because

1. the *Macrolepidoptera* are phytophages associated in all their developmental stages with the vegetation surrounding them,
2. the influence of other environmental factors is exerted on them through plants except for such accidental events as fire, flood, etc., and
3. the geobotanic regionalization unites areas with analogous or very similar environmental conditions, which admits of the supposition that the *Macrolepidoptera* find similar living conditions throughout the unit irrespective of the magnitude of the area occupied by this unit.

In some cases it was necessary to give up the rigorous observation of geobotanic division. This is, above all, true of islands, which owing to their isolation may have a distinct fauna, though their plant cover is the same as in the adjacent region of the continent. Separate units have been established for such islands. The fact that the present study covers the whole Palaearctic necessitates some generalization and simplification of the boundary lines of particular geobotanic regions.

In order to obtain as correct a geobotanic division as possible the following works were referred to: „Rastitelnyi pokrov SSSR“ (1956), „Flora SSSR“ (1934—1964), ALEKHIN (1951), ALEKHIN et al. (1961), ALEKHIN and WALTER (1936), BRAUN-BLANQET (1923), DIELS (1929), FABER and SCHIMPER (1993), GOOD (1953), HEGI (1933—1963) and WALTER (1955, 1962)[1].

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[1]. It should be emphasized that the problem of choice of a basis for the establishing of spatial units so as to „straighten up“ the boundaries of the ranges is not very significant. So far as the *Macrolepidoptera* are concerned, the application of the geobotanic division seems most correct. Some other divisions, e.g. the physiographic division or that made in respect of soil, may be suitable for other groups of animals, provided that they are based on the differentiation of homogeneous elements (or those closely correlated with each other) which are of vital importance to the animal group under study. Instead, it is essential to select such a criterion that it shall govern the shape and size of the range of a given group of animals to the highest degree. The main condition of occurrence of phytophages is the presence of food plants, whereas in the case of soil predators it may be the sort of soil. The basic object of study is the range, and the background against which it is considered is of rather secondary significance.

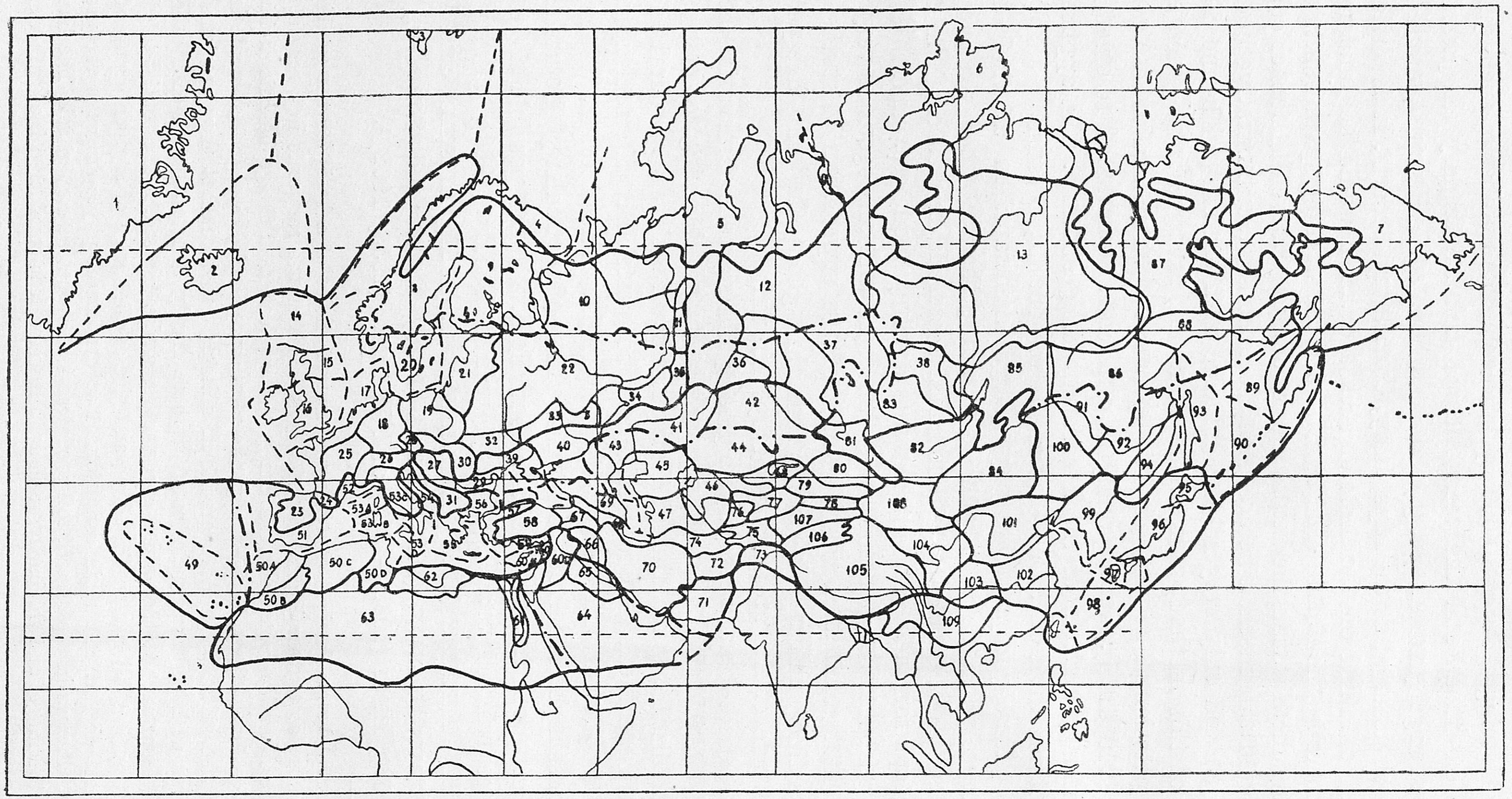

Fig. 1

The whole area of the Palaearctic has been divided into 118 working spatial units, most of which consitute separate geobotanic regions.

The working division of the Palaearctic area is presented in Fig. 1.

Further studies showed that virtually these units had been established correctly, which can also be evidenced, if by nothing else, by the very small number of subspecies occurring within one unit. Out of the total of above 5000 subspecies only 148 occur together in a single unit. In addition, the vast majority of them are mountainous subspecies, attached to various massifs or appearing on the opposite slopes of the same mountains.

The tabulation of the ranges of particular species formed a basis for further studies and made the statistical elaboration of the material possible. The very summing up of the particular columns of the table permitted the characterization of the *Macrolepidoptera* of the Palaearctic in respect of their specific abundance in different parts of this area. The selection of all the species the ranges of which are limited to single geobotanic units produced the picture of the di-

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Fig. 1. Working division of the Palaearctic based on geobotanic regionalization. 1. Greenland Region, 2. Iceland Region, 3. Spitsbergen, 4. Lapland, 5. Kanin-Gydan Region 6. Arctic Siberian Region, 7. Chukchi-Anadyr Region, 8. Central Scandinavian Region, 9. Karelo-Finnish Region, 10. Dvina Region, 11. Central Ural Region, 12. West Siberian Region, 13. Central Siberian Region, 14 Shetland Is., 15. Scottish Subregion, 16. British Subregion, 17. Nord Sea Lowlands Region, 18. Central European Region, central subregion, 19. Eastern subregion of Central European Region, 20. Northern subregion of Central European Region, 21. Baltic Subregion, 22. Central Russian Subregion, 23. Northern Iberian Region, 24. Pyrenean Region, 25. Western subregion of Central European Region, 26. Alpine Region, 27. Panonian Region, 28. Southern subregion of Central European Region, 29. Eastern Danubian Region, 30. Carpathian Region, 31. Western Balkan Region, 32. Volhynian Region, 33. Oka-Don Subregion, 34. Central Volga Subregion, 35. Southern Ural Region, 36. Tobol'sk Region, 37. Ob Region, 38. Angara Region, 39. Black-Sea Region, 40. Don-Kuban Region, 41. Ural (Mugodzhar) Region, 42. Irtysh Region, 43. Western subregion of Kazakh Region, 44. Eastern subregion of Kazakh Region, 45. Caspian Subregion, 46. Eastern Aral Region, 47. Kara Kum Region, 48. Balkhash Subregion, 49. Macaronesian Province, 50 A. Moroccan Subregion, 50 B. Atlas Subregion, 50 C. Algerian Subregion, 50 D. Tunisian Subregion, 51. Southern Iberian Region, 52. Provencal Subregion, 53 A. Corsica, 53B. Sardinia, 53 C. Apennine Region, 53 D. Sicilian Subregion, 54. Adriatic Region, 55. Aegean Region, 56. Thrace Region, 57. Moesia-Lydia Subregion, 58. Anatolian Region, 59. Taurus Subregion, 60 A. Cyprus Subregion, 60 B. Palestine Subregion, 60 C. Lebanon Subregion, 60 D. Syrian Subregion, 61. Egyptian Subregion, 62. Libyan Subregion, 63. Saharan Subregion, 64. Arabian Region, 65. Mesopotamian Region, 66. Kurdistan Region, 67. Armenian Region, 68. Abchazian-Hircanian Region, 69. Caucasian Region, 70. Northern Iran Region, 71. Sindian Province, 72. Afghan Region, 73. Kashmir and Punjab, 74. Turkmenia Region, 75. Pamir Region, 76. Fergana Region, 77. Kirgiz Region, 78. Eastern Tien Shan Subregion, 79. Kuldzha-Ala Tau Subregion, 80. Dzhungar Region, 81. Altai Region, 82. Altai-Changai Region, 83. Sayan Region, 84. Mongolian Region, 85. Zabaykal Region, 86. Uda Region, 87. Indigir Region, 88. Okhotsk Region, 89. Kamchatka Region, 90. Kurils, 91. Zeya Region, 92. Amur Region, 93. Sakhalin Region, 94. Ussuri Region, 95. Northern Region of Japanese Area, 96. Central Region of Japanese Area, 97. Southern Region of Japanese Area, 98. Ryuku, 99. Korean Region, 100. Manchurian Region, 101. Northern Chinese Region, 102. Central Chinese Region, 103. Szechwan Region, 104. Eastern Tibetan Region, 105. Central Tibetan Region, 106. Northern Tibetan Region, 107. Kashgar Region, 108. Gobi Region, 109. Yunnan, Sikkim.

stribution of endemic forms in the narrow sense of the word. However, neither the richness of local faunas nor the number of endemic species constitutes a basis for working out the lepidopterological regionalization of the Palaearctic. In order to obtain the right division the materials collected should be worked out statistically by comparing the compositions of the local faunas. The method of differential analysis of J. CZEKANOWSKI (1913) appeared to be most useful for this purpose. This method renders it possible to compare any number of elements in an objective manner. It facilitates the formation of a system of elements under study, for their characters are arranged by themselves according to their value. The method is quite objective because, if used faultlessly, it cannot give two different results. The conclusions made on the basis of the material worked out according to this method are easy to check. The analysis may be carried out by some other persons and the result will always be the same. The results obtained with differential analysis, being in themselves the solution of many problems, present valuable materials for interpretation as well. The arrangement of local faunas established in this way allows the evaluation of the importance of the floral factor to the distribution of the *Macrolepidoptera* and at the same time verifies the geobotanic division adopted in the study, throwing light upon the history and the essence of distinctness of individual botanic regions. The application of CZEKANOWSKI's method is undoubtedly made difficult by its laboriousness. It was, for example, necessary to make about 7000 calculations to compare 118 local faunas. Differential analysis is, above all, a segregating method, grouping elements with similar characters close to each other. In this case the quality of these elements is not essential. This method can be applied to segregate collections of concrete values as well as those of conventional values, coefficients, etc. St. KULCZYŃSKI (1940) was the first to introduce it into biogeography, and now it is applied widely, especially by phytosociologists, but hitherto has not been used in zoogeographic studies.

In investigations on the spatial differentiation of the Palaearctic fauna it is essential to apply a suitable coefficient, which would express this differentiation as well as possible. The coefficient of JACCARD and STEINHAUS, calculated by the formula

$$p = \frac{2c}{a+b} \times 100$$

where c is the number of species common to faunas a and b, a is the number of species in fauna a, b is the number of species in fauna b, and pointing to the faunal similarity of two regions examined, cannot be used for our purpose. It would be adequate, if all the local faunas had more or less the same number of species. However, in the presence of the wide range of the numbers of species in particular faunas, the differences in the dividend play too great a part, obscuring the picture of real connexions between the faunas. A comparison of the fauna of Scotland with that of the Shetland Islands may be used as an example. There are 155 species of the *Macrolepidoptera* in the

Shetland Islands and all of them appear in Scotland as well. Consequently, the actual affinity of the Shetland fauna to that of Scotland may be expressed by 100%. On the other hand, 445 species of the *Macrolepidoptera* are known from Scotland and so the coefficient of similarity of these two faunas is

$$\frac{2\times 155}{155+445}\times 100=\frac{310\times 100}{600}=51{\cdot}6$$

Thus both these faunas, being absolutely related, lie on the margin of mutual similarity. This is natural, because the fauna of Scotland differs from that of the Shetland Is. in having 290 species which are absent from the latter.

Since the faunal relationship of any areas is evidenced not by the number of species inhabiting them but by the homogeneity of the faunas, it seems more correct to base the studies on the criterion of faunal affinity. The formula of SZYMKIEWICZ defines the degree of affinity in the best, though perhaps not perfect, way (vide SZAFER, 1949).

$$p=\frac{a}{A}\times 100$$

where p is the coefficient of affinity, a the number of species common to faunas A and B, and A the number of species in the less abundant fauna (A). This coefficient defines the relationship of two faunas compared in a sufficiently clear manner. Its defect is that it refers only to the percentage share of the species of the more abundant fauna in the less abundant one, but not vice versa. In close studies on individual faunas these differences may be of great importance, but they are not significant to general regionalization. After all, we study the relationship of faunas and not the share of particular elements in these faunas. The relationship of the Shetland and Scotland faunas is absolutely irrespective of the fact that the share of the „Shetland species" in the Scottish fauna amounts to only about 34%.

The coefficients of affinity calculated for all the local faunas (of particular geobotanic regions) were next arranged, partly by the dendritic method (FLOREK et al., 1952), into a diagram, in which the most closely related faunas are grouped beside each other. Finally, the diagram was transformed into a map illustrating the spatial differentiation of the *Macrolepidoptera* of the Palaearctic.

THE STRUCTURE OF THE MACROLEPIDOPTERA FAUNA OF THE PALAEARCTIC [1]

A total of 13427 Macrolepidopteran species were found in the area of the Palaearctic (in its traditional comprehension) till 1958. It makes less than 60% of all the Lepidopteran species recorded from this territory.

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[1] All the numerical data given in this chapter have only relative values, for they represent the state of our knowledge in 1958. It is obvious that further faunistic studies, especially in territories the knowledge of which is still very poor, will bring about changes in numerical

It is interesting to compare the number of the Macrolepidopteran species from the Palaearctic with those in other faunal realms. The data concerning the abundance of the *Macrolepidoptera* in particular faunal realms have been taken from the works of Rebel (1918), Holdhaus (1929), Bourgogne (1951), and Seitz (1909—1942). This comparison is presented in Table 1.

Table 1

Number of *Lepidoptera* in particular zoogeographic realms

Realms	Number of *Lepidoptera*			
	total of *Lepidoptera*	%	of which *Macrolepidoptera*	%
Palaearctic	22 000	15·9	13 427	13·9
Nearctic	14 000	10·2	8 800	9·0
Total of Holarctic	36 000	26·1	22 227	22·9
Indo-Australian	35 000	25·2	22 700	23·3
Ethiopian	22 000	15·9	16 300	16·9
Neotropical	45 000	32·8	35 500	36·9
Total	138 000	100	96 727	100

It will bo seen from the foregoing data that the Palaearctic *Macrolepidoptera* form about 15% of the whole of this group. This value seems to be too high, because the tropical faunas are known far worse than the faunas in the moderate zone. Besides, taking into consideration the magnitude of the area occupied by the Palaearctic, it may be stated that its fauna is the poorest in species. The number of endemic families is very small in the Palaearctic fauna as well. So far as the *Macrolepidoptera* are concerned, these are only the *Lemoniidae*, *Endromididae*, and *Somabrachidae*.

The vast majority of the Palaearctic species of the *Macrolepidoptera* are monotypic, i.e. not differentiated into subspecies. This is supposed to result, above all, from the fact that the ranges of most species are relatively small. On the other hand, the small number of subspecies described so far is to some extent due to the definition of this systematic unit, which has not been stated precisely, and to the splitting tendencies so common among investigators, who describe each variety as a new species too hastily (e.g. A. Walker). The great majority of these errors have already been corrected, none the less there are

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relations both within single faunas and between them. Nevertheless, the data offered in this chapter seem to illustrate some general regularities in the geographic distribution of the *Macrolepidoptera* over the study area in a sufficiently convincing manner.

The omission of these data only because they will undergo some, but even then not very great, corrections, would restrict the possibility to obtain a general picture of the Macrolepidopteran fauna of the Palaearctic, its characters, and connexions both between particular local faunas and between adjacent areas.

Table 2

	Number	%
Monotypic species	9127	68·0
Polytypic species	4300	32·0
of which		
species containing 2 to 9 subspecies	4072	30·3
,, ,, 10 to 19 ,,	196	1·4
,, ,, above 20 ,,	32	0·9

still about 1000 species known only by name and from a usually vague description, the species that have been seen by nobody but their authors. The degree of the intraspecific differentiation of the Palaearctic *Macrolepidoptera* is shown in Table 2.

This table shows only the so-called great subspecies, whereas all the breeds or even aberrations, treated by some specialists as subspecies, have been omitted. For example, *Parnassius apollo* (L.) has 8 distinct subspecies, within which it is differentiated into more than 200 breeds. On account of their isolation these breeds are often treated as subspecies, and then a special unit should be erected for these 8 great subspecies in the system, standing between species and subspecies and resembling the notion „grex“ applied in botany.

The ranges of most Macrolepidopteran species are, as a rule, very small and for the most part they do not go beyond the boundaries of a single geobotanic region or occupy only a few neighbouring regions. The degree of attachment of the Macrolepidopteran species of the Palaearctic (with the exception of those it has in common with the non-Palaearctic areas) to the geobotanic units is illustrated in Table 3.

As will be seen from this table more than 80% of all the Macrolepidopteran species occur in small areas, usually similar in their geobotanic characteristics.

Table 3

Number of geobotanic units included in the range of species	Number of species	% of total
1	4602	39·9
2—3	2641	22·8
4—9	2131	18·5
10—19	940	8·1
20—29	417	3·6
30—39	321	2·8
40—49	232	2·0
50—59	131	1·1
60—69	77	0·7
above 70	56	0·5

There are only very few species which have extensive ranges, and this is another advantage of this group of animals for all kinds of regionalistic studies. If the species occurring also outside the Palaearctic were included in this table, the picture obtained would not undergo essential changes, because nearly 90% of these species appear in only a few adjacent regions. Only the share of the most widely distributed species would increase, but not very much, from 56 to 98. They are mainly Holarctic species of great ecological importance or cosmopolites occurring nearly all over the world. The dominancy of species with small ranges explains the causes of the slight intraspecific differentiation in this group of animals to some degree.

The differentiation of the faunas of particular geobotanic units is interesting in respect of the number of endemic species that they contain. The number of these species in particular faunas, as shown on the map (Fig. 2), is relative, because only the species whose occurrence in the given area was certain and confirmed were taken into account. On the other hand, the species described vaguely, the descriptive types of which were lost and the presence not confirmed, were left out. The inclusion of these „species", which are generally empty names, would only obscure the picture.

Most of the species having small ranges are grouped in the southern part of the Palaearctic, where they form four distinct centres, in the West Mediterranean, West Asia, Central Asia, and in the Far East. In the central and northern parts of the Palaearctic the number of these species is small or they are completely lacking. This seems to be quite natural, for these areas are generally poorly differentiated and rather late colonized. Naturally, some characteristic species occur there as well, but their ranges usually cover larger areas including several or some dozen geobotanic units.

The West Mediterranean centre embraces the faunas of North Africa, Macaronesia, and South Europe. These areas have been explored so well that the large number of endemic species does not result from the deficiency of data. The number of species with small ranges fluctuates from 10 to 169 in particular working units (except the Sahara). Their number is nearly doubled, if the species distributed somewhat more widely (in 2 or 3 neighbouring units) are taken into consideration. Real numbers only poorly illustrate the role of endemic species in particular faunas. The percentage share of these species in local faunas is more instructive (Fig. 3).

A comparison of these two maps will show rather far-reaching differences, especially as regards the European part of this centre. Besides the focus in Algeria, well defined on both the maps, there is another, which includes the Macaronesian Is., where the endemic species form more than 40% of the *Macrolepidoptera*. The significance of Africa increases considerably as compared with southern Europe, where the share of such species (except for southern Spain and Corsica) does not exceed 5%.

The second — West Asiatic — centre covers Asia Minor, Middle East, Egypt, and Iran. However large is the number of species with small ranges

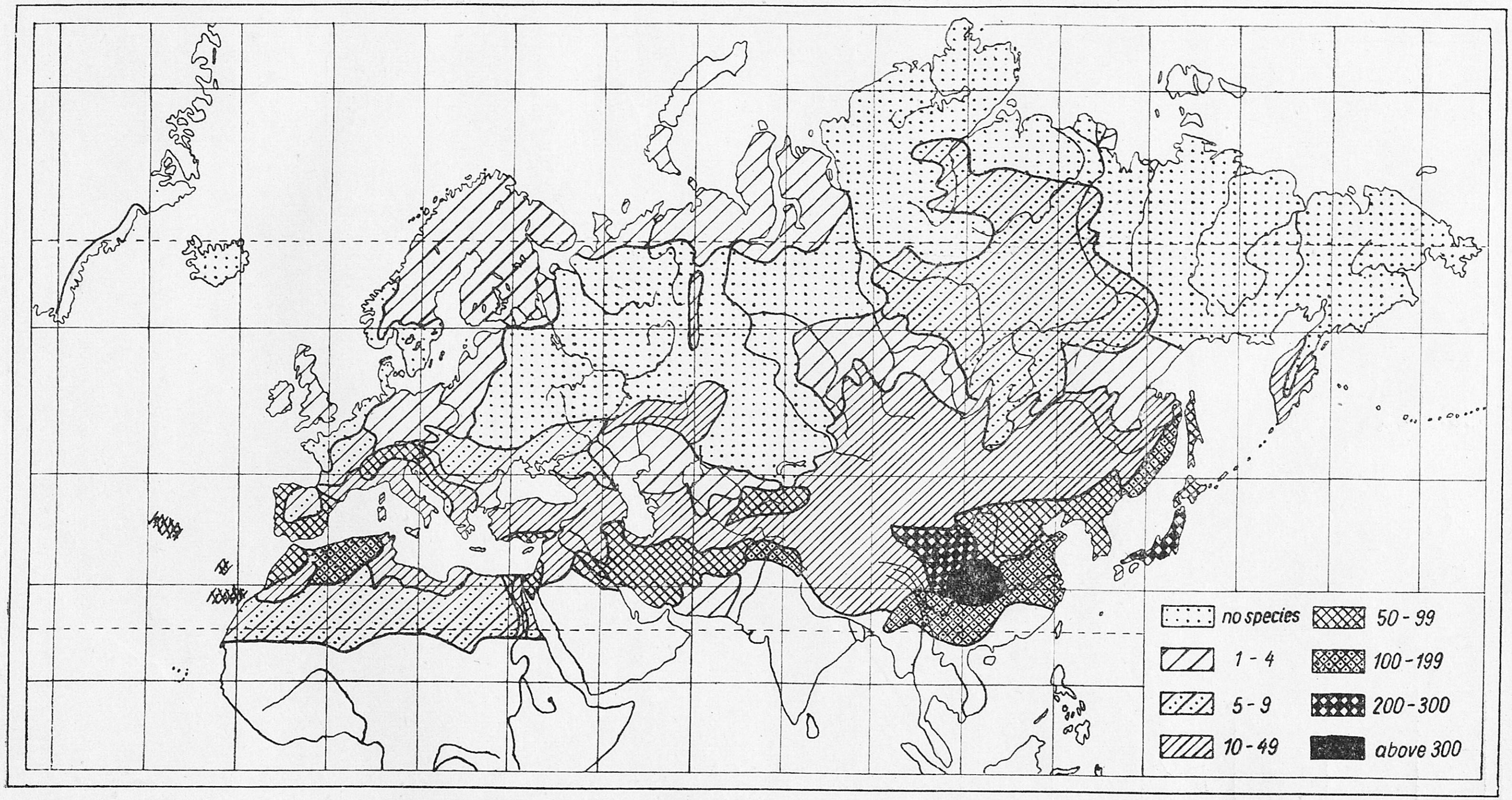

Fig. 2. Number of endemic species in particular local faunas

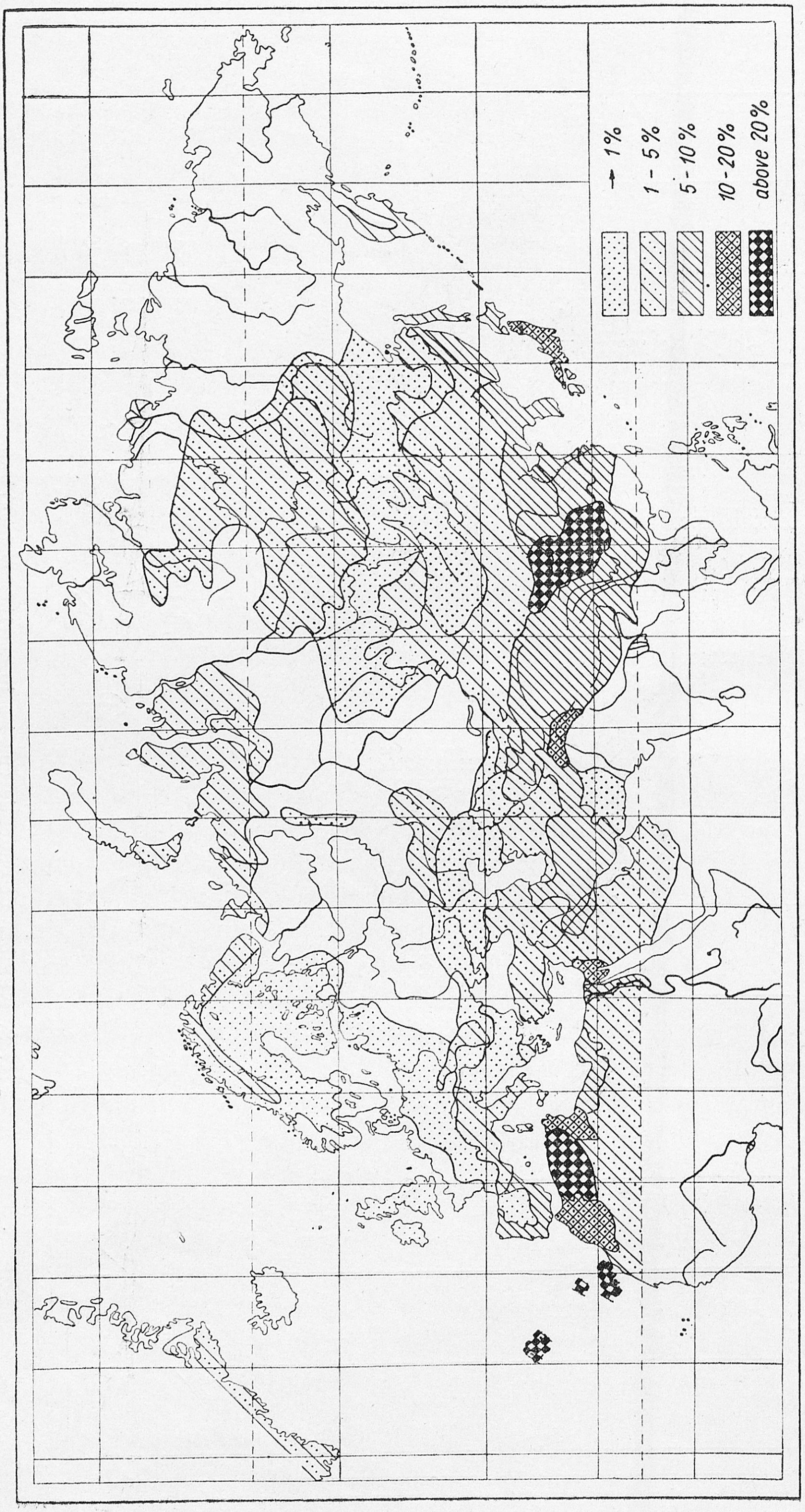

Fig. 3. Percentage share of endemic species in particular local faunas

in each of the faunas of this centre, their percentage share is not high. Only the fauna of Palestine, in which the endemic species form above 12%, is an exception.

The third centre consists of the mountains of Central Asia and its core lies in the mountains of Kashmir (188 endemic species, i.e., 17·3% of the Macrolepidopteran fauna). Besides Kashmir, there are numerous endemic species in Afghanistan, in the Fergana Basin and in the Tien-Shan Mts. However, the share of these species in the whole of the *Macrolepidoptera* is not considerable.

Finally, the fourth centre occupies the south-eastern part of the Palaearctic, including China, Japan, Sakhalin, Korea, and the Sikhote Alin Mts. The fauna of Szechwan and that of the adjoining Tibetan Plateau are particularly rich in endemic forms. These species are also numerous on the island of Honshu, whereas on the neighbouring islands both on the north and on the south they are considerably fewer.

An analysis of the data on the distribution of species with small ranges suggests the following conclusions:

1. The vast majority of these species occur in refuges of the Tertiary flora and fauna and so where the effect of glaciations was insignificant. On the other hand, the number of endemic species is very small in the territories which were covered by glaciers in the past, or those adjacent to them. This would indicate that they are for the most part relict endemic species and not neo-endemic ones.

2. The occurrence of species with small ranges is closely associated with areas which are well differentiated in so far as their relief is concerned. All the above-mentioned centres of occurrence of these species cover, above all, mountainous areas. The variety of environments, common in mountains, and their isolation are supposed to constitute an evident species-producing factor, and this is especially well seen in the central and northern parts of the Palaearctic, which were within reach of direct action of the glacier in the past. The Pyrenees have 17 endemic species (1·8%), the Alps 57 (3·9%), the mountains of the Balkan Peninsula 10 (0·8%) and the Carpathians 8 (1·3%), whereas the areas adjoining to them but not so well developed have only 1—3 such species in a single geobotanic unit. An analogical situation can be found, among other regions, in the Altay Mts., Sayan Mts., and in Kamchatka.

3. The process of differentiation, though on a much smaller scale, is observed in the European Arctic area and then in the territory where the glacier kept longest. Although the number of endemic species is small there, their share in the fauna of this area is fairly large, i.e., from 4 to 8%. It is an interesting fact that all these species are closely related with those occurring either in the Alps or in central Scandinavia. Consequently, they are of European and not Arctic Asiatic origin, though the Arctic Asiatic species form a high percentage of the total fauna.

4. The faunas of islands (with the exception of the Arctic zone) have a high proportion of endemic species. The farther an island lies from the continent

and the earlier its isolation was established, the larger is the number of these species. Local species are generally far more numerous on oceanic islands than on the islands of internal seas, however early these islands were cut off the continent. A permanent isolation, similar to that brought about by the sea, may also be caused by a partition in the form of a completely different type of vegetation. An example is Kamchatka; the relatively warm southern part of the peninsula is separated from the continent by a broad zone of highland tundra, which prevents any exchange between this region and the territories resembling it in environmental conditions but situated on the continent. In the fauna of southern Kamchatka the number of endemic forms amounts to 19 Macrolepidopteran species, which makes 3·6% of the total fauna. It is remarkable that most of these species are related to the species inhabiting the forest zone of North America. Only 4 species are derived from eastern Asia.

The number of Macrolepidopteran species in particular geobotanic units is very various, it ranges from 36 species in Iceland to 2574 in Szechwan. On the average about 900 species fall within a unit. The number of Macrolepidopteran species in particular working units is illustrated by Fig. 4.

The faunas of Arctic and desert areas are the poorest. The regions with faunas abounding in species are grouped in two separate complexes: the Europeo-West Asiatic complex and the East Asiatic one. It seems that the variety of localities plays the main role in this case. The fauna of Greece falling short of that of Bulgaria and the faunas of Sicily and Calabria poorer than that of central Italy as far as number of species is concerned would indicate this fact. In addition, there is an apparent correlation between the number of Macrolepidopteran species and the number of species of higher plants. Fig. 5, based on the calculations of WULFF (1935) completed with data from more recent publications, presents the approximate number of plant species occurring in particular geobotanic units. In spite of differences in details, these two maps (Figs. 4 and 5) show a clear-cut coincidence. There are three centres of very rich faunas and floras, well visible on both these maps, and the fourth, the floral Altay-Sayan centre, which can also easily be seen, though less distinctly, on the faunistic map. Does this coincidence indicate the conjugate evolutions of both these groups, i.e., the plants and the *Macrolepidoptera?* It does not seem to. Such an interrelation exists for certain, but it rather plays a secondary role. Had the evolution of these two groups been conjugated really, the Macrolepidopteran fauna would have had to differentiate as the flora differentiated. Each area rich in plants would be rich in animals as well, and the relation between the number of plants and that of the Macrolepidoptera ought to be more or less constant. This relation is however variable. The average number of plant species falling to one Macrolepidopteran species is given in Fig. 6.

In the majority of the geobotanic units this numerical relation fluctuates from one to three plant species coming to one Macrolepidopteran species, though there are fairly numerous areas in which this relation increases enormously. This is true both of the Arctic Zone, especially its western part, where this

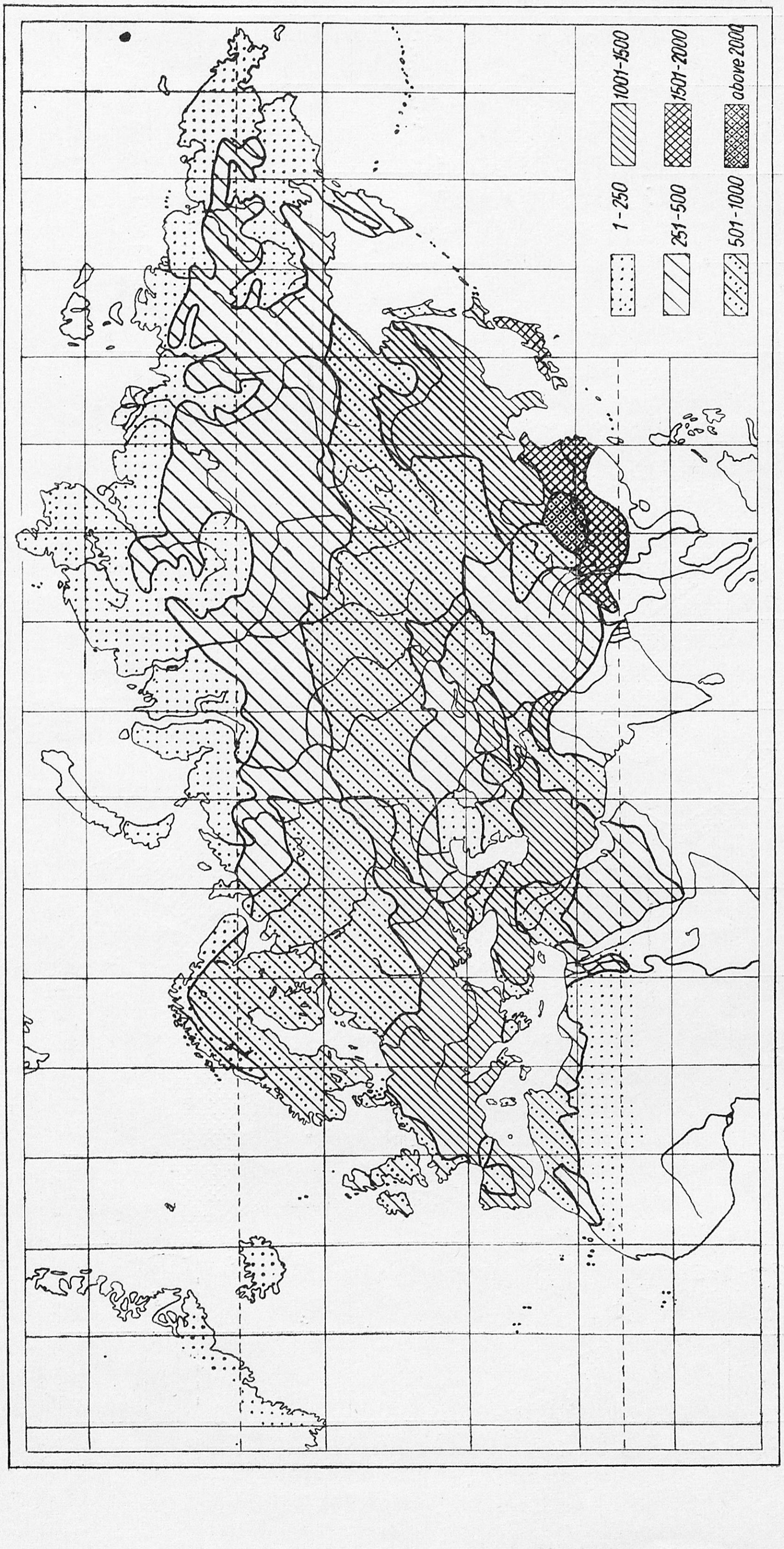

Fig. 4. Number of Macrolepidopteran species in particular local faunas

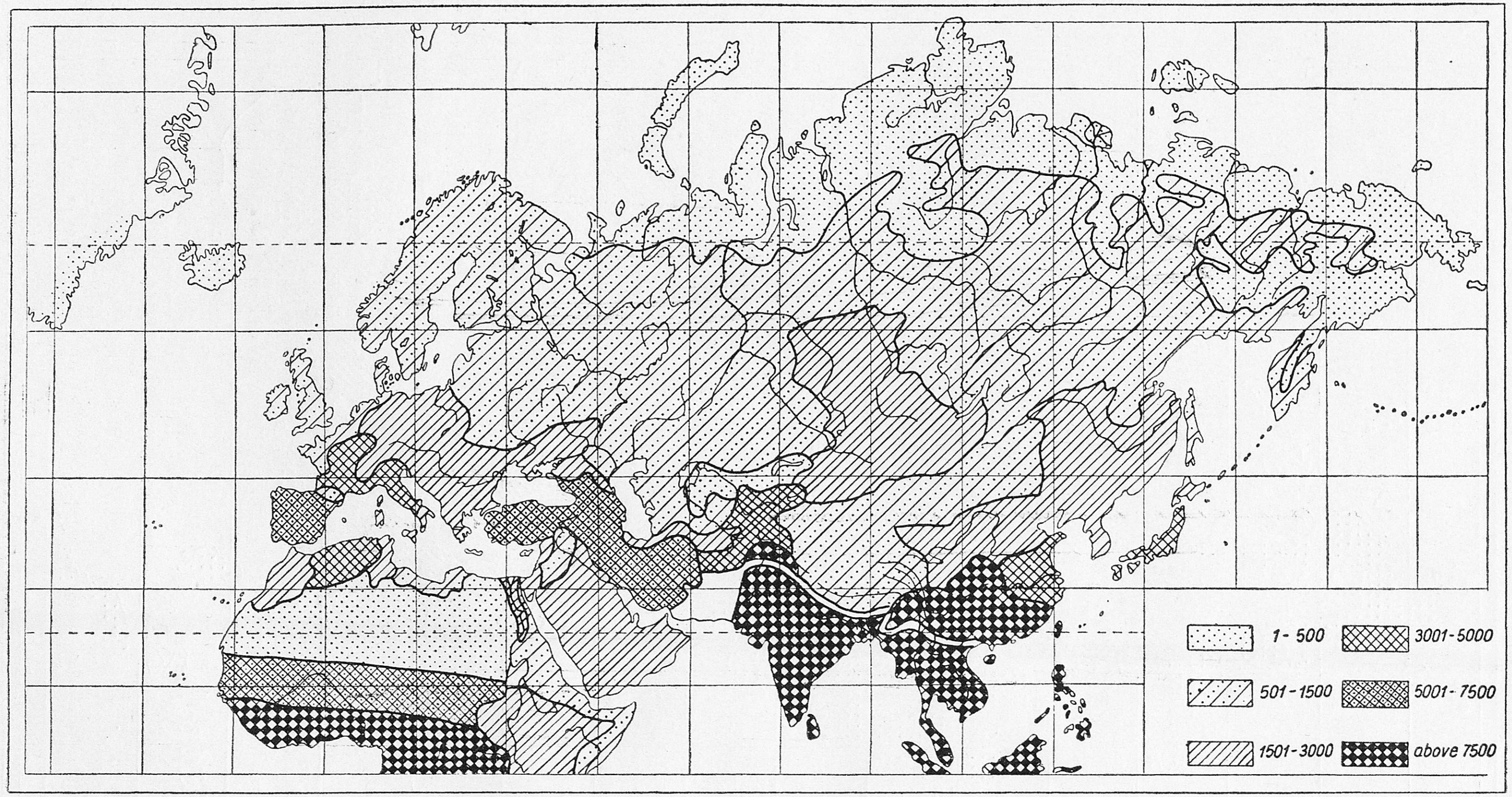

Fig. 5. Approximate numbers of higher plant species in the floras of particular working spatial units

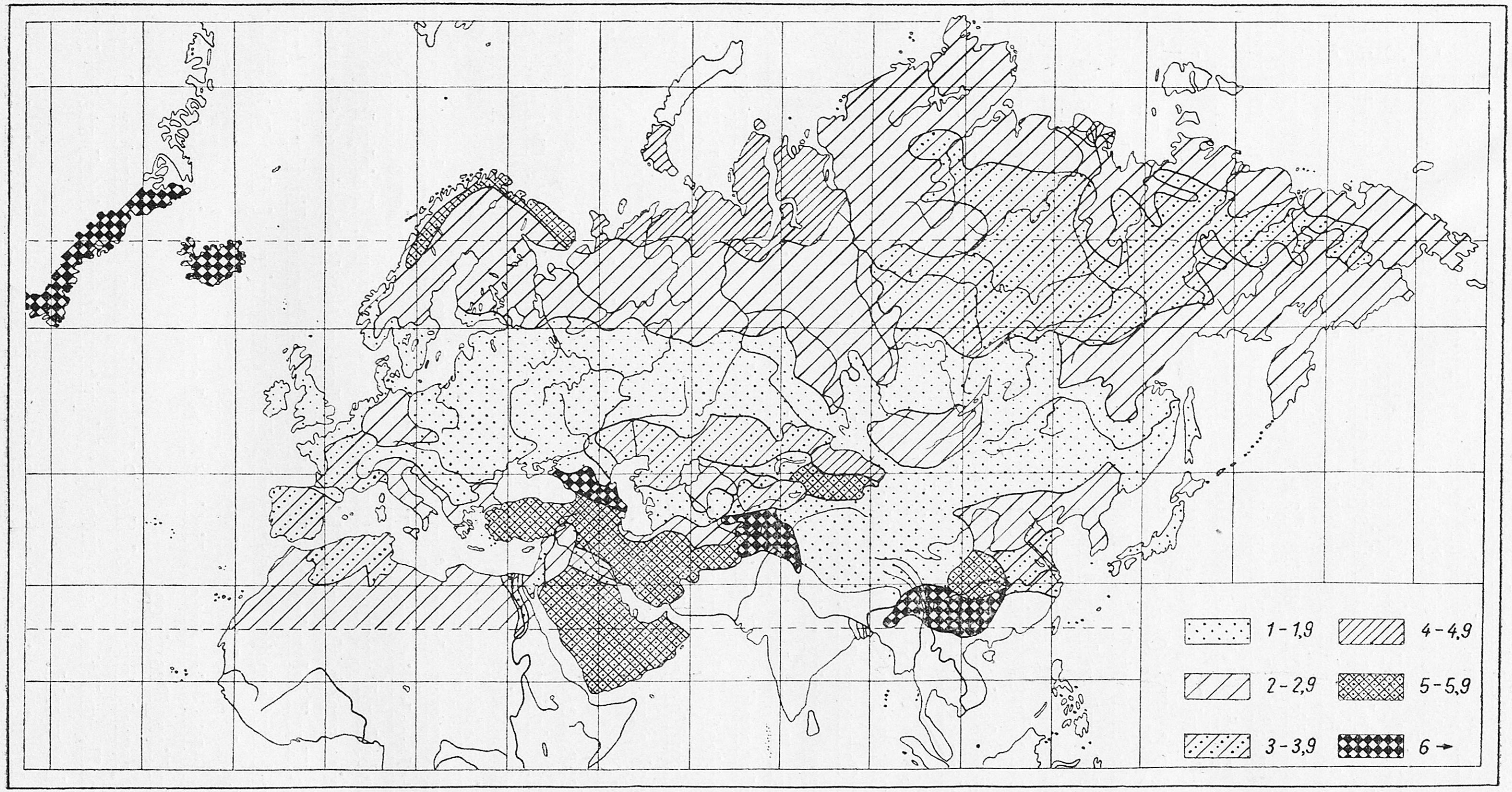

Fig. 6. Number of higher plant species for 1 Macrolepidopteran species in particular working spatial units

coefficient exceeds 4, and of central and eastern Asia, where more than 5 plant species come to one Macrolepidopteran species. In the first of these cases the difference might be ascribed to the faster process of speciation in plants as well as their easier adaptation to environmental conditions, whereas it is difficult to find the explanation of this phenomenon in the Asiatic territories. A typical example of this is the Caucasus Mts., from which hardly 869 Macrolepidopteran species (including only some dozen endemic ones) have been recorded, whereas the number of higher plants in this area exceeds 5700 species; consequently, 6·6 plant species fall to one Macrolepidopteran species. In the nearby Kopet Dahgh Mts., which are a refuge locality for the Tertiary flora and fauna, this relation is 2·6. The Caucasian fauna being sufficiently well explored, the cause of this fact cannot be ascribed to its bad knowledge, either. C. HORMUZAKI (1929, 1930), who also realized the exceptional poverty of the Caucasian *Macrolepidoptera* in species, explains it by different origins of the flora and the fauna. He holds the opinion that after the glacier had withdrawn, these mountains were colonized by the vegetation coming from the Armenian-Hircanian refuge, whereas the *Macrolepidoptera* came rather from the North. However, further detailed and universal investigations of the flora and fauna of this area are necessary to answer the question why the vegetation that encroached upon the Caucasus Mts. after the ice had melted did not bring its own Macrolepidopteran species with it.

The small number of species with ranges going beyond the boundaries of the Palaearctic and which, consequently, are also common to other faunal realms, indicates the autonomy of the fauna in a sense. Difficulties to carry out close studies caused that these species, i.e., both the Palaearctic species occurring also outside the Palaearctic and the non-Palaearctic ones that appear within this area, were treated together. The substitute subspecies which occur in the Nearctic and with reference to which there is a controversy whether they form distinct species or not, have been left out. Table 4 shows the number of species which the Palaearctic has in common with the non Palaearctic zoogeographic realms.

The percentage share of species which the Palaearctic has in common with the Oriental realm is given in Fig. 7. Most of these species occur in eastern Asia, in the borderland vague in its zoogeographic nature. Fairly large numbers of these species reach through China and Japan to the basin of the Amur River and to the Kuril Islands. Besides, they spread from India through Arabia to the Sahara and farther to Macaronesia. The connexion of the Sahara with India can also be observed in the flora of these areas, which, besides, became a basis for their combination into a distinct floral and geobotanic province, the so-called Sahara-Sindian Province.

In the remaining part of the Palaearctic area the number of these species is very small, and they are mostly ubiquitous forms, distributed widely nearly all over the world.

The share of species which the Palaearctic and the Nearctic have in common

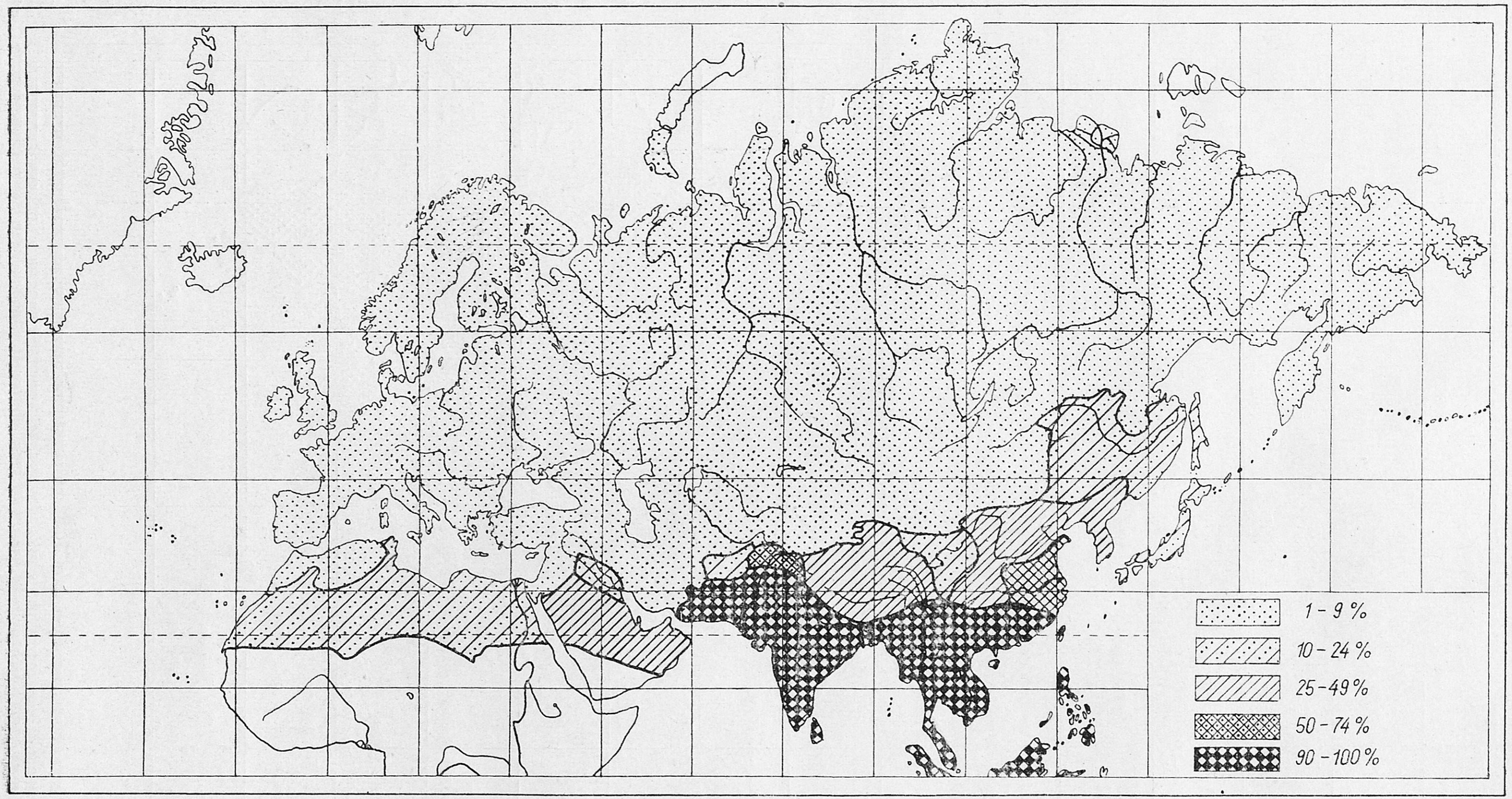

Fig. 7. Percentage share of *Macrolepidoptera* which local faunas of the Palaearctic have in common with the Oriental Realm

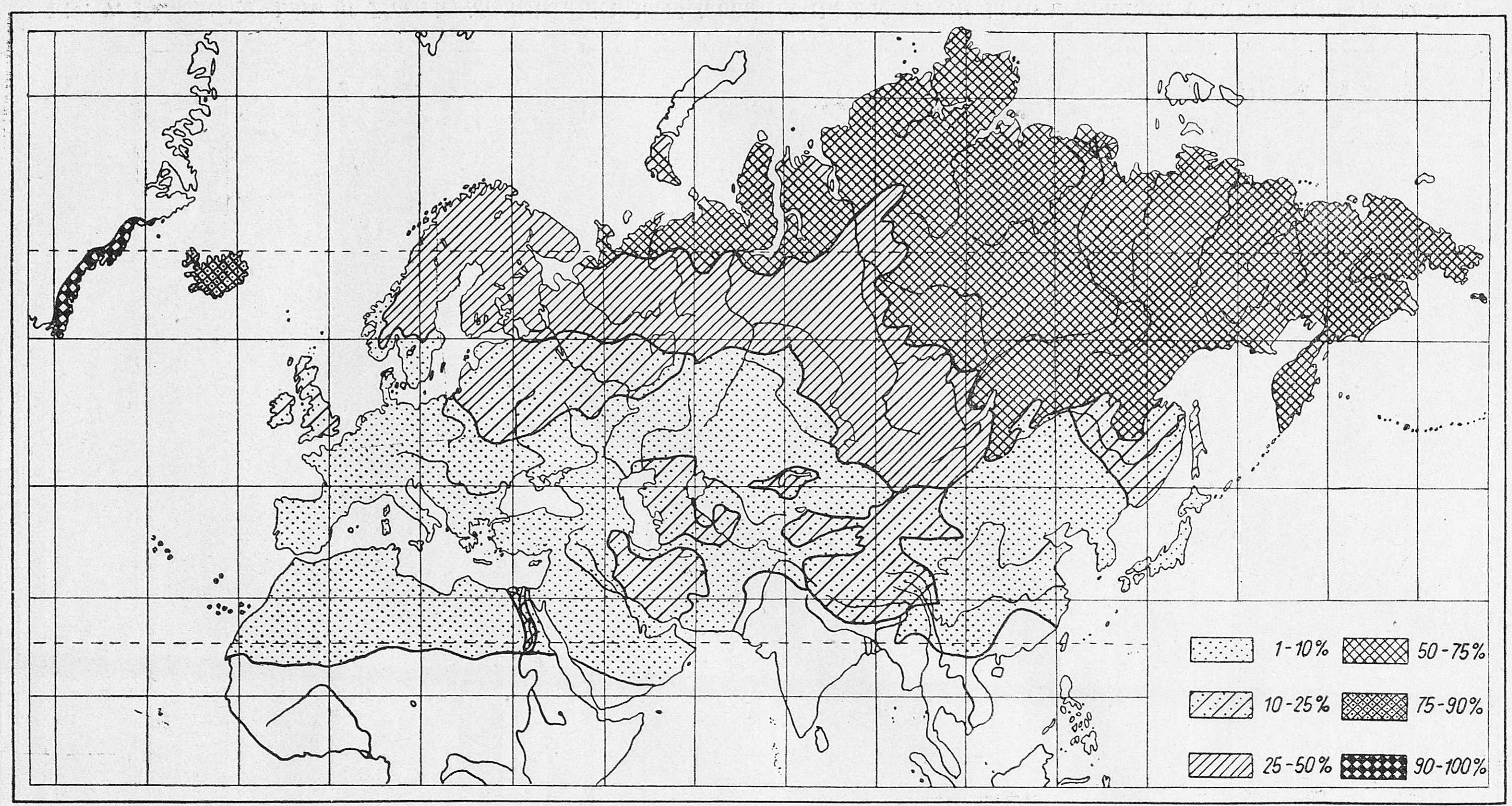

Fig. 8. Percentage share of Macrolepidopteran species which particular local faunas of the Palaearctic have in common with North America

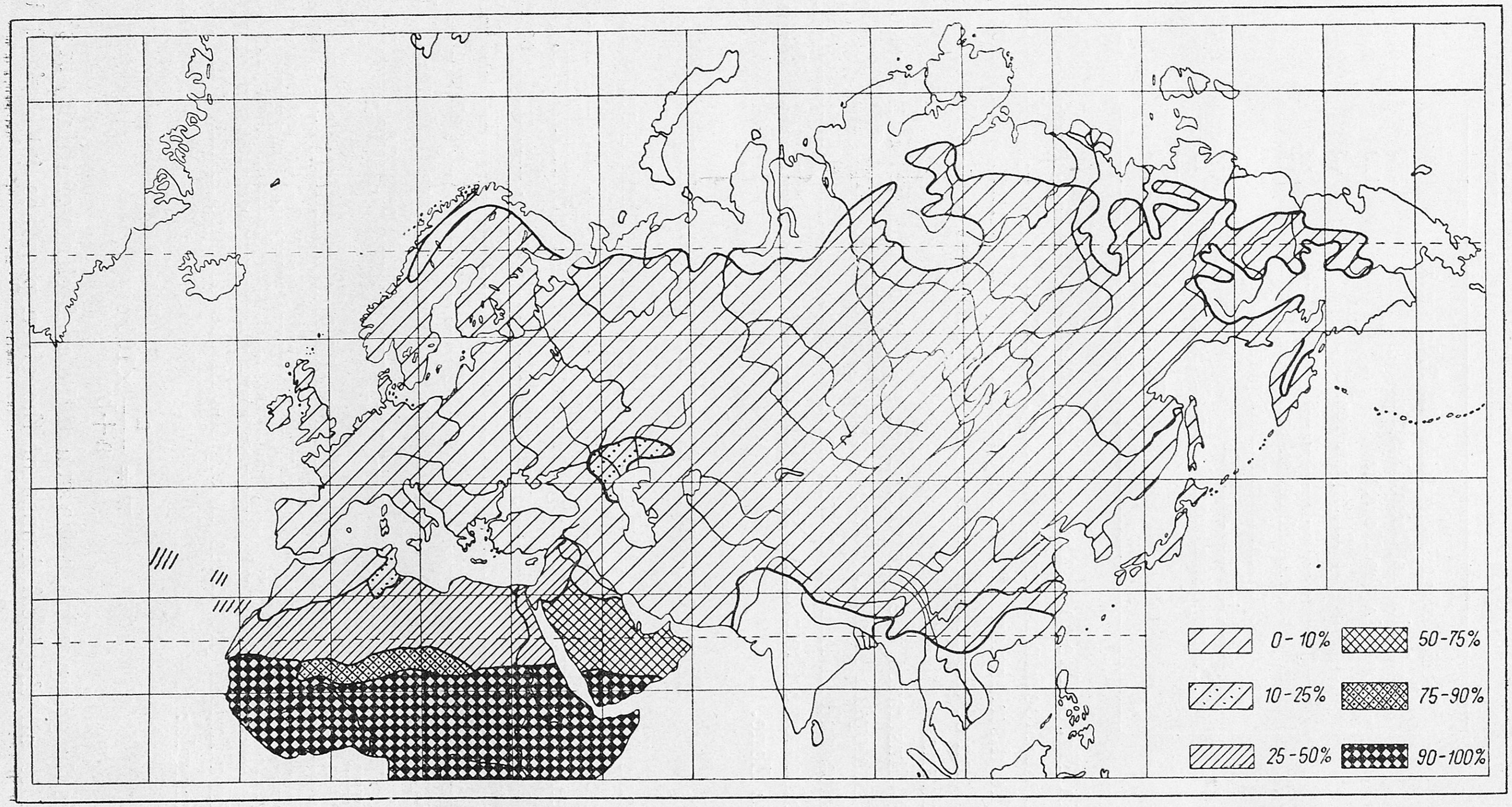

Fig. 9. Percentage share of Macrolepidopteran species which particular local faunas of the Palaearctic have in common with the zoogeographic Ethiopian Realm

Table 4

Species occurring outside the Palaearctic	
only in the Oriental realm	1593
only in the Nearctic	429
only in the Ethiopian realm	48
in the Oriental and Ethiopian realms	74
in the Oriental realm and Nearctic	13
in the Oriental and Ethiopian realms and in the Nearctic	10
Cosmopolites occurring in all the realms	12
Total	2179

is shown in Fig. 8. The comparatively large number of these species in the Arctic and the East Siberian faunas is striking. Unfortunately, the lack of data concerning the distribution of these species in North America does not permit the estimation of the actual share of Arctic species and that of Nearctic species in these faunas.

Fig. 9 illustrates the proportion of species which the Palaearctic shares with the Ethiopian Realm. These species play a more important role only in North Africa and in Arabia as well as in Macaronesia. In the remaining parts of the Palaearctic their share is slight and they are completely absent from the Arctic Zone.

REGIONAL DIVISION OF THE PALAEARCTIC

The basis of the regional division of the Palaearctic carried out with regard to the Macrolepidopteran fauna is the specific affinity of all the local faunas of this area. The faunas were recognized as related, after SZYMKIEWICZ (SZAFER, 1949), if their coefficient of affinity was higher than 50·0%. The table containing the coefficients of affinity calculated for all the 118 local faunas distinguished in this area was then rearranged into a diagram, in which the particular faunas were grouped according to the relations occurring between them (Table 5). This very diagram provides a detailed picture of the regional differentiation of the fauna under study.

Since some local faunas show a high coefficient of affinity for two or more outstanding groups, it was necessary to check carefully whether they were correctly positioned in the diagram. For this purpose the group value of elements of particular faunal provinces or regions in the definite fauna was calculated by the formula:

$$w = \frac{a}{a+b} \times 100$$

where w is the group value, a the sum of the coefficients of affinity of the fauna examined to all the local faunas of the given province (a) divided by the number of local faunas, and b the sum of the coefficients of affinity of the fauna examined to all the local faunas of the other province (b) divided by the number of local faunas.

(For example: The local fauna A has a high coefficient of affinity both to the faunas of the province B and to those of the province C. The sum of the coefficients of affinity of the fauna A with all the 10 local faunas of the province B as well as that with the 20 local faunas of the province C amounts to 500.

$$a = \frac{500}{10} = 50 \qquad w_a = \frac{50 \times 100}{50 + 25} = 66{\cdot}6$$

$$b = \frac{500}{20} = 25 \qquad w_b = \frac{25 \times 100}{50 + 25} = 33{\cdot}3$$

As may be seen, the fauna A, in spite of the high value of its coefficient of affinity with the province C, belongs to the province B, within which it is a transition zone to the province C).

The calculation of the group value permitted the classification of mixed faunas which constitute transition links to some other regional units between well-defined faunal complexes.

The arrangement of regional units obtained through an analysis of specific relationships into a hierarchic system making up the units of a higher order is a very difficult but essential task in studies of this type. Unluckily it was not always possible for the reasons discussed previously. Only the units standing highest in the hierarchy, characterized by entirely diverse types of faunas, could be distinguished. This permitted a relatively precise definition of the boundaries of the Palaearctic, naturally in so far as the *Macrolepidoptera* are concerned, because theoretically the boundaries for other groups of the animal kingdom may be different. The coefficient of specific affinity facilitates the distinction of provinces or regions but it does not provide sufficient material to determine interrelations between particular provinces. Supposing the fauna of the province A has no species in common with the faunas of the provinces B and C, but it shares 50% of genera with the province B and none at all with the province C. Judging only by the coefficient of specific affinity the faunas of these three provinces are equally alien to each other, though in reality the provinces A and B, unlike the province C, form a unit of a higher order, e.g., a subrealm. No such difficulties are encountered, if a province is divided into lower regional units, because the criterion of specific affinity reflects the existing resemblances and differences sufficiently well.

As a matter of fact the diagram constitutes the result of the present study, for it illustrates the regional differentiation of the Palaearctic *Macrolepidoptera* in an objective way. However, on account of its general handling of affinities it is not easy to make out. For this reason it became necessary to work the diagram, naturally after introducing some simplifications, into a map. This map (Fig. 10) shows only the essential outlines of the division of the Palae-

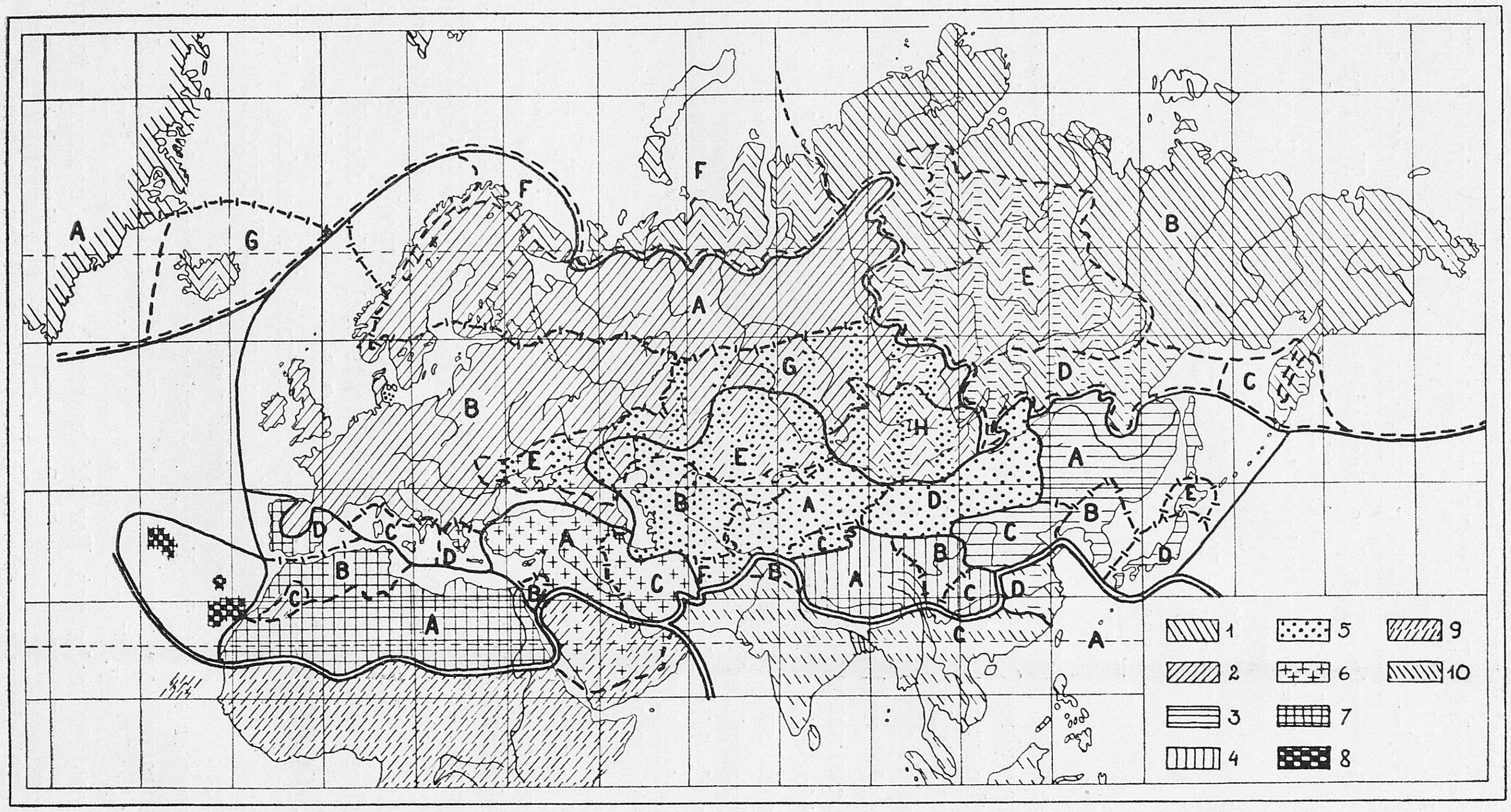

Fig. 10

arctic into units of a higher order, i. e., provinces, regions and transition zones of an indefinite order but not inferior to subregion. The establishing of lower subregional spatial units is possible only through a close examination of the faunas of particular regions, giving attention to faunal relationships and similarities as well as to chorology, history, etc., which goes beyond the scope of the present study.

On the basis of the close analysis of the distribution of the *Macrolepidoptera* and of relationships between particular Palaearctic faunas (sensu lato) this area can be divided into the following units:

- Holarctic Realm
  - Arctic Subrealm
    - Greenland Region
      - Iceland transition zone
    - Arctic Siberian Region
      - Kamchatka transition zone
      - Vitim-Aldan transition zone
      - Yakutsk transition zone
      - Gydan-Kanin transition zone
  - Palaearctic Subrealm
    - Europeo-West Siberian Province
      - Boreal Region
        - Arctic-Scandinavian transition zone
      - Europeo-Siberian Region
        - South Siberian transition zone
        - Altay-Sayan transition zone
      - North Mediterranean Region
        - Aegean transition zone
    - East Asiatic Province

Fig. 10. Zoogeographic regionalization of the Palaearctic based on the values of the coefficient of specific affinity of the Macrolepidopteran fauna: 1 — Arctic Subrealm: A — Greenland Region, B — Arctic Siberian Region, C — Kamchatka transition zone, D — Vitim-Aldan Transition zone, E — Yakutsk transition zone, F — Gydan-Kanin transition zone, G — Iceland transition zone. 2 — Europeo-West Siberian Province: A — Boreal Region, B — Europeo-Siberian Region, C — Northern Mediterranean Region, D — Aegean transition zone, E — Pontine transition zone, F — Arctic Scandinavian transition zone, G — Southern Siberian transition zone, H — Altai-Sayan transition zone. 3 — East Asiatic Province: A — Amur Region, B — Korean Region, C — Northern Chinese Region, D — Japanese Region, E — Ainus Region. 4 — Tibetan Province: A — Central Tibetan Region, B — Eastern Tibetan Region, C — Szechwan Region. 5 — Central Asiatic Region: A — Turanian Region, B — Aralo-Caspian Region, C — Altyn-Tag Region, D — Gobian Region, E — Kazakh transition zone, F — Afghan transition zone. 6 — West Asiatic Province: A — Asia Minor Region, B — Jordan Region, C — Iran Region. 7 — North African Province: A — Sahara Region, B — Mauritania Region, C — Atlas transition zone, D — Iberian transition zone. 8 — Macaronesian Province. 9 — Ethiopian Realm: A — Arabian transition zone. 10 — Oriental Realm: A — Formosan Region, B — Kashmir-Punjab Region? Province?, C — Sino-Burman Province, D — Central Chinese transition zone

      - Amur Region
      - Korean Region
      - North Chinese Region
      - Japanese Region
    - Tibetan Province
      - Central Tibetan Region
      - East Tibetan Region
      - Szechwan Region
    - Central Asiatic Province
      - Turanian Region
        - Afghan transition zone
      - Aralo-Caspian Region
        - Kazakh transition zone
      - Altyn Tagh Region
      - Gobi Region
    - West Asiatic Province
      - Asia Minor Region
      - Jordan Region
      - Iran Region
    - North African Province
      - Sahara Region
      - Mauritanian Region
        - Atlas transition zone
        - Iberian transition zone
    - Macaronesian Province
- Ethiopian Realm
        - Arabian transition zone
- Oriental Realm
    - Formosan Region
    - Kashmir-Punjab Province? Region?
    - Sino-Burman Province? Region?
      - Central Chinese transition zone

Arctic Subrealm

It embraces the whole far-northern zone of the Holarctic. In Eurasia the Arctic Subrealm includes the fauna of Arctic and alpine tundras and tundra-taiga transition zones (except Lapland), as well as a remarkable portion of the East Siberian taiga. It includes the faunas of Kamchatka, Greenland and Iceland, as well. The traditional Palaearctic part of this subrealm is differentiated distinctly into two virtually entirely indepen dent units. The first of them contains the faunas of Greenland and Iceland, the other embraces all the remaining faunas of the Eurasian portion of the

Arctic Subrealm. These two units probably belong to two different faunal provinces, but as the data from the American part of the subrealm are lacking, there are no grounds to treat them as higher regional units.

The number of Macrolepidopteran species in particular local faunas of this subrealm is very various, ranging from 3 species in Spitsbergen (because of this small number of species these islands have been left out in the present study) to 739 species in the Yablonovyy Range. The average number of Macrolepidopteran species in the fauna of a geobotanic unit amounts to 282. In respect of specific abundance, the Arctic Subrealm may be divided into three separate zones. The first of them includes the fauna of the both Arctic and alpine tundra and tundra-taiga transition area. The number of species in the particular faunas of this zone fluctuates between 36 (Iceland) and 97 (Chukchi-Anadyr geobotanic unit). The second zone is made up of the faunas of both highland and lowland larch taigas and forests of Kamchatka, in which Erman's birch *Betula Ermani* CHAM. is dominant. In this zone the average number of species falling to a local fauna is about 330. Finally, the third zone includes the faunas of highland larch forests of the southern taiga with a high proportion of Manchurian plant species. On the average 700 Macrolepidopteran species fall to a particular local fauna in this zone. Such a strong quantitative differentiation and its zonal arrangement suggest that the fauna of the larch taiga of East Siberia is related rather with the fauna occurring in the forests of North America than with the Arctic one. The more so as it does not seem very probable that the Arctic fauna of North America exceeds the analogous fauna in Eurasia in the number of species so much that more than 350 species of this fauna might occur also in East Siberia. It is more likely that at least a majority of these species are peculiar to the Nearctic Subrealm and not to the Arctic one. The solution of this problem would demand statistical-comparative studies of the fauna of whole North America. The classification of the Macrolepidopteran fauna of the larch taiga in the Arctic Subrealm is therefore only provisional and it indicates close relations between this fauna and North America.

The distinctive character of the Macrolepidopteran fauna of the subrealm under discussion is the high coefficient of affinity, which combines it with the fauna of the Nearctic in the wide sense of this word. The only exception is the fauna of Lapland, the relationship of which with the European-West Siberian Province is considerably closer than that with the Nearctic. The Arctic fauna shows also strong connexions with that occurring in the northern part of the East Asiatic Province and above all in the Amur drainage basin. The Arctic species appear there in fairly large numbers in the higher ranges of mountains (Bureye Mts., Sikhote Alin Range, mountains of Korea and Sakhalin). A relatively high degree of relationship exists also between the Arctic fauna and the Boreal Region of the European-West Siberian Province, and especially the fauna of the West Siberian taiga. In addition, numerous arctic species occur in the high parts of the Altai Mts., the Sayan Mts., and the mountains of North Mongolia. The connexions with other Palaearctic provinces are poor, the connecting elements being for the most part ubiquitous species, widely distributed all over the Palaearctic and even the Holarctic.

A. WAGNER (1845) was the first to recognize the Arctic Province as a separate province, which he called the Polar. In it he included also northern Scandinavia, the Central Ural, and, as in the present study, North-Eastern Asia. Later, the opinions, both on the independence of the Arctic Subrealm and on its boundaries, have undergone great changes. Most zoogeographers, recognizing the independence of this subrealm, confined it only to the tundra and the tundra-taiga transition zone of the Holarctic (ARLDT, 1907; PAGENSTECHER, 1897; MEISSENHEIMER, 1915; MARCUS, 1933; REINIG, 1937, and others). Other writers, e. g., HEILPRIN (1887) and DAHL (1921) united it together with the taiga fauna into the so-called Boreal Province. Finally, many zoogeographers, especially those in more recent times, cancelled this subrealm as an independent faunal unit. HOLDHAUS (1929) included it whole in the Euro-Siberian Subregion, whereas SCHILDER (1952, 1956) divided particular parts of the Arctic Zone among different provinces or regions of the Palaearctic. Though the southern boundary of this subrealm is still disputable, the tendencies to liquidate it should be categorically rejected. This subrealm is characterized by such a distinct fauna showing specific adaptations to hard living conditions, separate origin not quite explained yet, and the circumpolar type of ranges found for most of its species, that the union of this fauna with the Palearctic one is deprived of any grounds. A majority of the zoogeographers did not divide this subrealm into lower regional units and treated it as a homogeneous whole. Only occasionally, as e.g. in the work of DAHL (1921), the Nearctic part of this subrealm was opposed to the Palaearctic part. The Soviet zoogeographers, e.g., BOBRINSKY (1951) and GEPTNER (1945), distinguished three regions in the Palaearctic part: the Arctic European Region, from northern Scandinavia more or less to the Kara Gate, the Central Region, from the Kara Gate to the mouth of the Lena River, and the East Arctic Region, from the Lena to northern Kamchatka. In the opinion of these authors, the fauna of Greenland constitutes a separate region as well. On the whole, most zoogeographers agree to the fact that Greenland is the easternmost outpost of the Nearctic fauna. More recent studies (e. g. LINDROTH, 1957), however, show the existence of close relations binding this island to the Eurasian Arctic, at any rate in some groups of animals. Studies on the *Macrolepidoptera* do not corroborate this fact, but it may result from the nature of this group. On the other hand, the opinions on the zoogeographical membership of the fauna of Iceland are very divergent. Most of the authors include it in the Arctic Subrealm. Some of them, however, e.g. HETTNER (1935) and SCHILLER (1952, 1956), think that this fauna constitutes a part of the fauna of the Euro-Siberian Province. This opinion does not seem to be greatly convincing, though some data given by LINDROTH (1957) point clearly to the affinity of this fauna with the European one, which is to some degree confirmed also by the analysis of the Macrolepidopteran fauna of Iceland.

Since in their distribution the *Macrolepidoptera* depend upon the plant kingdom, which provides them both with food and with shelter, a discussion, however brief, of the regionalistic opinions of the phytogeographers and the emphasis laid on the differences and resemblances between the phytogeographic and lepidopterological regional divisions seem to be purposeful. Most of the phytogeographers, with the exception of DIELS (1929), who does not treat the Arctic Zone as a separate floral unit, agree as to the distinctness of the flora of the tundra and of the tundra-taiga transition zone. The only differences may be seen in the lines of demarcation. GOOD (1953) unites the floras of the Arctic Zone and the Subarctic Holarctic and marks out the southern boundary of this province so that it runs along the tract of the passage of the taiga into the tundra-taiga transition zone, except for Fennoscandia, where the spruce and birch forests of the Kola Peninsula and of Central Scandinavia have been included in the Arctic. In the Far East GOOD marks out the boundary of the Arctic Province across the northern part of the Koryak Range, and consequently the large area of tundra of northern Kamchatka, the Taygonos Peninsula and the Gydan (Kolyma) Range has not been included in this province by him. GOOD divided the Arctic Province into three regions: the Eurasian Region, the Greenland Region (with Iceland) and the Nearctic Region. HAYEK (1926) uses the name of the Arctic Subarea in a considerably narrower sense. He marks out its southern boundary between the proper tundra and the tundra-taiga transition zone, thus embracing this last zone in the Euro-Siberian area. The alpine tundra of East Siberia, according to him, belongs to this area as well. Similarly to GOOD, HAYEK divides the Arctic Subarea into three regions. KOMAROV (1934) agrees on the whole with HAYEK's opinion only that he divides the Arctic Zone of Eurasia not into three but into six regions: the Arctic Scandinavian, Arctic European, Novaya Zemlya, Arctic Siberian, Chukchi, and Anadyr regions. TOLMACHEV (1960) included both the tundra and the tundra-taiga transition zone in the Arctic Subarea and divided it into 26 separate floral regions. Of these regions 5 cover the vegetation of the islands in the northern Atlantic, 4 refer to the Nearctic part of the subarea under study, and 17 to its Eurasian part. In all the above-mentioned studies, unlike the geobotanic regionalistic ones, only the proper Arctic, i.e., excluding the alpine tundras of East Siberia, is treated as the Arctic area or subarea.

The following conclusions arise from a comparison of both floral and faunal regionalistic divisions of the Arctic discussed above with the division obtained from the analysis of the distribution of the Macrolepidopteran fauna:

1. The area in which the species common with North America (and so both circumpolar and Nearctic sensu stricto) predominate is remarkably larger than it has been assumed hitherto, because besides the tundra and the tundra-taiga transition zone it embraces the East Siberian larch taiga as well. This fact, eventually resulting in a great reduction of the Palaearctic area (no matter whether in favour of the Arctic or of the Nearctic), has not received proper attention in regionalistic studies as yet. The course of the north-eastern boundary of the Palaearctic should be checked for other groups of the animal kingdom,

as it may well be that the result obtained reflects only the specific nature of the group being examined.

2. Lapland, regarded as an integral part of the Arctic Subrealm both by phyto- and zoogeographers, has a Macrolepidopteran fauna referring very strongly to the European fauna, whereas it is weakly connected with the Arctic fauna of America. The supposition arises that this fauna, historically the youngest of the faunas of the Arctic Subrealm, has not developed fully yet. On the one hand, the influence of the Gulf Stream facilitates the acclimatization of the more enduring European species; on the other hand, typical circumpolar species have not managed to colonize this area yet (similarly to, e.g., the spruce in central Scandinavia, whose progress to the west can still be observed).

3. The Macrolepidopteran fauna of the Atlantic islands of the Arctic Zone forms a separate whole, differing remarkably from the fauna occurring in Arctic Eurasia. It is, however, evidently related with the Arctic fauna of America. It may be supposed that both Greenland and Iceland were colonized by the Macrolepidopteran species coming from Arctic America and not those of European Arctic origin as suggested by PAGENSTECHER (1897, 1909) or WARNECKE (1958), not to mention other authors. The European Arctic as well as the Boreal species came to these islands a relatively short time ago, most likely with man.

Palaearctic Subrealm

It embraces all the remaining provinces and regions established on the basis of the statistical analysis of the affinity of the Macrolepidopteran faunas. The species of the families *Endromididae* and *Lemoniidae*, endemic in the Palaearctic, occur in all these provinces. Only the species of the third endemic family, the *Somabrachidae*, appear exclusively in its southern part. The members of these families are unknown from both the Arctic Subrealm and the faunal realms bordering upon the Palaearctic. The Palaearctic Subrealm occupies a large area, which is greatly differentiated, and the faunas of its particular parts show great differences as well. Consequently, it seems reasonable to discuss each province separately rather than to offer the general characteristics of the whole Palaearctic.

Europeo-West Siberian Province. This province occupies nearly whole Europe along with its islands in the Mediterranean Sea, the Caucasus Mts. and western Siberia as far eastwards as Lake Baykal and Central Mongolia. On the north and east it neighbours on the Arctic Subrealm, on the south on the North African, West Asiatic, and Central Asiatic Provinces. Despite its fairly remarkable uniformity the fauna of this province shows apparent regional differentiation. Besides, the faunas of some border territories have sometimes a considerable share of species proper to the neighbouring provinces, forming distinct transition zones. On the basis of differences in the faunal composition this province has been divided into three regions, within which 6 areas of transitional faunas have been distinguished.

The Europeo-West Siberian Province embraces faunas occurring in diverse environments from the tundra of Lapland through both coniferous and deciduous forests to the Mediterranean scrubs and evergreen woods as well as the South European and West Siberian steppes. Though this province as a whole does not show any apparent connexions with the nature of the plant cover, the particular regions and transition zones are visibly associated with definite types of vegetation.

The Boreal Region includes the fauna of the European and West Siberian taiga, both the spruce forest with *Picea excelsa* L. or, in the east, *Picea obovata* Ml., and the fir or the Cembra pine forests.

The European Region embraces the faunas of coniferous forests of the European type (with pines and a mountainous variety of spruce dominant in them), mixed and deciduous forests, parklands and fertile Black-Sea steppes, the Macrolepidopteran fauna of which constitutes a transition zone at the level of subregion. The faunas of the South Siberian forests and parklands of the nature of a highland taiga or birch-aspen woods or Ural oak woods also come under this category.

The North Mediterranean Region contains the faunas of natural evergreen woods and their modifications resulting from human activity (maquis, garigue, phrygana shrub and shiblyak brush).

On the whole, the fauna of this province is rich in species, though their number in particular local faunas varies considerably. The fauna of Lapland is the poorest (155 species), whereas the largest number of species, 1438, occur in the Alps as well as in the Panonian Lowlands, from which 1296 Macrolepidopteran species have been recorded. An average of 880 species falls to a particular fauna of this region. A clear-cut quantitative differentiation of the faunas of individual regions is noticeable. The Boreal Region, whose faunas consist on the average of about 500 species each, is the poorest. Even the transition zones adjacent to this region have a remarkably larger number of species. This is only natural, because the differentiation of the territory and, consequently, of its environments is much greater in these zones and, besides, the ranges of species of different provinces overlap here, e.g., in the Altai Mts. or the Sayan Mts., which also contributes to the general richness of these faunas. The European Region with its average of 1000 species in a fauna is the richest. Also here the fairly great differentiation of the territory as regards both its flora and climate seems to be responsible for this state. It may be readily shown that the richest faunas in this region are those of the mountains and highlands lying at some distance from the range of the Pleistocene glaciations. The number of species recorded from the Pontine transition zone is somewhat smaller than in the neighbouring areas and, above all, than in the Balkan Peninsula, probably because the scenery of this zone is poorly differentiated. The Caucasian fauna, too, belongs to the European Region, and it exhibits a likeness to the faunas of the Balkan Peninsula. The North Mediterranean Region is much poorer than the European in so far as number of species is concerned. In this region the Macrolepidopteran fauna consists on the average of a little more than 800 species. Though its living conditions might seem far better than those in the European Region, both the isolation of its particular areas and the nearly complete destruction of the original vegetation and its replacement by shrub communities of various types explain the specific poverty of the there existing faunas in a satisfactory manner.

The number of endemic species (in the narrow sense of the word) is small in the particular faunas of the Europeo-West Siberian Province. In the northern part of the province, which was once under a strong influence of glaciations, the number of endemic species is very small or they are wanting at all. Besides they are mostly very small species of the family *Psychidae*. On the other hand, in the southern part and in the mountains the species with small ranges are relatively numerous. The faunas of the Boreal Region have hardly any endemic species (these are the most numerous in the fauna of the Central Ural, which has 3 of them). Their number in the transition zones adjacent to the Boreal Region is much larger. The endemic species are for the most part associated with mountains (the Altai Mts. — 22 species, the Sayans — 30), but their number is also large in the steppes of the southern Ural and in the Mugodzhar Mts. (12 species). In the European Region the endemic species are fairly numerous only in the mountains situated at a distance from the front of the glacier. There are 57 endemic species in the Alps, 25 in the Apennines, and 17 in the Pyrenees, but only 6 in the Carpathians and 2 in the mountains of Central Germany. Finally, unlike the plants and, perhaps, other animal groups, the Macrolepidopteran fauna of the Panonian steppes contains only a very small number of endemic species, namely, hardly 7. The North Mediterranean Region, probably because of the isolation of particular islands, has fairly many species with narrow ranges. The largest number of endemic species, 32 in all, occurs in the fauna of the islands of the Aegean Sea, especially that of Crete. Comparatively few endemic species, only 16, have been recorded from Sardinia. This may result from the comparatively poor knowledge of the fauna of this island.

The influence of the Europeo-West Siberian fauna can be observed in many neighbouring regions belonging to other zoogeographic provinces. On the other hand, the species of the neighbouring areas also appear in fairly large numbers in some faunas of the province in question. All in all, the fauna of the Europeo-West Siberian Province has the largest number of species in common with the Central Asiatic Province (on the average 30%) and the East Asiatic Province (on the average 28%), though it does not border on the last one. It has considerably fewer, but all the same fairly numerous (about 23%) species in common with the West Asiatic Province. However, its affinity with the North African, Macaronesian and Tibetan Provinces is very remote.

This is not the case with the particular regions and especially with the transition zones. The share of species alien from them is sometimes very large.

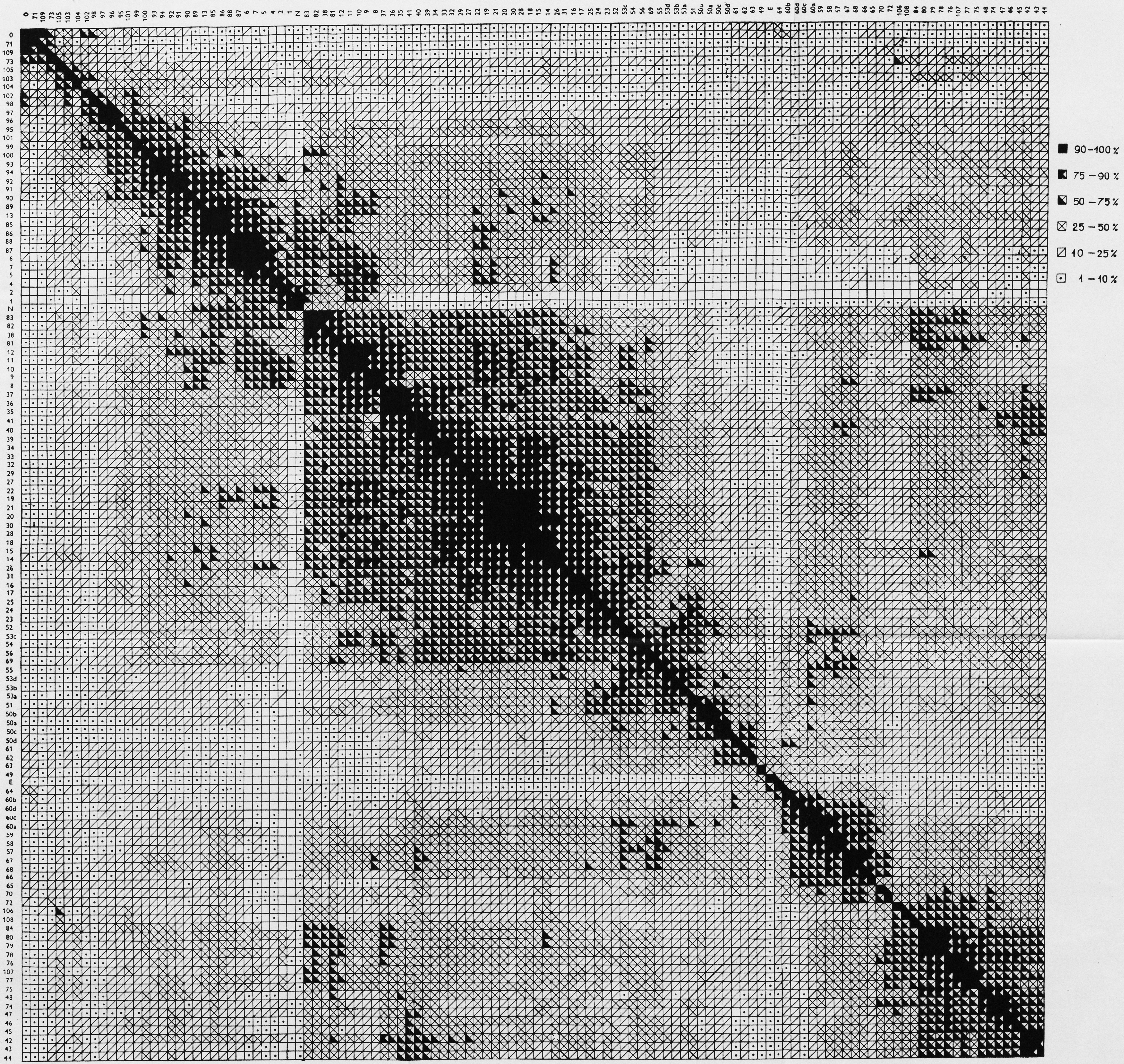

Table 5. Diagram to illustrate the relationship of the distinguished local faunas. The explanation of figures is given by fig. 1

There is a large number of such transitional faunas within the Europeo-West Siberian Province. The transitional fauna of Lapland has already been discussed in this paper. The South Siberian transition zone is characterized by a large admixture of Central Asiatic elements. The group value of these elements in the fauna of the zone under discussion amounts to 24—40%. This zone combines the faunas of the Ural and South Siberian parklands and flowering-plant-dominant steppes.

The Altai-Sayan transition zone, which besides the named ranges embraces also the mountains of northern and central Mongolia and the southern part of the drainage basin of the River Angara, constitutes one of the most interesting areas of the Palaearctic in so far as its Macrolepidopteran fauna is concerned, for it is made up of elements derived from various provinces. The Europeo-West Siberian elements have the highest group value for all the local faunas of this territory (about 29%). The Arctic elements have a group value of about 26%, the Central Asiatic of 24%, and the East Asiatic ones of about 16%. As can be seen, the differences between the shares of particular elements are not great there, and the dominance of the Europeo-West Siberian elements has only a relative value.

The Pontine transition zone, including the faunas of the Black Sea steppes, is a conglomerate of Europeo-West Siberian species with their group value averaging 43%, West Asiatic species with a value of 27%, and Central Asiatic ones, which have an average group value of about 30% in this zone. The diversity of the fauna of the Pontine zone can be best explained by the history of its origin and formation. The dominance of the Europeo-West Siberian elements, in some sense, corroborates TALYEV's hypothesis (1904) on the secondary nature of the steppes of these areas.

The Aegean transition zone covers southern Greece and the islands of the Aegean Sea, including Crete. In this zone the group value of the Europeo-West Siberian and West Asiatic elements is nearly equal and it amounts to 51·5% and 48·5% respectively. The large contribution of the West Asiatic elements, especially to the fauna of the Aegean Islands, seems to have been caused by historical factors (a comparatively recent isolation of these islands from the continent) and, to a considerably lower degree, by the secondary assimilation of the plant cover of the islands to that of the western coast of Asia Minor.

The opinions, held up to the present, on the regional division of faunas in the moderate zone of Eurasia diviate conspicuously from those presented in this paper. In most cases the differences relate to two problems: the homo- or heterogeneity of the faunas of the forest zone or the so-called Europeo-Siberian zone and the manners of zoogeographical approach to the faunas of the Mediterranean coast.

The problem of the homo- or heterogeneity of the so-called Europeo-Siberian fauna has been frequently discussed. Both in the studies of the nineteenth century (WAGNER, 1845; SCHMARDA, 1853; HEILPRIN, 1887, and others) and in those of the first years of the present century (ARLDT, 1907; PAGENSTECHER,

1909) the common opinion was that the faunas of the western part of the forest zone were distinct from those of the eastern part, i.e. the European faunas from the East Asiatic ones. A variety of boundaries marked out for the European part of this zone was brought about by the application of different methods and due to the basing of divisions on various animal groups. The vast majority of these zoogeographers assumed the Ural Mts. as the eastern boundary of the European Province. West Siberia was included (e.g. by SCHMARDA) in the Arctic Province or it was combined with East Siberia into a distinct regional unit. Only MURRAY, joined the fauna of West Siberia (including the Altai and Sayans) together with the European fauna into a single, Europeo-Asiatic, region in his study of 1866 on the geographic distribution of mammals. Of the most recent zoogeographic studies the regional division of the zone under discussion made by SCHILDER (1952, 1956) distinguishes itself by originality. SCHILDER combines the faunas of West Europe, the Mediterranean, and West Asia into one unit, the West Palaearctic Province, in opposition to the rest of the Palaearctic.

In Central Europe the boundary of this province traverses Poland, crosses the Carpathians and then turns abruptly to the east, towards the Black Sea, including Bulgaria in the West Palaearctic but not Romania. The faunas of the Baltic countries, Ukraine, and Crimea belong naturally to the East Palaearctic Province (extending as far as the Chukchi Penin. and Sakhalin), whereas those of the Caucasus Mts. and Iran are included in the western part. Before World War II the prevalent opinion, advocated chiefly by HOLDHAUS (1929) in the West and by KUZNETSOV (1950) in the East, was that the faunas of the forest zone of Eurasia are homogeneous. HOLDHAUS combined the faunas of nearly whole Europe and Siberia (not excepting the Arctic Zone) into one subregion — the Europeo-Siberian. Similar conceptions can be found in the studies by HETTNER (1935), AMSEL (1933) and KOZHANCHIKOV (1937). Two factors, above all, influenced the establishment of this opinion: 1. The physiognomic similarity of the plant cover in the eastern and western parts of this zone and, consequently, the similarity of ecological conditions; 2. The occurrence of numerous species of animals both in the area of the whole zone and in its eastern and western parts with a disjunction in Central Siberia (the so-called Europeo-Manchurian elements).

At first sight the European and the East Siberian vegetations really resemble each other. Physiognomically related coniferous, mixed and deciduous forests occur in both these territories. However, the number of plant species, especially that of trees, which they have in common is very small. According to these considerations the whole forest area of the Nearctic should be included in the Europeo-Siberian Subregion as well, though it has not a tree species in common with, e. g., Europe.

The number of the Macrolepidopteran species occurring both in Europe and in East Asia is in fact fairly large and amounts to about 800. It consists of widely distributed ubiquitous species, which constitute a connective element of all

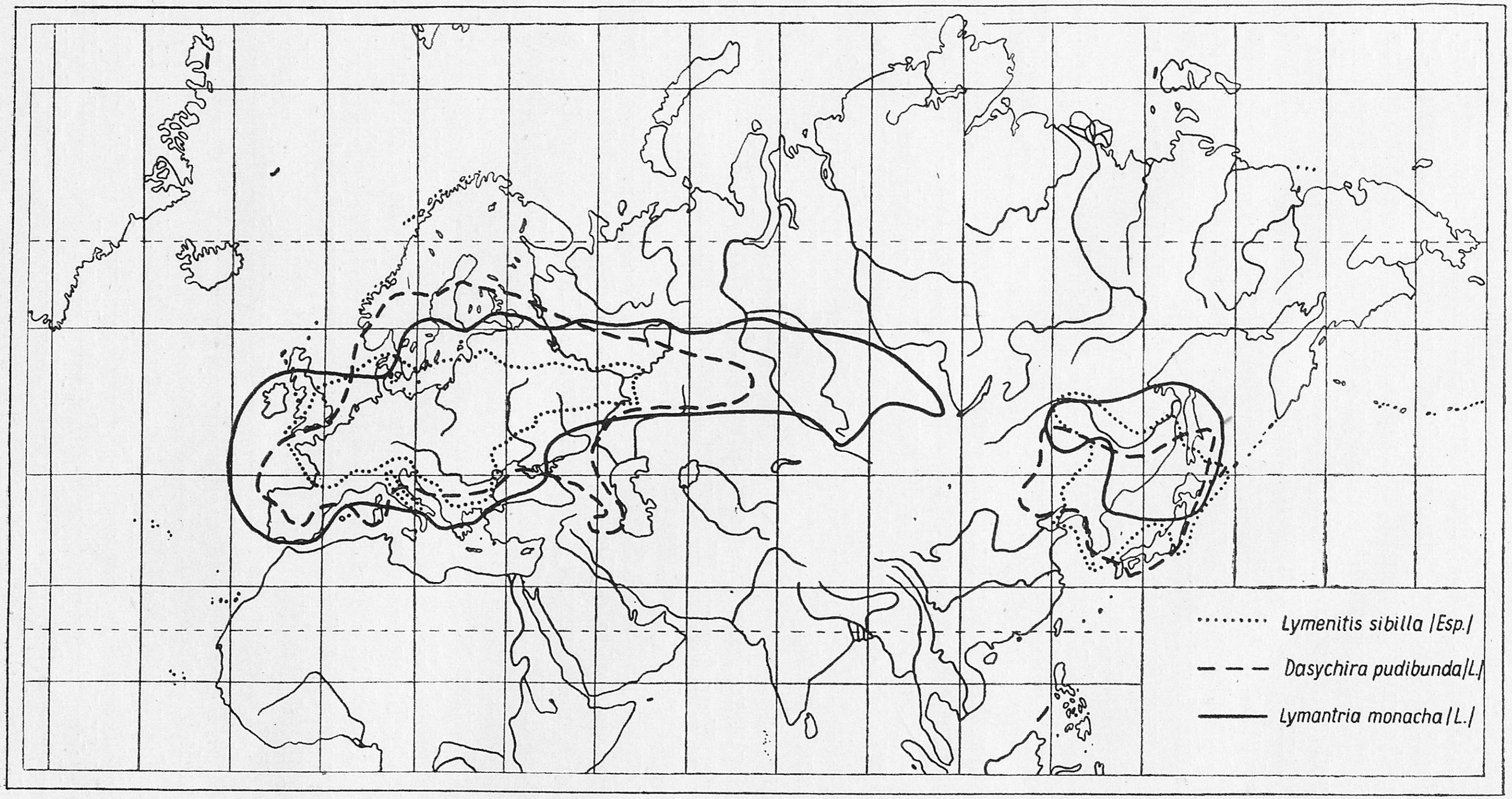

Fig. 11. Examples of the „Europeo-Manchurian“ type of ranges among the *Macrolepidoptera*.

the faunas of the Palaearctic, the species pertinent to the whole forest zone of Eurasia and, finally the so-called Europeo-Manchurian elements. Fig. 11 shows an example of a range of this type. Of these groups the Europeo-Manchurian species are the most numerous, their number being about 500, and are followed by the ubiquitous forms with their about 200 species. The species of the Europeo-Asiatic forest zone come last and their number is somewhat over 130. In the particular faunas, both European and East Asiatic ones, the share of the Europeo-Manchurian species does not exceed 20—35%. It is obvious that the existence of species with a range of this type indicates the common origin of these faunas, but it does not provide any objective grounds to combine the territories in question into a whole. A bias towards this type of a range must have brought about the fallacious conclusions.

The opinions of phytogeographers on the regionalistic division of this zone come near to each other. The vast majority of the phytogeographers recognize the floral homogeneity of the whole forest zone of Eurasia. This opinion results, above all, from the application of the geobotanic criterion in floral regionalization, as can be well seen from the studies of ENGLER (1919), DIELS (1929), and HAYEK (1926). GOOD (1953) divided the Europeo-Siberian Province into the European and the Asiatic Subprovinces. The first of them, reaching eastwards to the Ural, was divided into 7 regions: Western Europe, Central Europe, Scandinavia, Russia, Danube Basin, European Alps, and Caucasus. In the other subprovince, however, covering whole Siberia including Kamchatka, GOOD distinguished only 4 regions: Western Siberia, Altai-Transbaikalia, North-Eastern Siberia, and Kamchatka. The vegetiation of Manchuria and South-Eastern Siberia was classified by him in the Sino-Japanese Province and the South Russian steppes in the Central Asiatic Province. On the other hand, GOOD includes the vegetation of Georgia, Armenia, and Azerbaydzhan in the Caucasian Region. In his working division for the „Floras of the U. S. S. R.“ KOMAROV (1934) divided the forest zone of the U. S. S. R. into 4 provinces: The European Province (with 15 regions), the Caucasus (6 regions), Western Siberia (4 regions), Eastern Siberia (4 regions), and the Far East (6 regions). KOMAROV marked out the boundary of the European Province (embracing also the vegetation of the Black Sea steppes) more or less along the Ural, that of Western Siberia along the River Yenisey and the eastern slopes of the Altai Mts. The western boundary of Eastern Siberia ran approximately along the Stanovoy Range and the Gydan (Kolyma) Range so that the vegetation of Kamchatka, the Okhotsk Sea coast, the Amur drainage basin, Sakhalin and Manchuria was embraced in the Far East Province. The Caucasian Province, as in GOOD'S division, includes also whole Transcaucasia.

Finally, SOCHAVA (1953) divided the zone of the U. S. S. R. into 11 provinces: West Russian, East Russian, Ural, West Siberian, Altai-Sayan, Central Siberian, Verkhoyansk-Kolyma, East Siberian, Daurian-Mongolian, Amur-Primorsk, and North Pacific. Also in this case the division is based on geobotanic distinctions and not on floral ones.

To sum up, it may be stated that there is a distinct divergence between the opinions so far held by both zoogeographers and phytogeographers and the result obtained in the present study. The opinions on the faunal homogeneity of the forest zone of Eurasia held up to the present though questioned by some systematicians (Belishev, 1958; Kurentsov, 949, 1961) have not been confirmed on the material used in this study. It would be interesting to find whether this distinct division occurs also for the faunas of other groups of animals. In addition, it would be instructive to examine the complex of questions concerning the socalled Europeo-Manchurian elements, since the publications issued so far, both zoological (Hormuzaki, 1929, 1930; Reinig, 1937, 1950; Warnecke, 1958; Bartenef, 1933, 1934, and Berg, 1947) and phytogeographical (Wulf, 1935, 1944, and others), treat it rather vaguely. The explanation of this problem may greatly contribute to the deepening of our knowledge of the history of formation of the faunas and the phylogeny of particular systematic groups.

Another equally controversial problem is that of the homogeneity of the Mediterranean fauna and of the boundaries within which this fauna occurs.

A perfunctory survey of the results obtained will suffice to see the diversity of opinions of different authors on this matter. A great majority of both older and contemporary zoogeographers agree as to the faunal homogeneity of the Mediterranean area, but the boundaries of this zoogeographic unit marked out by them are not uniform. In this area Schmarda (1853) included the faunas of the whole Iberian Peninsula, the Apennine Peninsula, North Africa and West Asia as far eastwards as the Sind Desert. Pagenstecher (1909) and Arldt (1907) proceeded similarly and, in addition, they included the fauna of the whole Balkan Peninsula. Holdhaus (1929) follows them in respect of the range of the Mediterranean but he shuts out the northern part of the Iberian Peninsula. Finally, Amsel (1933) extends the Mediterranean area over a separate subarea, which is composed of the whole coast of the Black Sea, the eastern part of the Balkans, the northern part of Asia Minor, as well as the southern Ukraine including the Crimea. Hettner (1935) confines the Mediterranean area within considerably narrower limits. Although he retains the faunal unity of the coast of the Mediterranean Sea, he distinguishes a separate province for the North African-South Asiatic desert fauna of the Sahara, Arabia and southern Iran. He erects a distinct province, Macaronesia, for the faunas of the Azores, Madeira, the Canary Islands and the Cape Verde Islands. Kozhanchikov (1937) confines the Mediterranean Province to the faunas of South Europe and Asia Minor (with the southern Crimea) alone. He unites the faunas of North Africa, Arabia and Iran with that of central Asia into the Turanian-African Province. The division of Kozhanchikov is, in principle, based on the studies of Kuznetsov (1921) and Semyonov Tian-Shansky (1936), from which he differs only in details.

The views of phytogeographers do not generally deviate from those presented above. Engler (1919) treated the Mediterranean area pretty widely, embracing both the Macaronesian islands (as a distinct subarea) and the northern and western coasts of the Black Sea in it. He divides this territory into 6 provinces: the South-Western (including Morocco and the southern part of the Iberian Peninsula), Iberian, Liguro-Tyrrhenian, Central Mediteranean, South Mediterranean, and Armeno-Iran. DIELS (1929) reckons the Macaronesian, Saharan, West Asiatic and even Central Asiatic floras in the floral Mediterranean area as well. SZAFER (1949) raised this area, within the boundaries defined by DIELS, to the rank of a distinct floral realm. HAYEK (1926), however, regards only the floras of the coast as the Mediterranean Subrealm. Similarly, WALTER (1955) numbers only the vegetation of the coasts of the Mediterranean and Black Sea in the Mediterranean Province. Both these authors unite the floras of the Sahara, the West Asiatic deserts, Iran, and Baluchistan into a separate province, the Saharo-Sind Province. On the other hand, they include the vegetation of Turkey, Syria, Kurdistan, and northern Iran in the Central Asiatic Province. GOOD (1953) marks out the boundaries of the Mediterranean Province similarly to those defined by HAYEK and WALTER, and he divides this province into 4 regions: Lusitano-West Mediterranean, East Mediterranean, Morocco-Tunisian, and Libyo-Syrio-Egyptian. Interesting opinions have been put forward by POPOV (1927, 1963). He distinguished the area of the old Thetis's Basin as a distinct floral „dominion“, that is to say, he treated it as being on a par with the Holarctic or the Palaeotropic. In this realm, in addition to the coast of the Mediterranean Sea, he reckoned the Sahara, Arabia, Ethiopia (Abyssinia), western and central Asia. Originally, he included the Eurasian steppes in this realm as well, but then he treated them as a steppe province within the Holarctic. POPOV divided the Old-Mediterranean Realm into 5 provinces: the Mongolian, Iran, West Mediterranean, and African. LAVRENKO (1960) adopted POPOV's opinions in general outlines, but he degraded this area to the rank of a subrealm belonging to the Holarctic. He divided this subrealm into 3 areas: the Saharo-Gobian desert region, the Eurasian steppe region, and the Mediterranean. EIG (1931), basing on the studies of GRIESEBACH (1884) and DRUDE (1890), applied the following division of the Mediterranean Province: the Saharo-Sindian Region of the deserts and semi-deserts of northern Africa and western Asia, the Irano-Turanian Region embracing the vegetation of deserts and semi-deserts of Central Asia and south-eastern Europe, and the Mediterranean Region covering the xerophilous floras of the coasts of the Mediterranean Sea. Finally, he reckoned the vegetation of the Apennines and the northern part of the Iberian peninsula in the Europeo-Siberian Province, and that of the coasts of the Black Sea and of the Arabian Peninsula in the Sudano-Deccanian Region, which itself belongs to the Palaeotropic. WILHELM (1937), in his study devoted to the problem of differentiation of the vegetation of the Mediterranean coasts, presents the following division of this area: 1. the Canary Province, 2. the Mauritano-Iberian Province, 3. the West Mediterranean Province (containing 6 regions), 4. the Adriatic Province (2 regions), 5. the North-Eastern Mediterranean Province (3 regions), 6. the South-Eastern Province (2 regions), and 7. the Pontine Province (2 regions).

Table 6

Types of ranges expressed as percentages of the total flora

Types / Coasts	Omni-mediterran.	West Mediterranean	East Mediterranean	Europeo-Sib.-Mediterr.	Irano-Tur.-Mediterr.	Mauritanian	Africo-Oriental	Pontine	Endemic, and polychorous species
Southern Spain	22	15	—	18	9	6	9	—	21
Southern France	18	20	—	33	12	—	1	1	15
Corsica	21	18	—	28	11	—	2	—	20
Sardinia	31	18	—	19	13	—	2	—	17
Western Italy	26	25	—	28	7	—	1	—	13
Sicily	31	16	4	21	7	—	8	—	13
Dalmatia	28	10	2	28	14	—	—	—	18
Greece	26	7	16	26	10	—	2	1	12
Crete	23	6	18	25	8	—	4	—	16
Bulgaria	2	2	3	38	6	—	—	21	26
Crimea	—	—	2	33	7	—	—	34	24
Abchazia	4	—	—	38	17	—	—	23	18
Pontus	13	—	5	33	12	—	—	14	23
Cilicia	20	5	17	24	12	—	2	4	16
Cyprus	21	—	24	28	15	—	4	—	8
Syria	24	—	22	33	8	—	5	—	8
Egypt	19	1	18	29	4	—	18	—	11
Lybia	15	15	5	22	10	—	24	—	9
Tunesia	21	18	2	20	6	4	18	—	11
Algeria	21	23	1	23	9	5	5	—	9
Morocco	25	10	—	24	8	10	9	—	14
Canary Is.	16	8	—	17	3	8	18	—	30

The theoretical, both zoogeographic and phytogeographic, bases of these divisions are very various. Most of the zoogeographers adopted the occurrence of these or other guiding groups as a criterion for distinction of regional units or they based themselves on phytogeographical studies, assuming that the various ecological conditions must indicate the distinctness of the fauna. In Kozhanchikov's opinion, the genus *Epilecta* Hb. is such a guiding group for the Mediterranean Province, and for the Turano-African Province the genera *Estimaja* Ev., *Protaxernis* Kozh., *Ammogrotis* Sm. and *Dichagyris* Brs., of which 81 species occur all over the Palaearctic and only 50 in the Turano-African Province. The abundance of the Macrolepidopteran faunas classified by Kozhanchikov in this province is on the average about 700 species. Thus, the guiding group, on which he based his regional division, forms about 14% of the total of the *Macrolepidoptera* at most, that is, if all the guiding species occur together in the given fauna. This fact is a good example showing the exiguity of the bases on which generalizations are sometimes founded. Practically everything can be proved by the method of guiding groups, even that the flora of Kamchatka belongs to the Mediterranean Province. For this reason the discussion with those who plead these opinions is virtually impossible.

One of the striking results of the present study is the splitting of the Mediterranean fauna, which has hitherto been considered by most zoogeographers to be homogeneous. This result is, however, corroborated by the data given in many zoo- and phytogeographic studies, although the authors of these studies fall in with the homogeneity of this area.

Eig (1931) writes in his work on the flora of Palestine that only 15% of the plants occurring there have ranges covering the whole Mediterranaean area, 2·8% occur, in addition to Palestine, also in Mauritania, and 4·8% on the northern coasts of the Mediterranean Sea. Similarly, Amsel (1933), studying the Macrolepidopteran fauna of Palestine, found that the species occurring all over the Mediterranean form only about 20% and the Mauritanian species hardly 2·5%.

Comparing the vegetation of the sea coasts of the Mediteranean Province in the wide sense of the word in respect of their types of ranges, Wilhelm (1937) offers the data which are presented in Table 6.

A cursory survey of this table suffices to determine the existence of the evident differentiation of the Mediterranean flora, nearly completely conformable to the results obtained from the analysis of the distribution of the Macrolepidopteran fauna. The floras of the northern coasts of the Mediterranean Sea with an abundant share of West Mediterranean elements, those of the eastern coasts with East Mediterranean species and of the southern coasts with numerous both West Mediterranean and Mauritanian elements are evidently distinct. The flora of the coasts of the Black Sea differs so much in its nature from the Mediterranean flora that the combination of these two floras into a phytogeographic province seems to be a misunderstanding.

In my opinion, the correspondence of the results obtained from the faunistic analysis of these territories and those from the floral analysis carried out by different methods and based on different criteria confirms the purposefulness of the division of the Mediterranean area into a number of distinct provinces sufficiently clearly.

The East Asiatic Province. This province contains the Macrolepidopteran faunas of the Far East, i.e., those of Manchuria, the Amur drainage basin, Korea, North and Central China, Japan, Sakhalin, and the Kuril Islands. The fauna of this province is greatly differentiated. The specific composition of the Macrolepidoptera varies from one geobotanic unit to another so that virtually most of them should be treated as distinst faunal provinces. However, such division would be premature, because these faunas are not all known well enough. It seems more purposeful to combine them into one province both because of their common origin and history and on account of similar environmental conditions in which they occur. The influence of the oriental fauna, evidently marked at places, is also an element uniting them. The East Asiatic Province borders upon the Arctic Subrealm on the north, the Central Asiatic and Tibetan Provinces on the west and the Oriental Realm, or rather the Palaearctic-Oriental transition zone of central and eastern China on the south.

Five regions (perhaps of the rank of subprovinces) can be distinguished within the East Asiatic Province: 1. the Amur Region, embracing the faunas of the Amur drainage basin, Manchuria, the Ussuriisk land, Sakhalin and the Kurils; 2. the North China Region, covering, more or less exactly, the drainage basin of the River Hwang; 3. the Japan Region, including the faunas of the islands: Honshu, Kyushu and Shikoku; 4. the Ainus Region, containing only the Macrolepidopteran fauna of Hokkaido and 5. the Korean Region with the faunas of Korea and Kirin.

The vegetation of this province, formerly differentiated, has now been modified greatly by man, especially so in its southern part. Generally speaking, the boundaries of the province coincide more or less exactly with the ranges of the mixed and deciduous forests of the Far East. In the northern part of the province, above all in the mountains, large complexes of the East Siberian taiga and, in the higher zone, of the alpine tundraw ith dwarfish stone pines and Rhododendrons, have been preserved. In the Japan islands, mostly in the southern part, there are also some evergreen forests. The large steppe areas which covered the eastern part of the province in the past have been turned nearly entirely into cultivated fields.

The Macrolepidopteran fauna of the East Asiatic Province abounds in species. The smallest number of species, only 142, were found on the Kurils. This number should be treated with all reserve, because these islands are not well explored as far as their fauna is concerned. On the other hand, the largest number of the *Macrolepidoptera* was recorded from Honshu, where a single geobotanic unit has an average of about 1100 species and thus more than any other province of the Palaearctic. The average abundance of faunas in particular regions is almost the same. Only the Japanese Region is richer in species.

The distinctive feature of the Macrolepidopteran fauna of this province is a very large number of local species, which often possess very small ranges. Such species occur frequently in a single gorge or on a slope of a hill. All in all there are 125 endemic species known from the fauna of the Amur Region, 57 from the Korean Region, 55 from the North Chinese Region, 96 from the Ainus Region and 418 from the Japanese Region. Taking into account the whole Japanese archipelago (with the exception of the oriental Ryuku Islands) there are 608 Macrolepidopteran species living exclusively on these islands, which makes about 20% of the total fauna. The large abundance of endemic species is one of the causes of the relatively low value of affinities between particular faunas of this province.

Outside the boundaries of the province the East Asiatic Macrolepidoptera occur fairly abundantly on the southern slopes of the Yablonovyy and Stanovoy Ranges and in Central China, constituting a transition zone between the faunas of the East Asiatic Province, chiefly of northern China and Korea, and the Oriental Realm. Since the group value of the East Asiatic elements is not very high in the fauna of Central China (37%), this area should be counted in the Oriental Realm.

The East Asiatic Province was distinguished under various names by almost all zoogeographers. Nevertheless, the boundaries marked out for this unit did not coincide. The faunas of central and southern China, Szechwan and eastern Tibet were very often included in it as well (Figs. 1—10). Nearly all zoogeographers, however, have placed the Kurils outside this province. Some specialists, such as HOLDHAUS (1929) and PAGENSTECHER (1909), joined the fauna of the Amur drainage basin, the Ussuriisk region and Sakhalin to the Europeo-Siberian fauna and not to the East Asiatic or the so-called Manchurian one. The Russian zoogeographers treated this province widely, extending it not only over the Amur fauna but also over those of Mongolia and nearly whole China including Yunnan and Hainan. In the Palaearctic part of Asia SUSHKIN (1925) distinguished the so-called Asiatic-Alpine faunistic area and divided it into four provinces: the Mongolo-Tibetan, the Afghano-Turkestan, the Indo-Baluchistan, and the Sino-Japanese Provinces. He regarded the last-named province as the oldest and original part of the Palaearctic, the fauna of which has developed without disturbances since the end of the Mesozoic era. In his study on the geographic differentiation of the *Macrolepidoptera* KUZNETSOV (1929) considered the Manchurian Province within Wallace's boundaries and quartered it into the South Chinese, Central Chinese, Sino-Japanese and Amur Subprovinces. SEMYONOV TIAN-SHANSKY (1936) marked out three independent provinces: the Manchurian, Korean and Japanese. He extended the first of them also over the fauna of central China. Finally, in his monograph on the Far East KURENTSOV (1961) offers the regional division of this area on the basis of characteristic types of fauna. As a fauna type KURENTSOV takes an animal complex which in a definite area has ecologically similar conditions and has taken rise in consequence of general palaeogeographic changes. In the further part of his study KURENTSOV based himself evidently on geobotanic regionalization, establishing fauna types on the basis of environments. As a result, the regionalistic division offered by this author resembles the vicious circle, because he marked out a region on the basis of a fauna type, which type again has become distinctive by living in this region (e.g., the characteristic type of fauna of the Aldan Province, embracing a thin larch taiga, is the Angara type, the essential character of which is its occurrence in the larch taiga).

Phytogeographers rather agree in their opinions on the distinctness and range of the East Asiatic flora. They distinguish the vegetation of this part of the Palaearctic to form a separate phytogeographic subrealm, the co-called Orasiaticum. DIELS (1929) and ENGLER (1919) determine the southern boundary of this subrealm approximately along the River Yangtze, including also the flora of eastern Tibet in the Orasiaticum. However, HAYEK (1926) as well as GOOD (1953) and, out of the zoogeographers, REINIG (1937) extend the Orasiaticum over nearly whole southern China, the mountains of the Indo-Chinese Peninsula, Sikkim and the Himalaya Mts. GOOD divides this area, called by him the Sino-Japanese Province into 1. Manchuria and South-Eastern Siberia, 2. North Japan and South Sakhalin, 3. Korea and South Japan, 4. North China, 5. Central China and 6. Sino-Himalayan-Tibetan mountains. ALEKHIN (1951) divides the Sino-Japanese Province into five „floras“: the Manchurian (embracing, in addition to Manchuria proper, the Ussuriisk and Amur regions and northern Korea), Northern Chinese (corresponding to northern and central China), Central Chinese (containing the floras of Szechwan and Yunnan), Southern Chinese (with subtropical and tropical vegetation), and Japanese (including the vegetation of islands from Formosa to the Kurils and of southern Korea).

A comparison of the opinions published so far on the regional division of the Palaearctic part of East Asia with the results presented in this paper reveals a number of differences. Slight differences in the course of the northern boundary of this province do not seem significant, but divergencies are remarkable as far as the opinions on its southern boundary and, what follows, the southern boundary of the Palaearctic are concerned. Most zoogeographers have defined the southern boundary of this province in keeping with the traditional manner more or less exactly along the 28° parallel of N. latitude. However, in the light of the present investigations it seems that this boundary should be shifted far more to the north, approximately as far as the River Hwang. Besides, the fauna of the Szechwan Basin (Red Basin) and of the mountains surrounding it turns out to be so distinct that its association with the Eastern Asiatic fauna, practised so frequently, does not seem justified, at any rate as regards the *Macrolepidoptera*. Both the fauna and the flora of this territory are original in relation to those of eastern Asia, or even of the Holarctic (if we reject the hypothesis, more and more criticized, on the origin of the Holarctic fauna from the Angara region). None the less this fauna has undergone such a thorough differentiation that, in my opinion, there are no grounds to associate it with the East Asiatic fauna.

The Tibetan Province. This province embraces the Macrolepidopteran fauna of Tibet (except for the Altyn-Tagh Range) and of the Szechwan Basin and the mountains surrounding it. It is a very well differentiated area. The Central Tibetan Region, covering the fauna of poor alpine steppes and semideserts of Tibet proper, is the worst known area of the Palaearctic. The Himalayas constitute the southern boundary of this region, whereas the Przhevalski and Marco Polo Ranges border it on the north. In the parallel direction it stretches from the eastern slopes of the Karakoram Mts. approximately to the Mekong Valley. Another region is made up by the faunas of eastern Tibet, from the Tsaidam Uplands through Tsing-Hai (Koko-Nor) to the Nan Shan Mts.

and the Richthofen Mts. The fauna of the Szechwan Basin and the mountains surrounding it form the third region of this province.

The fauna of the Central Tibetan Region has the smallest number of species. Only 498 Macrolepidopteran species have been recorded from this area as yet. This figure should, however, been treated as an approximate one. Taking into consideration the low degree of exploration of this fauna, the poor and rather monotonous plant cover and the harsh climate of the Tibetan Plateau we must admit that the number of nearly 500 Macrolepidopteran species proves the richness of the fauna occurring there. The Szechwan Basin (Red Basin) is noted for the largest number of species not only in this province, but even in the whole Palaearctic. Owing to long-lasting investigations carried out mostly by German missionaries the fauna of this area is comparatively well known. So far, 2574 Macrolepidopteran species have been recorded from it. Also the flora of this territory has the largest number of species in the Holarctic, i.e., nearly 13 000 species of higher plants. The fauna of the East Tibetan Region, with its 930 Macrolepidopteran species, is considerably poorer. It has not been investigated very well except for the environs of Lake Tsing-Hai (Koko-Nor) and the Richthofen Range, which are fairly well known. For this reason the number of species in this area should increase as the investigations are continued.

The number of endemic species is very large in particular faunas of this province. It is the lowest and amounts only to 26 in the fauna of Tibet proper, which is therefore both the poorest in species and the youngest from the historical point of view. In eastern Tibet, where the plant cover is more differentiated and was only little destroyed in the Pleistocene, the number of endemic species is nearly eight times as large and amounts to 203 species. However, the fauna of the Szechwan Region has the largest number of endemic species. Up to now, 972 Macrolepidopteran species the ranges of which are in most cases restricted to particular plant associations or altitudes (CARADJA, 1935) have been recorded. Such species form about 30% of the Macrolepidopteran fauna existing there and they belong for the most part to endemic genera as well.

The comparatively high coefficient of specific affinity and the large number of endemic genera common to all the regions of this province evidently indicate the homogeneity of the faunas occurring there. The fauna of central Tibet, which developed last, supposedly took rise directly from the East Tibetan fauna, and this was in turn differentiated directly from the Szechwan fauna considerably earlier. Central Asiatic and Oriental species, so numerous on the southern slopes of the Himalayas or in Kashmir, contributed to the process of formation of the Tibetan fauna to a small extent only. On the borders alone, that is, in the Altyn-Tagh Mts. and in the south-western part of the Tibetan Plateau, the faunas have been slightly mixed. A number of Oriental species have penetrated into Tibet chiefly along river valleys and some Tibetan elements have been included in the forest faunas of the Altyn-Tagh Mts.

The Tibetan Province was regarded by most zoogeographers as a part of the Eastern Asiatic Subrealm and it was sometimes divided into parts. The eastern part used to be joined to the Eastern Asiatic Province and Tibet together with the Richthofen Mts. to the Centrasiaticum. Only HETTNER (1935) treated the Tibetan fauna as that of a distinct faunal province.

The opinions of phytogeographers on the spatial differentiation of the vegetation of this area are almost entirely concurrent. DIELS, GOOD, RIKLI and ENGLER classified the vegetation of the Szechwan Basin, the eastern slopes of Tibet and the Himalayas approximately as far northwards as the valley of the Brahmaputra in the Sino-Japanese Province, but they included the flora of Tibet, both of Tibet proper and of its eastern part, and that of the Richthofen Range in the Central Asiatic Province (Centrasiaticum).

Therefore, there is an obvious discrepancy between the results of investigations presented in this paper and the opinions so far held on the regional differentiation both of the flora and of the fauna of the area under discussion. This discrepancy, especially so far as the floral regionalization is concerned, is however rather apparent. It results, on the one hand, from the physiognomic similarity of the steppes of Tibet and of the Central Asiatic Subrealm and, on the other hand, from the historical connexions between the vegetation of whole eastern Asia and that of Szechwan. Studies of WARD (1935, 1936) and WULFF (1935, 1944) showed that the bulk of the vegetation of the Tibetan Plateau is of Eastern Chinese origin. It is composed of alpine species occurring in analogical localities in the mountains of China, Burma, and the eastern Himalayas. Instead, the number of Central Asiatic elements in the Tibetan flora is small; it amounts only to 11·6% of the total of species. A similar situation has been found in the flora of the environs of Lake Tsing-Hai, where according to HAO (1938), despite the Mongolian neighbourhood, a great majority of species are of Sino-Himalayan origin. All the Eastern Tibetan endemic species, the number of which reaches 25% of the total of plants occurring there, are of Sino-Himalayan origin as well.

The Kashmir-Punjab Region, bordering on this province on the west, and included by most zoogeographers in the Palaearctic Subrealm, should be classified in the Oriental Realm, with which it is associated by a very high coefficient of affinity for the Macrolepidopteran fauna.

Central Asiatic Province. This province combines the faunas of dry steppes, semi-deserts and deserts of the central part of the Palaearctic. It extends also over the areas of forest and parkland (steppe-forest transition) faunas of the mountains of Central Asia. The fauna of the Central Asiatic Province forms a number of distinct regional units.

The Turanian Region embraces the faunas of the mountains of Central Asia, that is, those of the Pamirs, Tien Shan, Alatau, Tarbagatay as well as of the Fergana, Kashgar, and Dzungar Basins. The fauna of the Afghan mountains has been included in this region provisionally as the Turano-West Asiatic transition zone.

The Aralo-Caspian Region covers the faunas of steppes, semi-deserts, and deserts situated between the Caspian Sea and the mountains of Central Asia. In addition, it contains the faunas of southern Turkmenia and the Kopet Dagh Mts. The fauna of the northern part of the region, occurring in esparto-dominant steppes and in *Artemisia*-dominant, short-grass steppes, is transitional Central Asiatic-Europeo-West Siberian in type.

The Altyn-Tagh Region is confined only to the range of the same name and characterized by a fairly remarkable admixture of Tibetan elements.

The Gobi Region includes the faunas of the low steppes, semi-deserts and deserts of West China and southern Mongolia.

The numbers of species in the faunas of particular regions are different. Generally speaking, the fauna of this province is pretty poor. The smallest number of species, only 439, were found in the Altyn-Tagh Region. This is undoubtedly due to the rather poor exploration of this area, for as regards the flora the region is rich enough for the number of species occurring there not to diverge from those in the Tien Shan Mts. or in the Pamirs. The faunas of the Gobi and Aralo-Caspian regions are poor as well. These regions embrace the faunas of environments characterized by extreme living conditions and little differentiated, though specifically abundant, floras. Where the conditions are less severe and the vegetation more diversified, the number of the Macrolepidopteran species increases. In the extremely poor argillaceous deserts between the Caspian Sea and the Aral Sea there are only 219 Macrolepidopteran species. In the sandy semi-deserts and deserts of northern Turkmenia, where the vegetation is noticeably richer, the number of Macrolepidopteran species amounts to 904 and in southern Turkmenia, with its abundant and diversified vegetation, even to more than 1100. The Turanian Region is the richest in this respect, its average being 830 Macrolepidopteran species for a local fauna. A close correlation between the number of Macrolepidopteran species and the differentiation of vegetation is visible also in this region. Only Dzhungaria, fairly rich in plants but poor in Macrolepidopteran species, departs from this principle.

Species with small ranges are fairly numerous in this province. They are mostly grouped in mountains, almost each massif of which has its own peculiar Macrolepidopteran species. The endemic species are the most numerous in the Fergana Basin (74 species), the Hindu Kush Mts. and Kandahar Mts. with their 65 species and the Tien Shan Range with 52 species come next. There are also many endemic species in southern Turkmenia, mainly in the Kopet-Dagh Mts. The faunas of steppes and deserts of the Aralo-Caspian Region are almost completely devoid of species having small ranges. Most of the *Macrolepidoptera* inhabiting this area are very widely distributed, from Gobi through the mountains of Central Asia up to the Kirgiz and Tartar steppes.

The Central Asiatic elements extend in large numbers into the European and South Siberian steppes. The role of these elements in the transition zones of the Europeo-West Siberian Province has already been discussed. Two types of transitional faunas can be distinguished within the Central Asiatic Province: the Central-Asio-Europeo-West-Siberian type occurring in northern and central Kazakhstan and the Central-Asio-West-Asiatic type characteristic of Afghanistan.

The total value of the Europeo-West Siberian elements in the Kazakh transition zone is not very high; it hardly reaches 30%. It is therefore equal to the value of the Central Asiatic elements in the transition zones of the Europeo-West Siberian Province, upon which it borders on the north and on the west. Both these zones constitute as if a separate whole in which the elements of one province dwindle gradually in favour of those of the other province.

In the fauna of the Afghan transition zone the value of the West Asiatic elements is very high, nearly equal to the value of the Central Asiatic elements, as they amount to 49·5% and 50·5%, respectively. The slight difference between the values of both these elements and a comparatively poor knowledge of the fauna occurring there do not allow its definite classification in one province or another. For this reason the assignment of the fauna of Afghanistan to the Central Asiatic Province should be treated only as temporary.

In most zoogeographic regionalistic studies carried out so far the fauna of Central Asia formed a separate faunal complex of the rank of a province, at least. Differences were perceptible only between the border-lines of the unit. Only ARLDT (1907) and PAGENSTECHER (1909) joined the fauna of Central Asia with that of East Siberia. KOZHANCHIKOV (1937) and GEPTNER (1945) thought that the fauna of Central Asia forms only a part of a large faunal complex embracing the animal kingdom of deserts and semi-deserts of the whole Palaearctic and they called it the Turano-African Subrealm (KOZHANCHIKOV) or the Saharo-Gobian Subrealm (GEPTNER). Another problem that has been discussed up to now is the zoogeographic membership of the fauna of steppes, both of the South-Siberian steppes and of the European ones. SEVERTSOV (1871), SUSHKIN (1925), SEMYONOV TIAN-SHANSKY (1936) and many other authors joined the steppe fauna of this area to the Europeo-Siberian one. However, SHULPIN (1940), GEPTNER (1945) and BOBRINSKIY (1951) held that this fauna constitutes a part of the Central Asiatic Province, to be exact, a part of the Central Asiatic Region of the Saharo-Gobian Province. Finally, KUCHERUK (1959) thought that the mammals of steppes and semi-deserts make up a separate homogeneous faunal complex which in turn forms an independent zoogeographic subrealm, the so-called Steppe Subrealm, extending from Hungary to Mongolia. Unfortunately, he analysed, however numerous, only species edificators, whereas the species occurring also out of steppes have not been included in his close analysis.

The opinions of phytogeographers on the floral membership of the vegetation of Central Asia coincide in general outlines with those put forward by zoogeographers. GRIESEBACH (1884) included both the Eurasian steppes and the deserts and semi-deserts of Tibet and western Asia in the floral Irano-Turanian Province. Analogical opinions can be found in the studies of RIKLI

(1934), **Braun-Blanquet** (1923), **Hayek** (1926), **Good** (1953) and other investigators. Of the Polish botanists **Gajewski** (1937) held the same view and included the vegetation of Podolia in the Irano-Turanian area in spite of the fact that, as he wrote himself, 62·8% of its species are of Europeo-Siberian origin. **Drude** (1890) and **Engler** (1919) distinguished the steppe zone from the Irano-Turanian Province, including it either in the European Province or in the Subarctic. This opinion is also shared by **Szafer** (1949). **Lavrenko** (1960, 1962), relying on the opinions of **Popov**, combines the vegetation of all the Palaearctic deserts and semi-deserts into one floral area, which he subdivides into 3 subareas: the Central Asiatic, embracing the vegetation of Mongolia, Tibet and the Gobi, the Irano-Turanian, in which he counts the vegetation of Central Asia, from the mountains in the east to central Anatolia in the west, and the Saharo-Sindian subarea, consisting of the deserts of Baluchistan, Iran, Arabia and the Sahara. The zone of steppes, both of the Black-Sea steppes and of the Siberian ones, forms, according to **Lavrenko**, a separate floral area. However, the views of **Lavrenko** are to a high degree subjective, for he based all his regional division on a few suitably selected guiding species. An analysis of the data presented by **Lavrenko** and concerning the percentage share of species of particular families in the floras of the zone under discussion shows clearly that the so-called Saharo-Gobian Area is a highly artificial formation.

A comparison of the opinions so far published on the problem of differentiation of the faunas and floras of Central Asia with those offered in the present paper indicates that:

1. There is, as a rule, a concurrence of the opinions of most zoogeographers and those given in the present paper, especially as regards the geographic independence of the fauna of Central Asia.
2. Nevertheless, there are marked differences between the Irano-Turanian Province, as determined by phytogeographers, and the zoogeographic Central Asiatic Province. Apart from the extreme views held by **Lavrenko** (in zoogeography by **Geptner** and **Kozhanchikov**) all phytogeographers place the vegetation of Anatolia, Transcaucasia and Iran in the Irano-Turanian Province, whereas the fauna of the *Macrolepidoptera* of these areas is quite distinct and shows hardly any similarity to the fauna of Central Asia.
3. The Macrolepidopteran fauna of steppes is obviously transitional in nature. Therefore, it cannot constitute a distinct regional unit of a higher rank.

West Asiatic Province. This province embraces the Macrolepidopteran faunas of Asia Minor, western and central Iran and the northern part of the Arabian Peninsula. The *Macrolepidoptera* of south-eastern Iran and Baluchistan are nearly all of Oriental origin, and for this reason the region, the so-called Sindian, should be counted in the Oriental Realm. The West Asiatic Province splits into three regions showing a high degree of independence.

The Asia Minor Region covers the faunas of upland steppes and evergreen forests of Asia Minor, Transcaucasia, Kurdistan and Armenia. It extends also over the Macrolepidopteran faunas of semi-deserts and deserts of Syria, Lebanon and Mesopotamia. The fauna of Cyprus, which little differs from that of the Taurus Mts., belongs to this region as well.

The Jordan Region is made up of the eminently specific fauna of Palestine, the Jordan Valley, the Naguib Desert and the Sinai Peninsula.

The Iran Region includes the faunas of steppes and evergreen forests of south-western and central Iran and the Tertiary refuge forests of the Elburz Mts., Talish Mts. and Hircania.

The Macrolepidopteran fauna of this province is fairly well known. The faunas of Kurdistan and central Iran have been explored most poorly. The number of species occurring in particular geobotanic units if fairly large. The faunas of Cyprus (517 species) and Mesopotamia (540 species) are the poorest, whereas those of Georgia (1197 species) and Armenia (1142 species) are the most abundant.

Endemic species are pretty numerous in almost all the local faunas. Their number is the largest in the Iran fauna; 70% of these species occur exclusively in the Elburz Mts. and in the Talish. Somewhat fewer endemic species appear in the Jordan Region. In the Asia Minor Region the largest numbers of species with small ranges have been found in the Taurus Mts. and in Mesopotamia. It is rather strange, because this area is open to penetration from the neighbouring territories and as regards its flora it is distinguished by nothing. The fewest endemic species are in the faunas of Cyprus and of the western coasts of Asia Minor.

Outside the province, West Asiatic elements play rather an important role in the faunas of the Aegean and Afghan transition zones. The contribution of these elements to and their role in the faunas mentioned have already been discussed. Besides, a fairly close affinity joins the *Macrolepidoptera* of this province, above all, of the Jordan Region together with the Arabian fauna, and this last belongs to the faunal Ethiopian Realm. However, since the group value of western Asiatic elements in this fauna is not high and amounts hardly to 36%, the whole territory of the so-called „Arabia Felix“ should be incorporated in the Ethiopian Realm as a transition zone.

The opinions of both zoogeographers and phytogeographers on the spatial differentiation of West Asia have already been presented. It should be only mentioned in general that nearly all zoogeographers joined the West Asiatic and the Mediterranean faunas together, whereas phytogeographers included only the vegetation of the coasts of Middle East in the Mediterranean Subrealm or Realm. They reckoned the flora of Anatolia and Iran in the Irano-Turanian flora and that of Transcaucasia and Armenia in the Europeo-Siberian.

An analysis of the distribution of the *Macrolepidoptera* does not support either of the views. The *Macrolepidoptera* of West Asia form an obviously distinct whole and they are only slightly related with the neighbouring faunas. In consequence, no objections can be raised against the faunal autonomy of this province, naturally as far as the Macrolepidopteran fauna is concerned.

	Total of *Macrolepidoptera*	Species they have in common with the Ethiopian realm.		Species they have in common with the Neotropical realm.	
		Number	%	Number	%
Madeira	76	23	30·2	7	9·2
Azores	42	13	31·0	4	9·4
Canaries	176	51	28·8	2	1·3
Total of Macaronesia	236	53	22·3	10	4·2
Ascension	12	8	66·7	2	16·7
St Helena	36	22	61·2	2	5·6
Cape Verde Is	53	43	81·1	1	1·9

The regional distinctness of this province has also been confirmed by detailed phytogeographic studies carried out by Eig (1931), Zohary (1957) and Wilhelm (1937).

North African Province. This province unites the faunas of the whole Palaearctic part of Africa, from the Sinai Peninsula to the coasts of the Atlantic. It embraces also the fauna of the southern and western part of the Iberian Peninsula (the so-called Andalusian and Lusitanian faunas).

The fauna of this province exhibits a distinct differentiation into two separate regions:

The Saharan Region with the faunas of deserts, semi-deserts and oases of the Sahara, Libya and Egypt and the Mauritanian Region, which embraces the faunas of whole Maghreb, occurring both in steppes and in maquis, in evergreen forests and in coniferous ones. This region extends also over two transition faunas: those of the Atlas and of southern Iberia.

Most local faunas of this province are poor in species. This is connected with its relatively little floral differentiation and the nearly complete annihilation of the original vegetation in this territory. The former forests and parklands have been replaced by little differentiated gramineous and shrubby vegetation.

The number of the Macrolepidopteran species is the smallest in the Sahara (224), it increases slightly in Egypt, but reaches its highest value for the fauna of the Iberian transition zone (over 1000 Macrolepidopteran species). It fluctuates about 800 for the faunas of Maghreb.

This province, however, abounds in endemic species (since the fauna of this province is well known owing to detailed explorations carried out by many entomologists, the endemism of these species does not raise any doubts). The largest number of endemic species (169) occur in Algeria, mainly in two centres: in the Aurès Mts. and Kabylia. The fauna of the Iberian transition zone comes second in this respect (71 species). Here the endemic species are mainly grouped in the Sierra Nevada and in Algarve. The fauna of the Sahara is the poorest

Table 7

Species exclusively Palaearctic		Species they have in common with Macaronesia		Endemic species	
Number	%	Number	%	Number	%
46	60·6	x	x	19	25·0
25	59·5	x	x	8	18·9
123	69·9	x	x	52	29·6
173	73·5	x	x	103	43·5
1	8·3	6	50·0	1	8·3
6	16·6	17	47·2	6	16·6
2	3·8	14	26·4	7	13·2

in endemic species; it has hardly 7 of them, of which 5 appear only in the Ahaggar Mts. and 2 in the Tibesti.

In its fauna the North African Province shows a slight relationship to the faunas of West Asia and Ethiopia. This is above all true of the *Macrolepidoptera* of Egypt. The proportion of the Ethiopian species in the Maghreb fauna is very small. The fauna of the province under discussion, especially that of the Mauritanian Region, shows a considerably greater affinity to that of the Europeo-West Siberian Province. The last-named region embraces two remote zones of mixed faunas. The first of them is the Macrolepidopteran fauna of the southern part of the Iberian Peninsula. The group value of North African elements in this fauna amounts to 56% and that of the Europeo-West Siberian elements to 44%. The area of this zone, though within somewhat narrower boundaries, is incorporated in North Africa also by phytogeographers.

The second transition zone covers the High Atlas. The group value of Europeo-West Siberian elements is somewhat lower for this zone than in southern Spain and amounts to 42%. Taking into account the distance of this zone from the boundaries of the Europeo-West Siberian Province, the number of these species and their value in the fauna of the Atlas Mts. are striking. They seem to be, for the most part, relicts of the Ice Age. It would be instructive to examine the ranges of European species occurring as relicts in the Atlas Mts. more closely. For it would throw some light upon the role of the North African refuge in the formation of the Eurpean fauna in the Holocene.

The opinions of zoo- and phytogeographers both on the regional division of this province and on its autonomy have already been discussed. A vast majority of zoo- and phytogeographers classify North Africa in the Mediterranean Subrealm. Of the zoogeographers only HETTNER (1935) divides this area into two parts, whereas the Russian zoogeographers include the fauna of this territory in the enormous Saharo-Gobian (or Turano-African) Subrealm. Phytogeographers, e. g. GOOD (1953), divide the African part of the Mediterranean into two regions, the boundaries of which agree more or less exactly with those given in the present paper. Only WILHELM (1937) has distinguished three separate provinces in North Africa. Most phytogeographers join the flora of the Sahara and central Egypt together with the vegetation of the West Asiatic deserts. This view cannot be corroborated on the basis of the Macrolepidopteran material, neither is it justified from the historical standpoint.

Macaronesian Province. This province is made up of the specifically poor but very peculiar faunas of the Canary Is., Madeira, and the Azores. The faunas of the Ascension I. and St. Helena I. also show a close relationship to the fauna of the Macaronesian Province. However, the high proportion of tropical African species rather suggests the inclusion of these faunas in the Ethiopian Realm. As regards the *Macrolepidoptera* of the Cape Verde Is., they are nearly all of Ethiopian origin. The correlations between the Macrolepidopteran faunas of the southern islands of the Atlantic are illustrated in Table 7.

The fauna of this province is poor in species. So far, only 236 Macrolepidopteran species have been recorded from the islands of this province. The large number of endemic species, 43·5% of the total of the *Macrolepidoptera* occurring there, is characteristic of this fauna. The number of endemic species in the particular islands is given in Table 7. There are only 16 exclusively Ethiopian species occurring nowhere in the Palaearctic out of the Macaronesian Province (6·8% of the total fauna). These are mostly grouped on the Canary Is. On the other hand, 8 neotropical species occur only on the Azores and Madeira. The large share of endemic species and the presence of neotropical and Ethiopian elements are distinctive features of this fauna.

The fauna of Macaronesia as well as that of the Cape Verde Is. was generally reckoned by zoogeographers in the Mediterranean Subrealm. No one but HETTNER (1935) treated the fauna of the islands under discussion as a separate regional unit. Phytogeographers have, however, recognized the Macaronesian vegetation as a separate floral province since long ago, and they include in it also the flora of the Cape Verde Is. GOOD (1953), for instance, divides the Macaronesian Province into four regions: the Azores, Madeira, the Canary Is., and the Cape Verde Is. However the opinions on the autonomy of this province are fully supported by the Macrolepidopteran material, the inclusion of the Cape Verde Is. in the Macaronesian Province and, consequently, in the Palaearctic causes much doubt.

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STRESZCZENIE

Badania nad regionalnym zróżnicowaniem fauny motyli Palearktyki zostały podjęte w trojakim celu:

1. Poznania przestrzennego zróżnicowania oraz wzajemnych związków zachodzących między faunami motyli różnych części Palearktyki.

2. Wypracowania metod badawczych, eliminujących w maksymalny sposób czynniki subiektywne. Metod, które można by było stosować zarówno w przypadku makroregionalizacji opartej o inne grupy świata żywego, jak też w mikroregionalizacji, tj. w skali krajobrazów, facji itp.

3. Stworzenie obiektywnych przesłanek do szczegółowych badań chorologicznych i historyczno-biogeograficznych.

Do chwili obecnej ukazało się wiele prac poświęconych tej dziedzinie zoogeografii. Jednakże osiągnięte wyniki były częstokroć zupełnie sprzeczne. Przyczyną tych rozbieżności między poszczególnymi opracowaniami, opartymi niejednokrotnie o tę samą wyjściową grupę systematyczną, było stosowanie różnych kryteriów delimitacji jednostek faunistycznych, różnych mniej lub bardziej subiektywnych metod, a przede wszystkim opieranie się prawie wyłącznie na dowolnie wybranych grupach przewodnich tzw. edyfikatorów.

Praca niniejsza stanowi próbę opracowania regionalnego podziału Palearktyki, opartą o możliwie jak najbardziej obiektywne kryteria. Zastosowano metodę chorologiczną i statystycznej analizy pokrewieństw. Podstawowym obiektem badań jest areał gatunku, a przedmiotem — fauna określonych jednostek geobotanicznych. Areały wszystkich znanych do roku 1958 gatunków tzw. motyli większych zostały przetransponowane na arkusze zbiorcze i przyporządkowane wydzielonym uprzednio na podstawie zróżnicowania szaty roślinnej przestrzennym jednostkom roboczym w liczbie 118. Zestawiony w ten sposób materiał poddano analizie statystycznej w celu określenia wartości współczynnika pokrewieństwa każdej z faun lokalnych w stosunku do wszystkich pozostałych. Jako podstawę obliczania współczynnika pokrewieństwa gatunkowego przyjęto wzór D. SZYMKIEWICZA:

$$x = \frac{a \times 100}{A}$$

gdzie: x = współczynnik pokrewieństwa, a = ilości gatunków wspólnych faun obszarów A i B w faunie gatunkowo uboższej (A), A = sumie gatunków fauny uboższej z dwu porównywanych.

Otrzymane wartości zostały następnie uporządkowane w diagram Czekanowskiego. Diagram ten przedstawia obraz rzeczywistego zróżnicowania fauny motyli tzw. większych badanego obszaru. Obraz ten w zgeneralizowanej formie jest przedstawiony na mapie.

Struktura fauny motyli większych Palearktyki

Ogółem do roku 1958 znanych było z obszaru Palearktyki 13 427 gatunków motyli tzw. większych. W tej liczbie monotypowych, tj. nie zróżnicowanych na podgatunki, było 9127, posiadających od dwu do dziewięciu podgatunków — 4072, a powyżej 9 podgatunków — 228.

Większość gatunków *Macrolepidoptera* występuje jedynie na niewielkich terytoriach, nie przekraczających obszaru pojedynczej jednostki geobotanicznej (4600 gatunków) lub obejmujących kilka sąsiednich (4772). Liczba gatunków szeroko rozsiedlonych w całej prawie Palearktyce oraz kosmopolitów jest bardzo niewielka i nie przekracza 300.

Liczebność faun motyli w poszczególnych jednostkach geobotanicznych jest bardzo różna. Waha się od 36 gatunków w Islandii do 2574 gatunków w kotlinie Syczuanu.

Gatunki endemiczne, tj. występujące wyłącznie w pojedynczej jednostce geobotanicznej, najliczniejsze są w ostojowych ośrodkach flory trzeciorzędowej, a mianowicie w Azorsko-Kanaryjskim, Mauretańskim, Małoazjatycko-Irańskim, Kaszmirskim, Wschodniotybetańskim i Japońskim. Ponadto stosunkowo znaczną liczbę gatunków endemicznych posiadają fauny motyli niektórych młodych pasm górskich z wyjątkiem Kaukazu.

Gatunki motyli, których zasięgi przekraczają tradycyjnie ujęte granice Palearktyki, potraktowane zostały z konieczności sumarycznie, tj. łącznie palearktyczne występujące również poza nią jak i pozapalearktyczne, stwierdzone na obszarze Palearktyki. Najwięcej gatunków wspólnych (1702 gatunki) ma fauna Palearktyki z zoogeograficznym Państwem Orientalnym. Grupują się one głównie w Azji Wschodniej oraz w Kaszmirze i południowo-wschodnim Iranie.

Gatunków wspólnych z zoogeograficznym Państwem Etiopskim jest w Palearktyce bardzo niewiele, bo jedynie 132. Występują one głównie na Półwyspie Arabskim i w dolinie Nilu.

Gatunki wspólne z nearktyczną częścią Holarktydy grupują się przeważnie w strefie arktycznej i w północno-wschodniej Syberii.

Wreszcie gatunków kosmopolitycznych, występujących poza Palearktyką, we wszystkich bez mała państwach zoogeograficznych jest zaledwie 12.

Regionalizacja zoogeograficzna Palearktyki

Podział regionalny Palearktyki, uzyskany na podstawie analizy statystycznej pokrewieństw faun motyli większych, różni się znacznie od dotychczas stosowanych. Zasadnicze cechy przedstawianego podziału są następujące:

1. Obszar, w którym dominują gatunki wspólne z Ameryką Północną, jest znacznie większy niż się to dotychczas przyjmowało, gdyż poza strefą tundr i lasotundr obejmuje również obszar modrzewiowej tajgi wschodniosyberyjskiej. Fakt ten powoduje w konsekwencji znaczne ograniczenie obszaru Palearktyki. Niestety z powodu braku danych faunistycznych z Ameryki Północnej nie można na razie z należytą pewnością ustalić, czy fauny północno-wschodniej Syberii nawiązują do Krainy Arktycznej czy też Nearktycznej Holarktydy.

2. Strefa arktyczna Fennoskandii, dotychczas na ogół traktowana jako integralna część Krainy Arktycznej, ma faunę motyli znacznie silniej spokrewnioną z europejską niż z arktyczno-amerykańską.

3. Granice prowincji Europejsko-Zachodniosyberyjskiej zostały w porównaniu z dotychczasowymi poglądami dość znacznie zmienione. Przede wszystkim nie została potwierdzona koncepcja jednorodności fauny leśnej Eurazji w wyniku wydzielenia faun Azji Wschodniej tworzących odrębne prowincje, a których odrębność nie budzi żadnych zastrzeżeń. Ponadto fauny północnych pobrzeży Morza Śródziemnego, stepów Europy południowo-wschodniej i arktycznej Fennoskandii, które dotychczas zaliczane były do innych prowincji Palearktyki w wyniku przeprowadzonej analizy, powinny być włączone do prowincji Europejsko-Zachodniosyberyjskiej.

4. Dawna Prowincja Śródziemnomorska, traktowana dotychczas przez wszystkich zoogeografów, w tym również i lepidopterologów, jako jednorodna całość stanowi faktycznie, w odniesieniu do fauny motyli, cztery całkowicie odrębne prowincje wykazujące jedynie nikłe wzajemne pokrewieństwo faunistyczne.

5. Prowincja Wschodnioazjatycka, łączona przez wielu zoogeografów z europejską w tzw. Euro-Syberyjską, stanowi całkowicie odrębną jednostkę regionalną rangi co najmniej prowincji. Południową granicę tego obszaru, a tym samym i wschodniej Palearktyki, w porównaniu z dotychczas przyjmowaną należy, przynajmniej w odniesieniu do fauny motyli, przesunąć dość daleko na północ.

6. Wyodrębniona została również jako całkowicie samodzielna jednostka zoogeograficzna fauna Tybetu oraz Kotliny Syczuańskiej, łączona dotychczas bądź to ze wschodnioazjatycką, bądź środkowoazjatycką.

7. Fauny Kaszmiru, Pendżabu, doliny Indusu, pustyni Sind oraz południowo-wschodniego Iranu, zaliczane zazwyczaj do Palearktyki, wykazują wysoki współczynnik pokrewieństwa gatunkowego z zoogeograficznym Państwem Orientalnym i doń powinny być włączone.

РЕЗЮМЕ

Исследования региональных различий фауны Палеарктики были предприняты с тройной целью:

1. Познания пространственных различий и взаимосвязей существующих между фаунами разных частей Палеарктики.

2. Выработки методов исследований в максимальной степени исключающих субъективные факторы. Методов, которые можно было бы применять как при макрорегионализации, основанной на других группах животного мира, так и при микрорегионализации, т. е. в масштабе ландшафтов фаций и т. д.

3. Выработки объективных предпосылок для подробных хорологических и историко-биогеографических исследований.

До настоящего времени в этой области зоогеографии выдано много работ. Однако полученные результаты часто были совершенно противоречивы. Причиной противоречий между работами, опирающимися неоднократно на этой же самой, исходной систематической группе, было применение разных критериев делимитации фаунистических единиц, разных в большей или меньшей степени субъективных методов, а главным образом то, что авторы основывались почти исключительно на произвольно избранных ведущих группах т. н. эдификаторах.

Настоящая работа представляет собой опыт разработки регионального подразделения Палеарктики, основанный на возможно наиболее объективных критериях. Применен хорологический метод и статистический анализ видового родства. Основным изучаемым объектом является ареал вида, а предметом — фауна определенных геоботанических единиц.

Ареалы всех известных до 1958 года видов т. н. *Macrolepidoptera* нанесены на сборческие листы и приделены выделенным предварительно на основании растительного покрова 118-ти пространственным рабочим единицам. На основании составленного таким образом материала проведен статистический анализ для определения величины коэффициента видового родства каждой из локальных фаун по отношению ко всем остальным. Как основание подсчёта коэффициента видового родства принята формула Д. Шимкевича,

$$x = \frac{a \times 100}{A}$$

где: x = коэффициент родства, a = количество видов фаун общих для территорий A и B в фауне более бедной в отношении количества видов (A), A = сумме видов фауны более бедной из двух сравниваемых.

Полученные величины послужили для составления диаграммы Чекановского. Эта диаграмма представляет собой картину действительных различий фауны *Macrolepidoptera* исследуемой территории. Эта картина в обобщенной форме представлена на карте.

Структура фауны *Macrolepidoptera* Палеарктики

До 1958 года на территории Палеарктики было в общем известно 13427 видов. В том числе монотипных, т. е. не делящихся на подвиды, было 9127, имеющих от двух до девяти подвидов — 4072, а свыше 9 подвидов — 228.

Большинство видов *Macrolepidoptera* встречается только на небольших территориях, не превышающих величиной территории одной геоботанической единицы (4600 видов) или вмещающих несколько соседних (4772). Количество видов широко распространенных почти во всей Палеарктике и космополитов очень невелико и не превышает 300.

Численность фаун *Macrolepidoptera* в отдельных геоботанических единицах очень разнообразна. Колеблется от 36 видов в Исландии до 2574 видов в котловине Сечуань.

Эндемические виды, т. е. распространение исключительно в одной геоботанической единице, наиболее многочисленны в остаточных центрах третичной флоры, а именно в Азорско-Канарийском, Мавританском, Малоазиатско-Иранском, Кашмирском, Восточно-Тибетском и Японском. Кроме того, довольно значительно количество эндемических видов в составе фаун некоторых горных цепей, исключая Кавказ.

Виды чешуекрылых, распространение которых больше традиционных границ Палеарктики, по необходимости показаны суммарно, т. е. вместе как палеарктические распространенные вне ее, так и внепалеарктические, найденные на территории Палеарктики. Больше всего общих видов (1702 вида) входит в состав фауны Палеарктики с зоогеографической Ориентальной области. Они группируются главным образом в восточной Азии, в Кашмире и юго-восточном Иране.

Видов общих с зоогеографической Эфиопской области очень мало, только 132. Они распространены главным образом на Арабском полуострове и в долине Нила.

Виды общие с неарктической частью Голарктиды группируются главным образом в арктической зоне и северо-восточной Сибири.

Наконец космополитических видов, которые встречаются вне Палеарктики, во всех зоогеографических государствах существует только 12.

Зоогеографическая регионализация Палеарктики

Региональное подразделение Палеарктики, полученное на основании статистического анализа родства фаун *Macrolepidoptera*, значительно отличается от применяемых до настоящего времени.

Главные черты предлагаемого подразделения следующие:

1. Территория, на которой преобладают виды общие с Северной Америкой, больше чем это принималось до сих пор, так как, кроме зоны тундр и лесотундр, она вмещает также территорию лиственничей восточно-сибирской тайги. Этот факт ведет за собой значительное ограничение территории Палеарктики. К сожалению, из-за недостатка фаунистических данных по Северной Америке еще нельзя с достаточной уверенностью установить родство фаун северо-восточной Сибири с арктическими или неоарктическими фаунами Голарктиды.

2. Фауны арктической зоны Фенноскандии, до сих пор рассматриваемой как интегральная часть Арктической, гораздо сильнее связана с европейской чем с арктическо-американской.

3. Границе Европейской — Западно-Сибирской провинции по сравнению с существующими до настоящего времени взглядами значительно изменены. Прежде

всего выделены фауны Восточной Азии, образующие отдельные провинции, обособленность которых не подлежит сомнению. В результате этого не подтверждается концепция однородности лесной фауны Евразии. Кроме того, в результате проведенного анализа фауны северных побережий Средиземного Моря, степей юго-восточной Европы и арктической Фенноскандии, которые до сих пор присоединяли к другим провинциям Палеактрики, следует причислить к Европейской Западно-Сибирской провинции.

4. Прежняя Средиземноморская провинция, рассматриваемая до сих пор всеми зоогеографами как единое целое, в действительности в отношении фауны чешуекрылых представляет собой отдельные провинции, обладающие только незначительным фаунистическим родством.

5. Восточно-Азиатская провинция, соединяемая многими зоогеографами с европейской в т. н. Евро-Сибирской, образует совершенно обособленную региональную единицу со значением по крайней мере провинции. Южную границу этой территории, а тем самым и границу восточной Палеактрики следует передвинуть по сравнению с принимаемой до сих пор, по крайней мере по отношению к фауне чешуекрылых далеко к северу.

6. Выделена также как совершенно самостоятельная зоогеографическая единица фауны Тибета и Сечуаньской котловины, которую до сих пор соединяли то с восточно-Азиатской, то с средне-Азиатской.

7. Фауны Кашмира, Пенджаба, долины Инда, пустыни Синд и юго-восточного Ирана, причисляемые обыкновенно к Палеарктике, показывают высокий коэффициент видового родства с зоогеографической Ориентальной областью и должны быть присоединены к ней.

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