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Use of General Zoogeographical Subdivisions in Particular Zoogeographical Researches for the Example of the Palaearctic Antlion Fauna (Neuroptera, Myrmeleontidae)

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Abstract—Some terms of general and special zoogeography, such as "fauna," "elementary fauna," "faunistic center," and "range" are defined. Characteristics of the main subdivisions used in general zoogeography are given; the complete list and map are provided for the Palaearctic Kingdom. A method of special zoogeographical regionalization based on an analysis of general biogeographical subdivisions is demonstrated, using the Palaearctic antlion fauna as an example. The similarity dendrogram method reveals 15 elementary faunas and 12 faunistic centers of antlions; these are characterized as centers of diversity and/or speciation.

Biogeography, and zoogeography as its part, use a specific body of concepts. However, the usage of many, if not most, terms varies between countries and even between different authors within a country, whereas the same concept often has several names. The terms of zoogeography are used to denote concrete or abstract objects and phenomena, which can be organized in a hierarchy or merely ranked. In this paper, we consider the main concepts of zoogeography and the reasons for selection and usage of particular terms.

Fauna is a concept of zoogeography and biocenology, denoting the set of taxa of the animal group in question (taxonomic, ecological, etc.), known to exist in the geographical territory, aquatoria, or ecosystem studied. Therefore, the term "fauna" requires at least two epithets: taxonomic and topical. The first (taxonomic) characteristic is omitted in this communication, because we are always dealing with the fauna of the family Myrmeleontidae, considered on the species level; when discussing the distribution of genera, tribes, and subfamilies, the relevant epithets are used. The topical epithets serve to distinguish different faunas within the subdivisions of general zoogeography (regional and provincial faunas, e.g., "Mediterranean fauna") or special zoogeography (elementary faunas, e.g., "Turanian fauna"). A fauna is merely a list of taxa occurring in a particular territory; therefore, a fauna cannot be plotted on a map.

Subdivisions of general zoogeography are particular areas of land (or water) of various ranks, which can be plotted on a map and given specific names. The largest subdivisions of land of the same rank as, e.g., Palaearctic are termed Kingdoms in this work, their names corresponding to those of Regions, as used by many zoogeographers (Cox and Moore, 1980; Belyshev and Kharitonov, 1983). Thus, the subdivision of land into kingdoms results in a scheme, resembling the assembles of biophylotic kingdoms, proposed by Vtorov and Drozdov (1978). However, the latter classification appears to be too detailed, and the 9 kingdoms distinguished by Vtorov and Drozdov can be reduced to the classical 7 kingdoms (Wallace, 1876; Cox and Moore, 1980), one of which is named the Palaearctic Kingdom.

The general characteristics of the distribution of antlion fauna are revealed within the scope of special zoogeography, which represents one of the many aspects of general bio- or zoogeography (Pesenko, 1991).

The term **"elementary fauna"** is derived from "faunal element" (Holloway, 1974; Dennis *et al.*, 1998; etc.) and denotes the assembly of species from a particular taxon, which exists in a territory distinguished by methods of numerical clustering, and is totally or partly distinct from similar assemblies existing in all adjacent territories. Thus, the elementary fauna differs from the "faunal group" sensu Holloway (the faunistic component of a faunal element) in that a territory occupied by a particular elementary fauna cannot be even partly occupied by other elementary faunas. In this aspect, the term "elementary fauna" most closely corresponds to "faunal region" sensu Dennis *et al.* (1998).

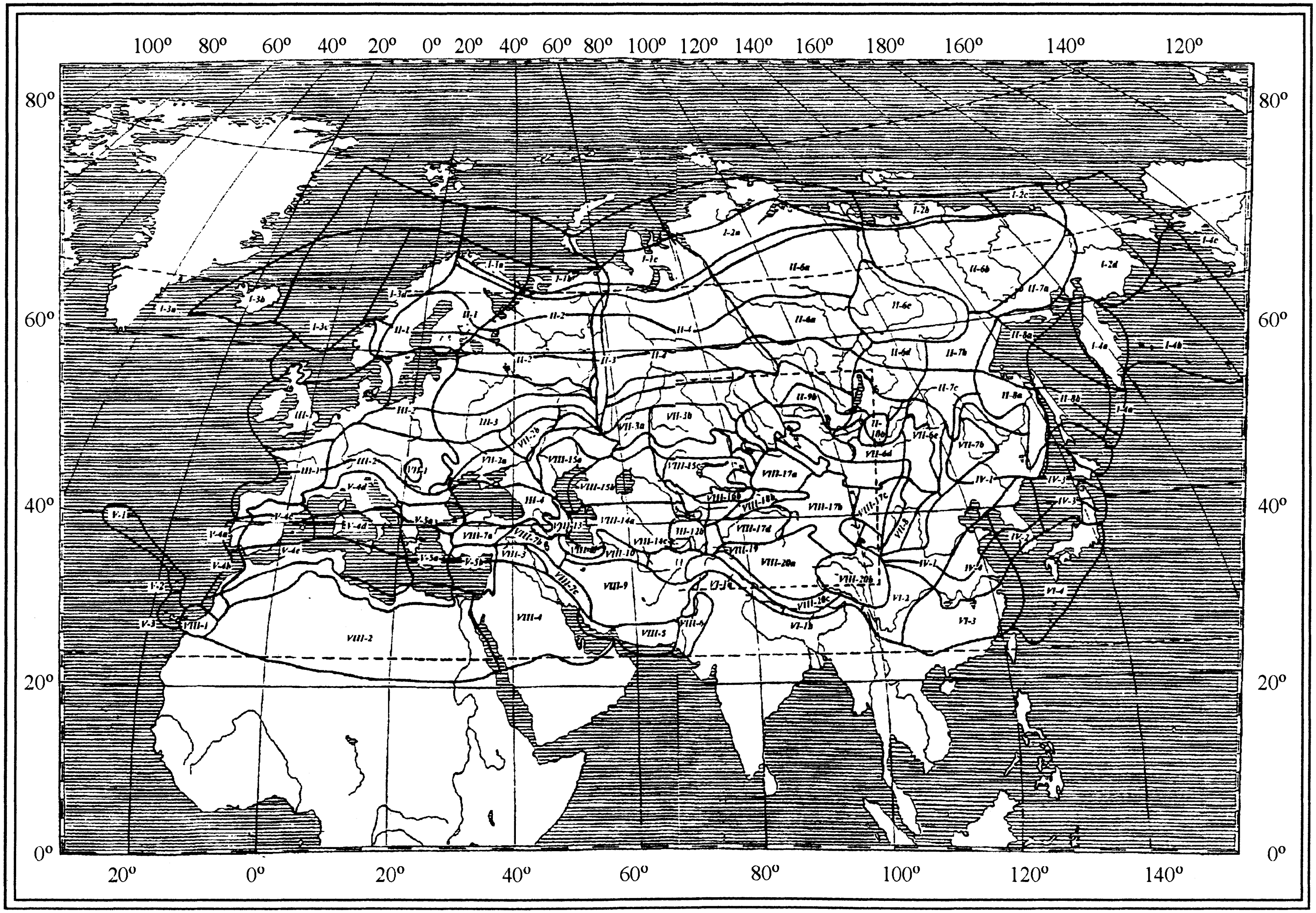

Fig. 1. General biogeographical subdivisions of the Palaearctic Kingdom. Designations of regions (Roman numerals), provinces (Arabic numerals), and subprovinces (Roman letters) correspond to those in Table 1. The area delimited by dashed line is enlarged in Fig. 2.

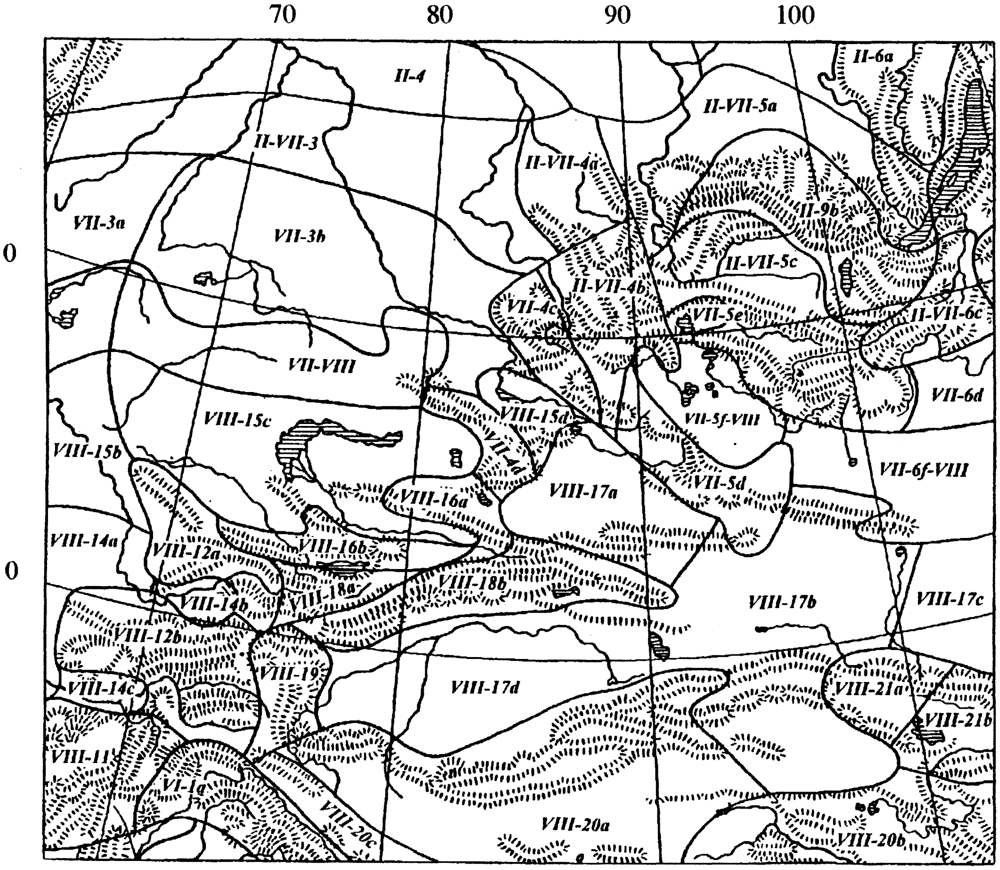

Fig. 2. General biogeographical subdivisions of the central part of the Palaearctic Kingdom. Enlarged fragment of the map shown in Fig. 1. Designations as in Fig. 1.

The term **"faunistic center"** is used in this work in the interpretation of Holloway (1974); it means a territory distinguished by numerical clustering of species of the taxon studied, based on their geographical distribution and area of their concentration. Therefore, a faunistic center is essentially a center of distribution and/or origin of an elementary fauna. A faunistic center can be plotted on a map, in which case it will coincide with, or be included in the territory occupied by the elementary fauna. Using different criteria of analysis, one can distinguish between diversity centers and speciation centers. The most detailed scheme of faunistic centers for the Palaearctic was worked up by De Lattin (1967).

Our study of elementary antlion faunas resembles in methodology investigations of the structure of the faunas of Rhopalocera within the Palaearctic Kingdom (Kostrowicki, 1965) or Europe (Dennis *et al.*, 1998). The most significant methodological difference consists in that the primary areas distinguished in these works represent geobotanical (Kostrowicki) or landscape-based (Dennis *et al.*) subdivisions, rather than biogeographical ones. The faunal regions outlined by these authors do not agree in number or shape with the territories occupied by elementary antlion faunas. These differences result from the specificity of the taxa studied, which quite agrees with the principles of special zoogeography. At the same time, the principles of general zoogeography are confirmed in all these studies, because many specific zoogeographical boundaries coincide with the zonal and sectoral boundaries of general biogeography.

The region (territory, water area, etc.) inhabited by a taxon is termed "areal" in Russian and German literature; such regions are studied by chorology. In the biogeographical literature published in English, this term is not used, because the related word "area" is too general in meaning. The English terms "range" and "distribution" also are polysemantic, because of which we prefer to use the word "areal," following the Russian biogeography tradition and the fundamental work by De Lattin (1967)[1].

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[1] Translator's comment: hereinafter, the Russian term "areal" is always translated as "range."

Table 1. Zoogeographical subdivisions of the Palaearctic Kingdom, after Emeljanov (1974); numbers in parentheses for Fig. 3 and Table 2 are given after Krivokhatsky (1998b).

	I. Circumpolar Tundra Region
	IA. Hyperborean Tundra Subregion
	1. Western Hyperborean Plain
	1a. Lapland
	1b. Nenets
	1c. Lower Ob
	2. Eastern Hyperborean mixed
	2a. Dolgany
	2b. Indigirka
	2c. Chaun
	2d. Anadyr
	IB. North Atlantic Subregion
	3. North Atlantic mixed
	3a. South Greenlandian (Nearctic)
	3b. Icelandic
	3c. Faeroe-Shetland
	3d. Norwegian (mixed with II 1)
	IC. North Pacific Subregion
	4. North Pacific mixed
	4a. Kuril-Kamchatka
	4b. Commander-Aleutian
	4c. Alaskan (Nearctic)
	II. Eurosiberian Taiga (boreal) Region
	IIA. Western Siberian Subregion
(1)	1. Bothnian mixed
(2)	2. Zyriansk Plane
(3)	3. Ural Mountain
(4)	4. Ob Plane
(5)	5. Altai (complex with VII 4)
	5a. Kuznetsk (mixed with VII 3)
	5b. Russian Altai (mixed with VII)
	IIB. Eastern Siberian Subregion
(6)	6. Angara mixed
	6a. Tunguska
	6b. Kolyma
	6c. Yakutian
	6d. Vitim
(7)	7. Okhotsk–Maritime Mountain
	7a. Northern Okhotsk–Maritime
	7b. Maya
	7c. Zeya
(8)	8. Okhotsk Mountain
	8a. West Okhotsk
	8b. East Okhotsk
(9)	9. West Mongolian complex
	9a. Cis-Sayan
	9b. Sayan
	9c. Zaisan
(10)	10. East Mongolian (complex with VII 6)
	10a. Northern Transbaikalian (mixed with VII 6a)
	10b. Khentey
	10c. West Khentey (mixed with VII 6c)
	III. European Nemoral Region
(11)	1. West European mixed
(12)	2. Central European mixed
(13)	3. East European Plane
(14)	4. Euxine Mountain
	IV. Stenopean Nemoral Region
(15)	1. West Stenopean mixed
(16)	2. Korean Mountain
(17)	3. North Japanese Mountain
(18)	4. Yellow Sea Lowland
	V. Hesperian Evergreen Forest (subtropical) Region
	VA. Macaronesian Subregion
(19)	1. Azorean Mountain
(20)	2. Madeiran Mountain
(21)	3. Canarian Mountain
	VB. Mediterranean Subregion
(22)	4. West Mediterranean mixed
	4a. Lusitanean
	4b. Moroccan
	4c. Iberian
	4d. Latin
	4e. Atlas-Betian
(23)	5. East Mediterranean Mountain
	5a. Aegean
	5b. Levant
	VI. Orthrian Evergreen Forest (subtropical) Region
	VIA. West Himalayan Subregion
(24)	1. Himalayan Mountain
	1a. West Himalayan
	1b. East Himalayan
(25)	2. Yunnan mixed
	VIB. East Orthrian Subregion
(26)	3. South Chinese mixed
(27)	4. South Japanese Mountain
	VII. Scythian Steppe Region
	VIIA. West Scythian Subregion
(28)	1. Pannonian Plane
(29)	2. Pontian Plane
	2a. West Pontian
	2b. East Pontian
(30)	3. Kazakhstan Plane

Table. (Contd.)

3a. West Kazakhstan
3b. East Kazakhstan
(31) 4. Altai (complex with II A)
4a. Kuznetsk (mixed with IIA, VII 3)
4b. Russian Altai (mixed with II 5)
4c. Kalbin
4d. Tarbagatai
VIIB. East Scythian Subregion
(32) 5. West Mongolian (complex with IIB)
5a. Cis-Sayan (mixed with II 10)
5b. Sayan
5c. Trans-Sayan (mixed with II 9)
5d. Ubsunur
5e. Ubs (mixed with VIII 17)
5f. Khara Usu (mixed with VIII 17)
(33) 6. East Mongolian (complex with IIB)
6a. Northern Transbaikalian (mixed with II 10)
6b. Khentey
6c. Cis-Khentey (mixed with II 10)
6d. Khalkha
6e. Barga
6f. North Gobi (mixed with VIII 17)
(34) 7. Dunbey mixed
7a. Western Dunbey
7b. Eastern Dunbey
(35) 8. Ordos Plane
VIII. Sethian Desert Region
VIIIA. Sahara-Arabian Subregion
(36) 1. Tekni Plane
(37) 2. Sahara Plane
(38) 3. Syrian Plane
(39) 4. Sumerian Plane
(40) 5. Mekran mixed
(41) 6. Sind Plane
VIIIB. Irano-Turanian Subregion
(42) 7. Middle Eastern (= Levant) mixed
7a. Angorean
7b. Armenian
7c. Zagrossan
(43) 8. Hyrcanian Mountain
(44) 9. Iranian mixed
(45) 10. Khorasan Mountain
(46) 11. Afghan Mountain
(47) 12. Turkestan Mountain
12a. Northern Turkestan
12b. Southern Turkestan
(48) 13. Kura-Araks mixed
(49) 14. South Turanian Plane
14a. Kumistan
14b. Ferghana
14c. Tajik
(50) 15. North Turanian Lowland
15a. Caspian
15b. Aral
15c. Balkhash
15d. Zaisan
(51) 16. Alatau Mountain
16a. Cis-Ili
VIIIC. Central Asian Subregion
(52) 17. Gobi Plane
17a. Dzhungarian
17b. Central Gobi
17c. Alashan
17d. Kashgar
(53) 18. Inner Tien Shan Mountain
18a. Central Tien Shan
18b. East Tien Shan
(54) 19. Pamir high Mountain
(55) 20. Tibetan high Mountain
20a. Chantan
20b. Sikan
20c. Trans-Himalayan
(56) 21. Nan Shan Mountain
21a. Western Nan Shan
21b. Eastern Nan Shan

When comparing antlion ranges, groups of species were clustered according to their occurrence, and a similarity dendrogram was built (Krivokhatsky, 1998b). The species were united in hierarchical clusters, characterized by similar (or even identical) ranges. A similar approach was taken by Holloway (1974) in studying the distribution patterns of the Indian Rhopalocera. However, Holloway did not use the "range" concept; his "faunal elements" represented unique territories, inhabited by similarly distributed species and overlapping with other unique territories, rather than sets of species with similar distribution. Thus, from our viewpoint, Holloway proposed a mapping method for the groups of ranges obtained by clustering.

Our zoogeographical analysis of the Palaearctic antlion fauna was based on the general scheme of zoogeographical regionalization of the Palaearctic Kingdom (Emeljanov, 1974), with some modifications; the

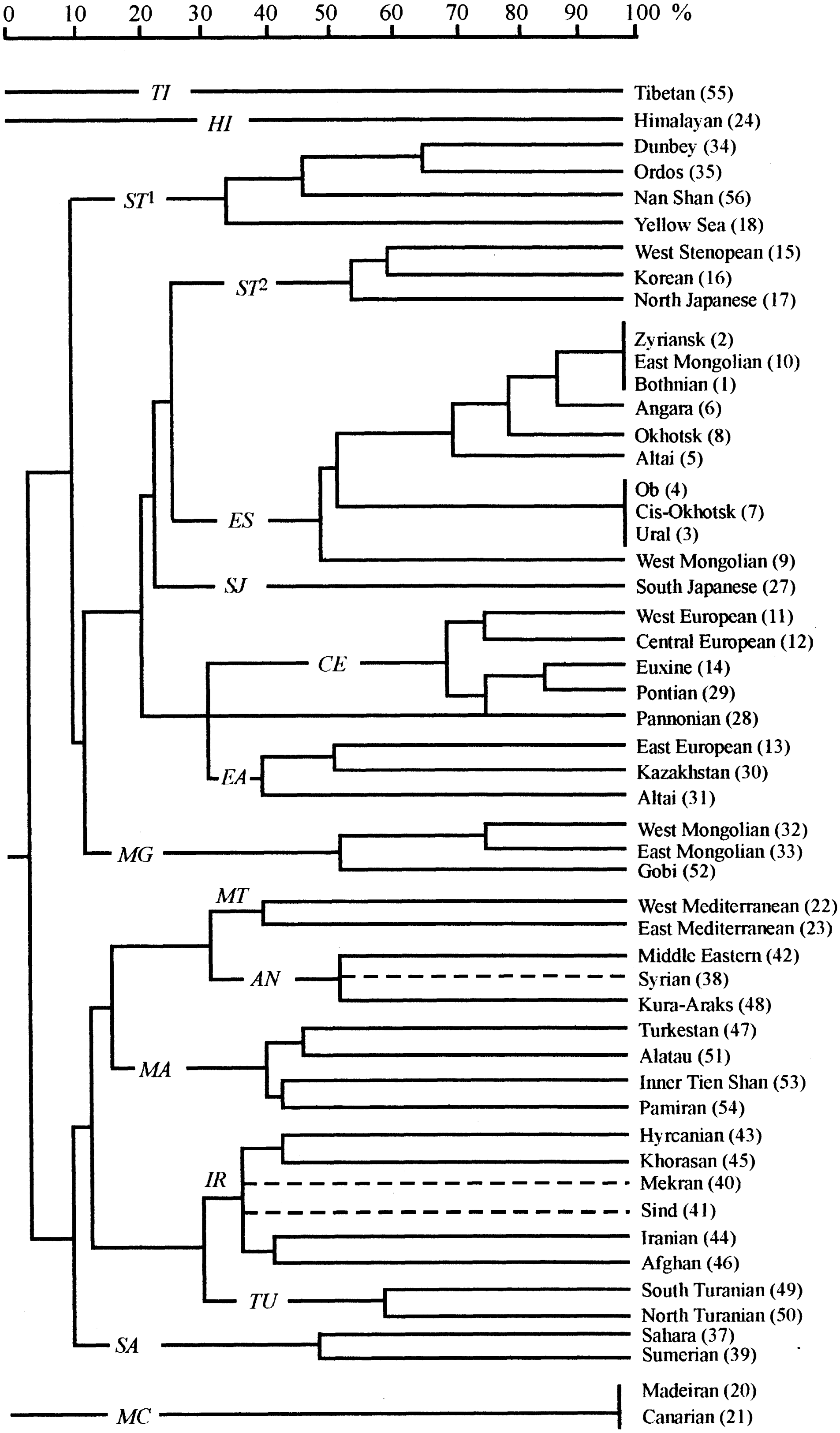

Fig. 3. Generalized faunistic similarity dendrogram of Palaearctic provinces, based on the dendrograms obtained using Czekanowski coefficient for 355 antlion species. Numbers in parentheses correspond to those in Table 1.

Table 2. Main parameters of the elementary antlion faunas of the Palaearctic Kingdom

Fauna	Numbers* of provinces occupied by the fauna	Number of species			
		total	common to all provinces	broad endemics	narrow endemics
Eurosiberian (*ES*)	1–10	4	1	0	0
Central European (*CE*)	11, 12, 14, 28, 29	23	7	0	(?)2
East European–Altai (*EA*)	13, 30, 31	13	2	0	0
Stenopean (*ST*)	15–18, 34, 35, 56	12	5	1	4
Southern Japanese (*SJ*)	25–27	6	0	0	2
Himalayan (*HI*)	24	11	0	0	9
Tibetan (*TI*)	55	6	0	0	4
Macaronesian (*MC*)	20, 21	5	2	2	3
Mediterranean (*MT*)	22, 23	101	27	4	47
Turanian (*TU*)	49, 50	46	28	4	3
Mongolian–Gobi (*MG*)	32, 33, 52	31	7	6	5
Sahara-Arabian (*SA*)	37, 39	132	45	21	63
Middle Asian (*MA*)	47, 51, 53, 54	42	5	0	6
Iranian (*IR*)	40, 41, 43–46	113	30	10	25
Anatolian (*AN*)	38, 42, 48	56	5	3	3
Unknown affiliation	36				
Data absent	19				

* Names of provinces are given in Table 1, with the corresponding numbers provided in parentheses.

map was specially designed in a more convenient projection. The subdivision of the Palaearctic Kingdom into zoogeographical regions, subregions, provinces, and subprovinces (Figs. 1, 2; Table 1) was based on climatic zonation combined with the landscape characteristics and features of plant and animal geography (Emeljanov, 1974).

During the 25 years since the publication of this biogeographical scheme, it has been used as a basis by a number of Russian entomologists. This scheme now has two main aspects of usage. Firstly, the outlines and names of biogeographical regions and provinces are used in zoogeographical and chorological descriptions of regional faunas of various insect taxa and in analysis of their zoogeographical relationships (Falkovitsh, 1979; Vinokurov, 1979; Emeljanov, 1980; Volkovich and Alexeev, 1994; Krivokhatsky *et al.*, 1996; Krivokhatsky, 1998a, 1998b; etc.). In some of these works, the entire Palaearctic fauna of the groups studied was analyzed (Homoptera, Orgeriinae: Emeljanov, 1980; Neuroptera, Myrmeleontidae: Krivokhatsky, 1998b).

Secondly, the principles of the sectoral, zonal, and provincial differentiation, accepted by A.F. Emeljanov as a basis for his biogeographical regionalization, and the zonal and sectoral boundaries determined by him are presently used in specific ecological and geosystemic studies of the whole regions of the Palaearctic Kingdom. The most substantial example of such an approach is a study of the insect fauna of Asian Beringia (Matis, 1986).

In the present work, the general biogeographical scheme of the Palaearctic Kingdom, proposed by Emeljanov, was for the first time used for establishing particular subdivisions of special zoogeography. The practical use of this regionalization scheme for compiling a data matrix for the antlion distribution over the zoogeographical provinces of the Palaearctic Kingdom was difficult because of the presence of transitional zones and mixed provinces. Specific methods for solving the complicated problems of antlion zoogeography were presented, together with the resulting matrix, in a previous publication (Krivokhatsky, 1998b).

Since the antlions are very unevenly studied, the faunas of separate localities and small territories could not be compared in such a way as to establish the specific zoogeographical regionalization of the entire Pa-

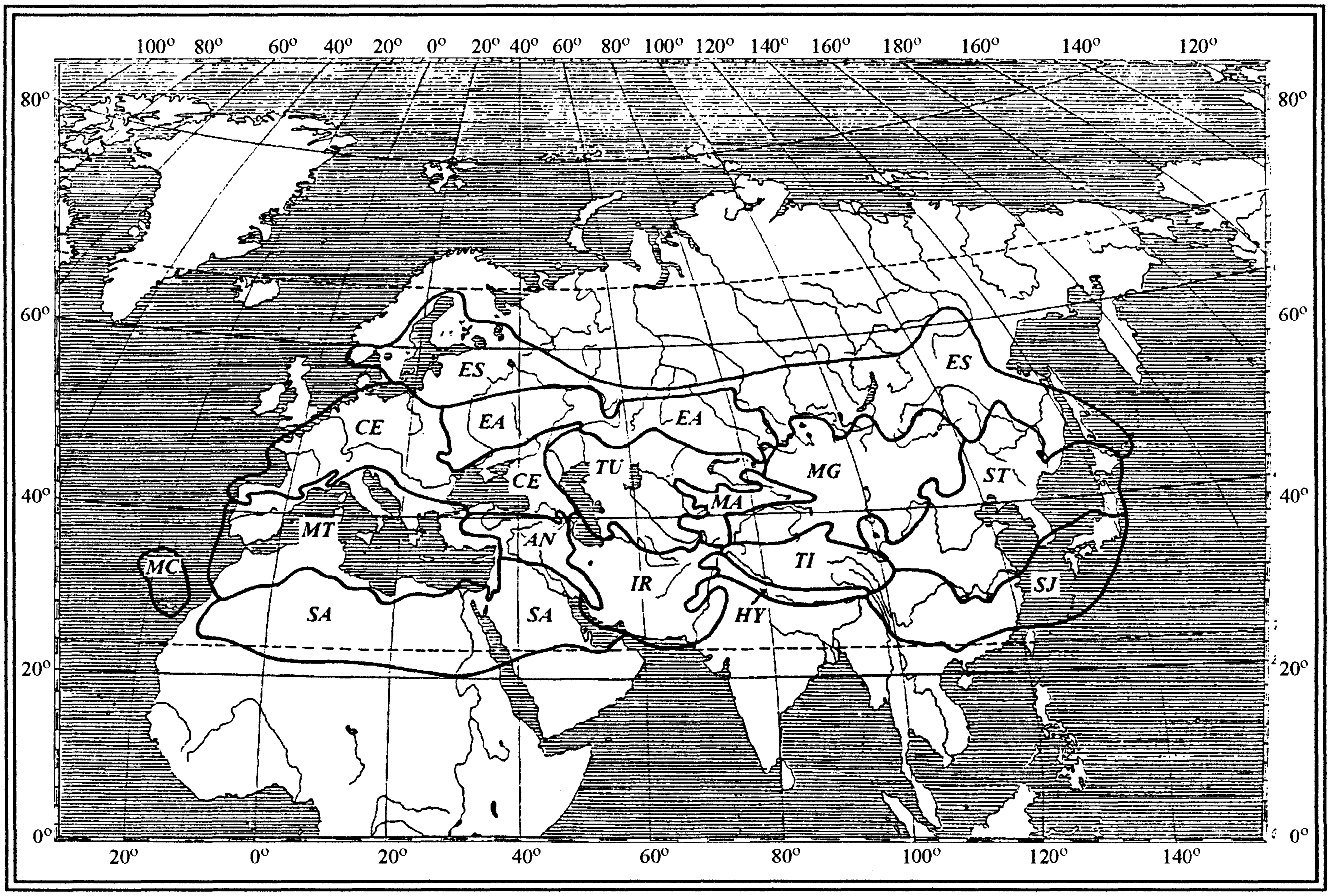

Fig. 4. Boundary between the southwestern and northeastern groups of antlion faunas, based on Czekanowski coefficient (solid line) and Sörensen coefficient (dashed line).

laearctic Kingdom on the basis of local samples. The distribution of species within the best studied territories was analyzed to the level of subprovinces, as done previously for Mongolia (Krivokhatsky *et al.*, 1996). An analysis of the distribution of antlion species and subspecies in the Aral region was performed in even greater detail, resulting in the establishment of infrasubprovincial subdivision (Krivokhatsky and Piryulin, 1997).

The faunas of the Palaearctic provinces were compared by means of the similarity dendrogram method based on the pairwise Czekanowski, Sörensen, and Jaccard coefficients. The distribution matrix of 355 antlion species over the provinces was processed using the program created by I.S. Plotnikov (Zoological Institute, Russian Academy of Sciences), which performed average linkage clustering of similar faunas, based on qualitative (presence or absence of each species in each province: Sörensen and Jaccard coefficients) or quantitative (frequency of occurrence, estimated in arbitrary units: Czekanowski coefficient) characteristics. The clustering method, based on the similarity matrices, was the same for all variants of data processing.

Of the entire set obtained, we selected three dendrograms, which were most distinct and therefore best suited for considering the reasons for similarities and differences between provincial faunas (Krivokhatsky, 1998b). The main dendrogram in our analysis was the similarity dendrogram derived with use of the Czekanowski coefficient from the estimated occurrence of 355 antlion species. The choice of the method was determined by the fact that the quantitative method gives (unlike the qualitative one) a smaller weight to occasional records of species in the periphery of their ranges, while the principal role in the clusterization of similar faunas belongs to mass and common species. Other dendrograms were used to account for the differences in the cluster composition when considering faunas of particular zoogeographical regions. As a result of this work, the zoogeographical regions (i.e., general zoogeographical subdivisions) of the Palae-

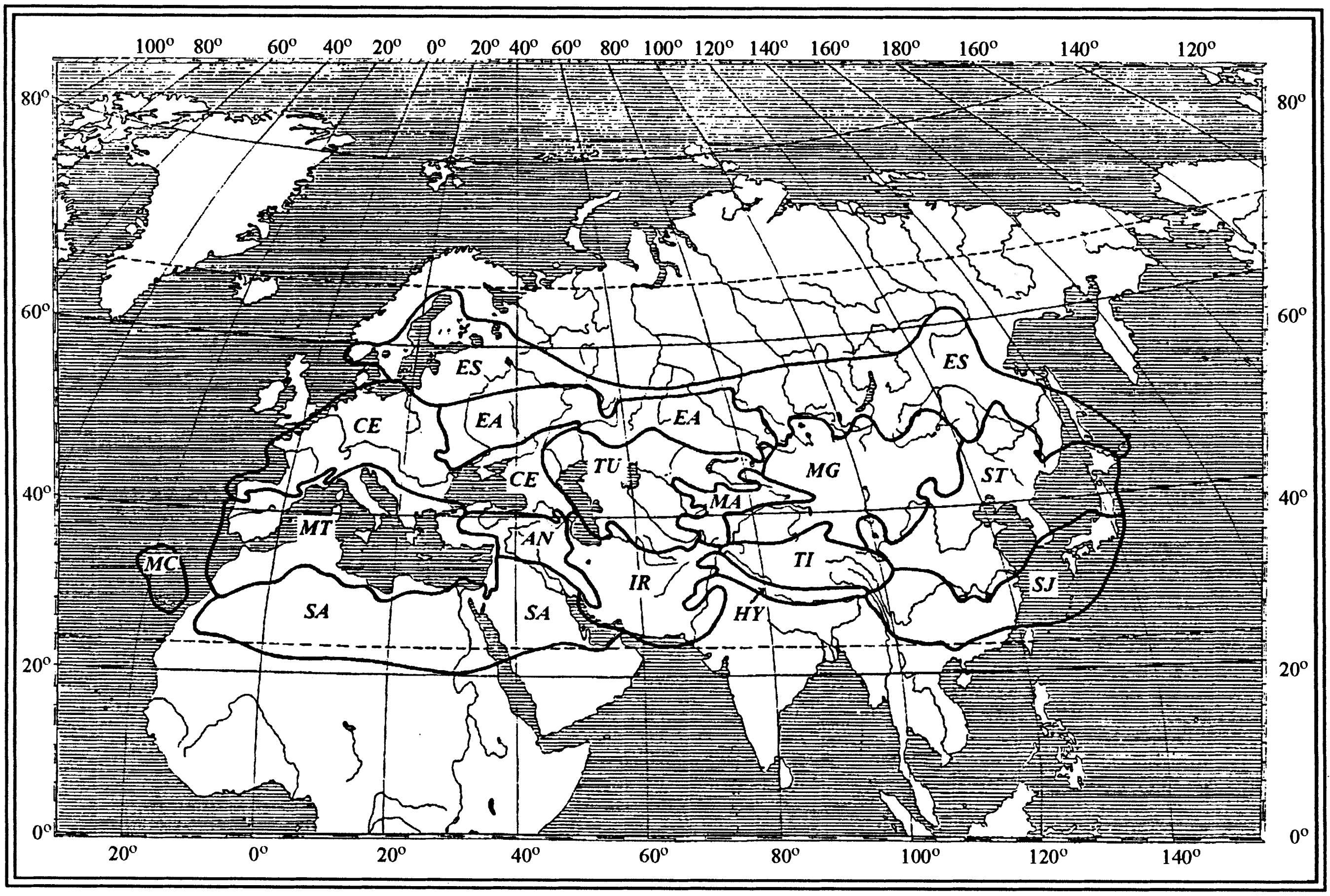

Fig. 5. Elementary antlion faunas in the Palaearctic. Eurosiberian (*ES*), Central European (*CE*), East European–Altai (*EA*), Stenopean (*ST*), Southern Japanese (*SJ*), Himalayan (*HI*), Tibetan (*TI*), Macaronesian (*MC*), Mediterranean (*MT*), Turanian (*TU*), Mongolian–Gobi (*MG*), Sahara-Arabian (*SA*), Middle Asian (*MA*), Iranian (*IR*), and Anatolian (*AN*).

arctic Kingdom were compared and characterized on the basis of provincial antlion faunas (Krivokhatsky, 1998b).

Out of the 355 species recorded in the Palaearctic Kingdom, only 7% are also distributed in the neighboring Ethiopian (19 species) and Oriental (7 species) Kingdoms. A broad Palaearctic distribution, covering 2 or more regions, is typical of 95 species, or 26%. The remaining 265 species (or 74%) are specific to separate regions, being either broad regional, or narrow provincial endemics. Endemism is characteristic of not all regions, but only the Stenopean nemoral (6 species), Hesperian (49) and Orthrian (10) Evergreen Forest, and Sethian Desert Regions (195). The presence of endemics in the Scythian Steppe Region requires further verification, whereas the European Nemoral and Euro-Siberian Regions definitely lack endemic forms. The Sethian Region, characterized by the highest degree of endemism (72%) on the species level, also has 11 endemic genera.

A comparison of provincial faunas with respect to species composition allowed the provinces to be clustered according to the greatest similarity principle. Only some of the obtained clusters corresponded to zoogeographical regions including all their provinces (Fig. 3). A considerable part of the clusters proved to be heterogeneous with respect to the provinces included. Each case when provinces from different regions clustered together (Krivokhatsky, 1998b) was discussed in order to reveal the faunistic links between regions—general zoogeographical subdivisions. In this work, each cluster is regarded as a unique subdivision of the special zoogeography of antlions, and is characterized by the corresponding unique elementary fauna. Thus, the faunistically similar territories, considered in the special zoogeography of antlions and corresponding to separate clusters of original dendrograms (Krivokhatsky, 1998b) and the generalized dendrogram (Fig. 3), are composed of provinces, or elementary territories used in the analysis. The faunas corresponding to each cluster represent the elementary faunas of antlions.

When the original matrices of the antlion species distribution in the Palaearctic Kingdom were compared with the resulting dendrograms, most of the elementary faunas proved to be associated with centers of diversity (criterion of total species number) and centers of speciation (criterion of endemism), i.e., with faunistic centers. The values of these criteria for 15 elementary faunas are shown in Table 2. The elementary faunas are named after the major zoogeographical regions and provinces occupied by these faunas. The names of the faunistic centers, except for specially discussed cases, correspond to those of the elementary faunas.

The previously published dendrograms (Krivokhatsky, 1998b) comprise two major branches, the northeastern and southwestern ones. If the estimated occurrence of widespread and endemic species is taken into account (Czekanowski coefficient), then the southwestern branch includes only the Sahara-Turanian Desert and Mediterranean Hesperian Subtropical Provinces. However, if analysis is based on a qualitative (Sörensen coefficient) and quantitative comparison, with endemic forms disregarded, then the southwestern branch also includes the neighboring provinces of European Nemoral Region and western (European) provinces of Scythian Steppe Region. These Central European provinces, lying between the two boundaries (Fig. 4), cover the ranges of the widespread, primarily boreal-nemoral and steppe species, which have the highest abundance in quantitative comparison, and also of the rare subtropical arid species, which occur sporadically in xerophytic areas; the significance of the last group increases in the qualitative comparison.

Thus, the zoogeographical boundary based on the Czekanowski coefficient is more significant from the faunistic viewpoint. This boundary, also clearly observable in the generalized dendrogram (Fig. 3), largely coincides with the general zoogeographical sectoral boundary between the West and East Palaearctic; at the same time, the southwestern zone of the Palaearctic, separated by this boundary, almost completely covers the Ancient Mediterranean area (Fig. 4). It is significant that a similar pattern of subdivision into southwestern and northeastern zones was obtained by analysis of regional antlion faunas on the genus level.

The northeastern zone revealed by a quantitative comparison of faunas corresponds to 6 separate clusters in the dendrogram (Fig. 3); each cluster is formed either by all provinces of a single zoogeographical region (10 provinces of the Eurosiberian Taiga Region), or by adjacent provinces of other regions. In the map presented in Fig. 5, these clusters correspond to the subdivisions formed by provinces with most similar antlion species composition (from 30 to 100%). Each subdivision is occupied by elementary faunas, which may be uniform (with the similarity between provincial faunas usually exceeding 50%) or heterogeneous, including centers of greatest faunistic diversity (diversity centers), which can also be regarded as speciation centers if they possess high number of endemic taxa (Fig. 7).

The southwestern zone sometimes shows a rather variable composition of its main clusters, depending on the method of data processing. However, analysis of this variation unambiguously reveals 6 elementary faunas corresponding to the clusters in the generalized dendrogram (Fig. 3).

The Eurosiberian elementary fauna occupies the largest and most northerly territory (the northern boundary of the antlion distribution lies to the south of the northern boundary of the Eurosiberian Province). This elementary fauna is characterized by the lowest species richness, including 1–3 species in each province. All 4 known species, including *Myrmeleon formicarius* L., which is indicative species for northeastern Palaearctic faunas, have very broad multiregional ranges.

The Central European elementary fauna covers 5 Central European provinces of the European Nemoral and Scythian Steppe Regions. It includes 23 more or less widespread species; the presence of 2 endemic species is doubtful (Krivokhatsky, 1998b). Seven species, or nearly one-third of the fauna, are uniformly distributed in all the 5 provinces: *Distoleon tetragrammicus* (F.), *Euroleon nostras* (Geoffr.), *Megistopus flavicornis* (Rossi), *Myrmecaelurus trigrammus* (Pall.), *Myrmeleon inconspicuus* (Rmb.), *M. formicarius*, and *Nohoveus zigan* (Asp., Asp., Hz.). Qualitative comparison of the faunas shows that the Central European elementary fauna is largely derived from the Mediterranean and Anatolian faunas. Some species, *Acanthaclisis occitanica* (Vill.), *Creoleon plumbeus* (Ol.), and *Synclisis baetica* (Rmb.), which occur in nearly all provinces occupied by the Central European elementary fauna, are autochthons of other provinces.

The East European–Altai elementary fauna includes 13 species, none of which is endemic; it repre-

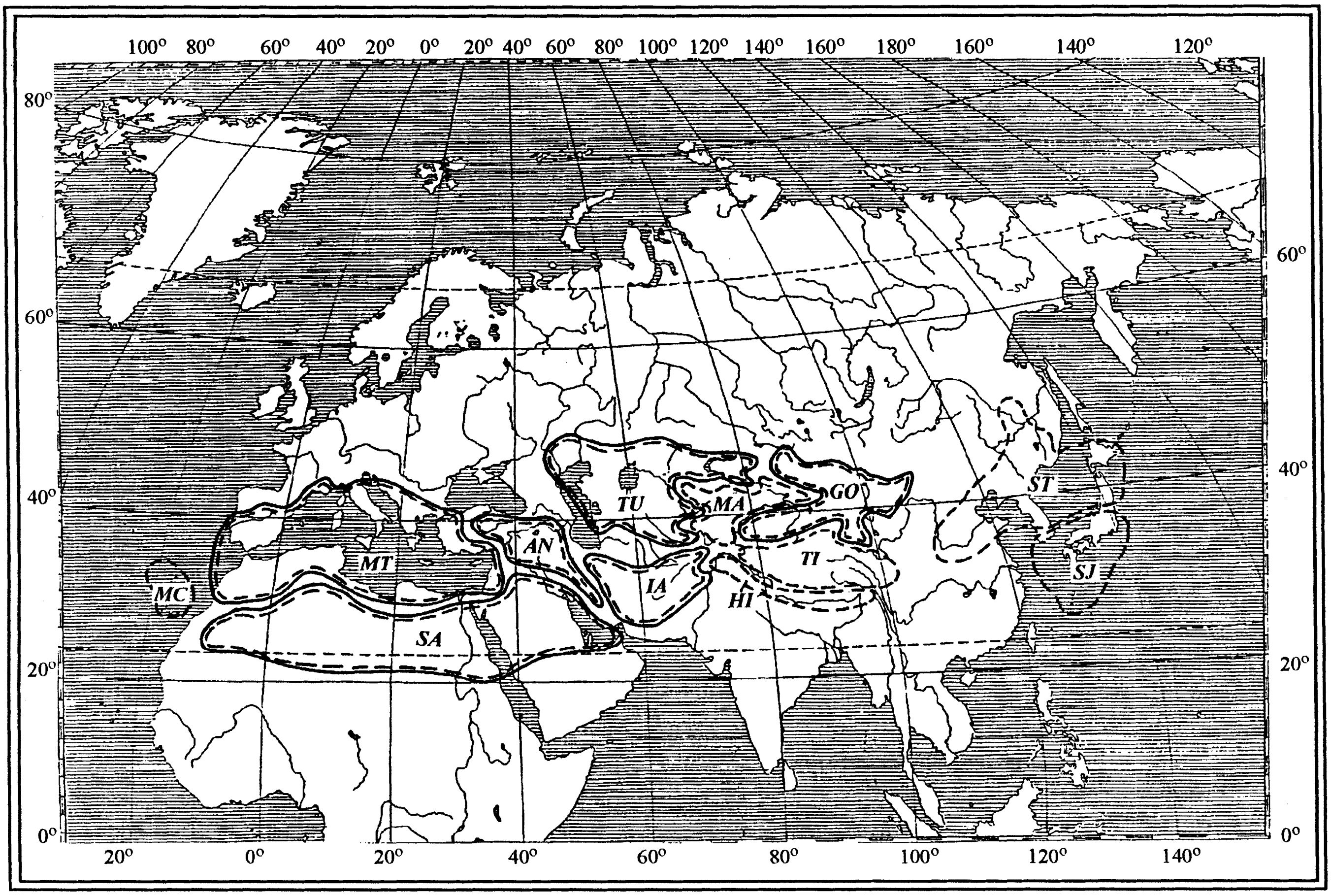

Fig. 6. Diversity centers (solid line) and speciation centers (dashed line) of antlions in the Palaearctic. Stenopean (*ST*), Gobi (*GO*), Southern Japanese (*SJ*), Himalayan (*HI*), Tibetan (*TI*), Mediterranean (*MT*), Macaronesian (*MC*), Sahara-Arabian (*SA*), Iranian–Afghan (*IA*), Turanian (*TU*), Anatolian (*AN*), and Middle Asian (*MA*).

sents a depauperate derivative of the Central European elementary fauna, occupying an intermediate position between this fauna and the poorest Eurosiberian elementary fauna. The indicator species is *Deutoleon lineatus* (F.), which occurs in all 3 provinces occupied by this fauna.

The Stenopean elementary fauna is heterogeneous (it occupies 7 provinces of 3 regions, including the entire Stenopean Region) and peculiar (5 endemic species in Stenopean Region). One species, *Euroleon coreanus* Okam., is the indicator of this fauna. Despite the relatively low species richness (12 species), the territory occupied by the West Stenopean, Korean, and North Japanese Provinces is considered a separate **speciation center**. The existence of this center is additionally confirmed by the presence of several autochthonous species, which presently have a broader distribution: *Euroleon coreanus, E. polyspilus* (Gerst.), and *Dendroleon similis* (E.-Pet.).

The Mongolian–Gobi elementary fauna is distributed in an inner territory of the Asian continent, occupied by the West Mongolian and East Mongolian Provinces of the Scythian Steppe Region and Gobi Province of Sethian Desert Region. The last area obviously represents a separate **Gobi diversity and speciation center**, comprising 11 endemic species and one entirely endemic genus *Mongoleon* Hz. This fauna has a strong influence on the faunas of the West Mongolian and East Mongolian Provinces, owing to the unstable boundary between the Gobi Desert and Scythian Steppe Region; this phenomenon, resulting from climatic fluctuations, has been observed even in the historical time (Gumilev, 1991). The reverse effect, namely migration of steppe elements (species of the genera *Myrmeleon* L. and *Nohoveus* Nav.) into northern areas of the Gobi Desert, was demonstrated earlier for a number of widespread species of Scythian origin (Krivokhatsky *et al.*, 1996). The indicators of the Mongolian–Gobi elementary fauna are, in addition to

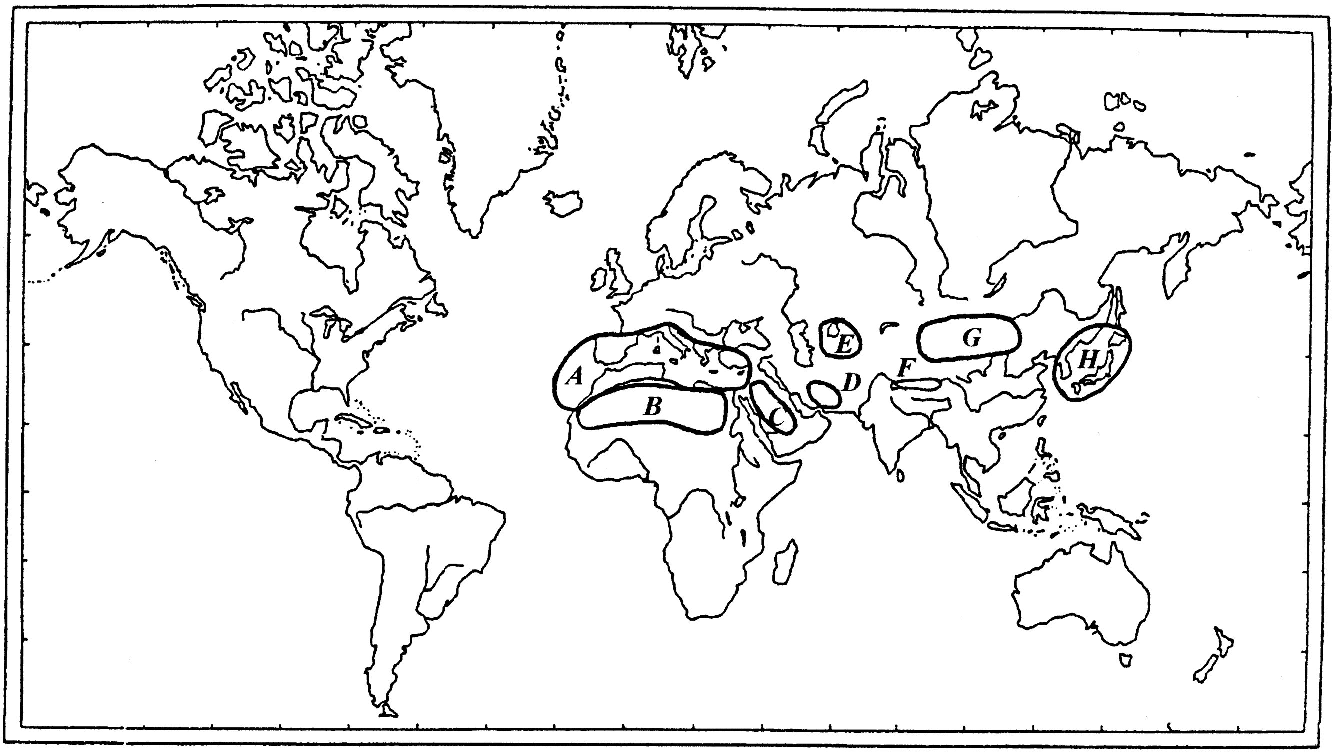

Fig. 7. Main distribution centers of antlion genera in the Palaearctic Kingdom (after Hölzel, 1986). Mediterranean (*A*), Afroeremian (*B*), Syroeremian (*C*), Iranoeremian (*D*), Turanoeremian (*E*), Nepalese (*F*), Mongolian (*G*), and Manchurian (*H*).

4 species of the genus *Mongoleon*, the species *Aspoeckiana venusta* Hz., *Lopezus fedtschenkoi gobiensis* Hz., *Mesonemurus guentheri* Hz., *M. mongolicus* Hz., and *Nohoveus atrifrons* Hz.

The South Japanese elementary fauna has been very poorly studied outside the South Japanese Province proper, and its distinctive status is subject to discussion. Consequently, this fauna is represented by a single province in the dendrogram. It includes 6 widespread species and 2 species endemic to the South Japanese Province: *Dendroleon pupillaris* (Gerst.) and *Epacanthaclisis moivanus* (Okam.). In view of these findings, a separate **speciation center** can be distinguished in this province.

The Himalayan elementary fauna, like the preceding one, lies in the territory of the Orthrian Region, but is restricted to a single province. Owing to its mountain position, this fauna has a high degree of endemism (9 out of the 11 known species). Therefore, the Himalayan Province includes a **speciation center**, which is characterized by the endemic species originating from different zoogeographical kingdoms. For example, the genus *Layachima* Nav., represented in the Himalayan fauna by the endemic species *L. nebulosa* Nav., is of Oriental origin. The species *Hagenomyia sagax* (Walk.) has a broad Oriental distribution and belongs to the autochthonous Oriental genus. At the same time, this fauna includes endemic species from the autochthonous Palaearctic genera *Indophanes* Bks. and *Epacanthaclisis* Okam. Thus, the Himalayan elementary fauna originated as a result of an interaction between the faunas of the Palaearctic and Oriental Kingdoms in the zone of their contact.

The Tibetan elementary fauna comprises 6 species, 4 of which are endemic. In the dendrogram, this fauna is represented by a separate branch, not included in either northeastern or southwestern group. Two species recorded in this fauna, *Acanthaclisis pallida* McL. and *Epacanthaclisis continentalis* E.-Pet., occur also in a number of southwestern elementary faunas; whereas the endemic species *Solter griseipennis* (Nav.) belongs to an autochthonous Mediterranean genus. In view of these facts, the Tibetan elementary fauna may be regarded as belonging to the southwestern group. However, the endemic species of the genera *Distoleon* Bks. and *Myrmeleon* are taxonomically close to their East Palaearctic congeners. Thus, the Tibetan elementary fauna has a separate **speciation center** and can be described as intermediate between the northeastern and southwestern Palaearctic faunas.

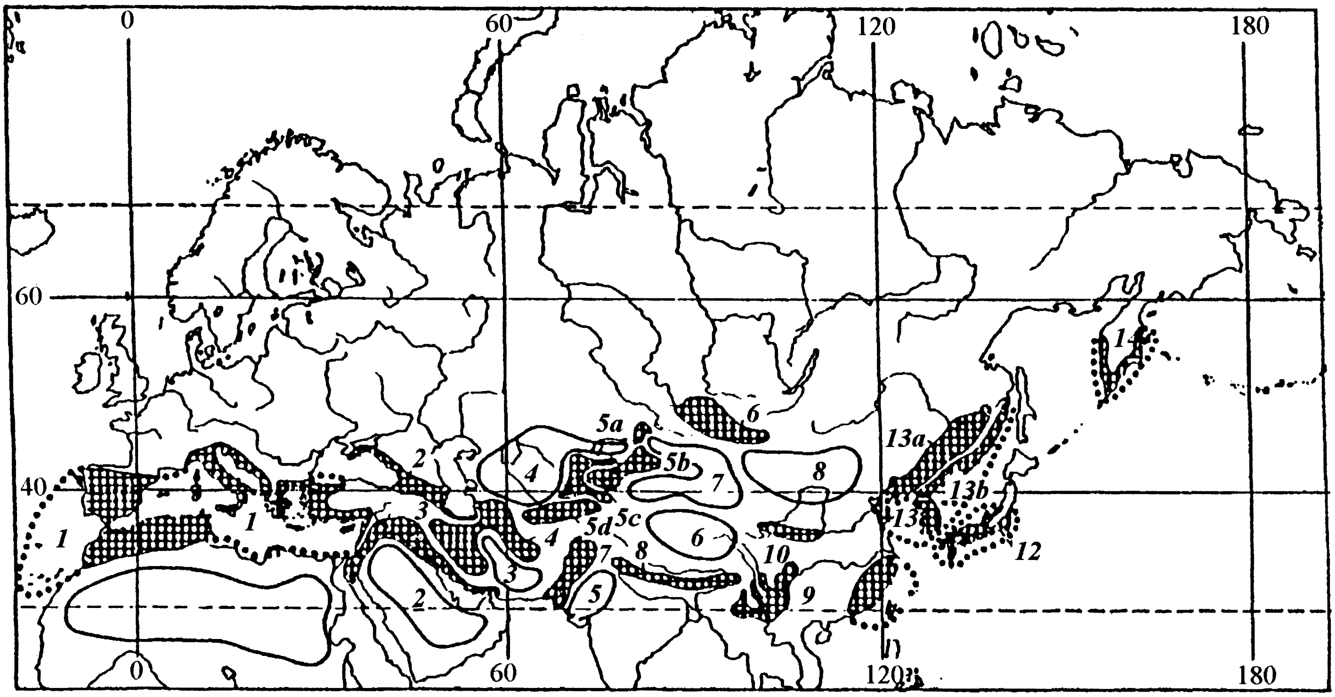

Fig. 8. Main distribution centers of species of Lepidoptera Rhopalocera in the Palaearctic Kingdom (after De Lattin, 1967). Arboreal centers (shaded): Mediterranean (*1*), Caspian (2), Syrian (*3*), Iranian (*4*), Turkestan (*5*), Mongolian (*6*), Sind (*7*), Nepalese (*8*), Yunnan (*9*), Chinese-Tibetan (*10*), Chinese-Pacific (*11*), Japanese (*12*), Manchurian (*13*), and Kamchatka (*14*). Eremic centers (unshaded): Afroeremian (*1*), Syroeremian (2), Iranoeremian (*3*), Turanoeremian (*4*), Sindoeremian (*5*), Tibetoeremian (*6*), Mongoloeremian (*7*), and Sinoeremian (*8*).

The Mediterranean elementary fauna is in all cases restricted to the West and East Mediterranean Provinces of the Hesperian Region. This territory contains a faunistic **(diversity and speciation) center**, characterized by high species richness (101 species) and considerable degree of endemism (51 species). More than half of the Mediterranean elementary fauna is represented by indicator species, whose list was published earlier (Krivokhatsky, 1998b) and need not be repeated here. This fauna is most closely linked with the Anatolian and Central European faunas.

The Sahara-Arabian elementary fauna occupies Sahara and Sumerian Provinces of the Sethian Desert Region, which constitute the largest **diversity and speciation center** of eremic antlions (132 species, 84 of these are endemic). The two provinces form a separate cluster in all dendrograms, showing the strongest affinity to the Iranian fauna with account taken of the abundance of widespread species.

The Iranian elementary fauna unites the faunas of the Iranian, Khorasan, and Afghan Provinces in all variants of data processing. If widespread species are given a greater weight in analysis, this cluster includes also Sind and Mekran Provinces; other methods of processing result in the inclusion of the Hyrcanian Province as well. The Iranian elementary fauna occupies the second place (after the Sahara-Arabian fauna) in species richness, being at the same time more heterogeneous: even the typical widespread species occupy not all of its provinces, and only a single species, *Neuroleon tenellus* (Klug), is uniformly distributed in all the 6 provinces. Ten out of the 35 endemic species are widespread in the region, whereas other 25 species are non-uniformly distributed over the provinces; 12 narrow endemics are known only from the Afghan Province. In general, the territory of the Iranian and Afghan Provinces is characterized by the greatest species richness (49 and 52 species, respectively) and endemism degree (13 and 18 species). Therefore, the **Irano-Afghan center of diversity and alpine speciation** occupies a smaller territory than the Iranian elementary fauna as a whole.

The highly specific sandy desert **Turanian elementary fauna** occupies the provinces of North and South Turan, showing a high faunistic similarity. This fauna has the corresponding **center of diversity** (46 species) **and speciation** (7 endemics). The Turanian elementary fauna was recently described in ample detail (Krivokhatsky and Piryulin, 1997). The most common indicator species of this fauna are *Cueta plexiformia* Kriv., *Lopezus karakumicus* Kriv., and *Myrmecaelurus major* McL.

The mountain **Middle Asian elementary fauna** includes 42 species, 6 of which are endemic, and occupies the territory of 4 provinces of the Sethian Region: the Turkestan, Alatau, Inner Tien Shan, and Pamir ones. Each of its endemics is distributed within a single province; therefore, the Middle Asian **diversity and speciation center** is characterized by narrow mountain endemism.

The Anatolian elementary fauna unites the faunas of the Syrian, Middle Eastern, and Kura-Araks Provinces and constitutes a separate **center of diversity** (56 species) **and speciation** (6 endemics). This fauna is to a considerable extent intermediate, being closest to the Mediterranean one; its indicator species (*Creoleon plumbeus*, *Neuroleon tenellus*), and many other common forms, also occur in the provinces inhabited by all neighboring faunas.

The Canarian and Madeiran Provinces of the Hesperian Region form a totally independent branch in dendrograms, and contain the entirely endemic **Macaronesian elementary fauna**, with its own **speciation center**. This fauna includes only 5 species and forms no diversity center. This fauna is close to, and is a derivative of the Mediterranean fauna; the latter includes all species related to the Macaronesian endemics.

Thus, the method of similarity dendrograms allowed the Palaearctic antlion fauna to be divided into 15 elementary faunas (Fig. 5), with 12 corresponding faunistic (diversity and/or speciation) centers (Fig. 6).

Using this method, we refined the number and geographical position of the centers distinguished by Hölzel (1986) based on mere superposition of generic ranges (Fig. 7). The "main distribution centers" recognized by Hölzel sometimes have the same position as those revealed in our work (Irano-Afghan–Iranoeremian; Turanian–Turanoeremian; Gobi–Mongolian; Stenopean–Manchurian; Himalayan–Nepalese), but always differ in the outline. In our opinion, the splitting of the Sahara-Arabian center into the Afroeremian and Syroeremian ones in the analysis of distribution at the species (and not generic) level is insufficiently justified; on the other hand, the completely distinct Macaronesian and Mediterranean faunistic centers can hardly be regarded as one (Mediterranean) center. In addition, the species similarity dendrograms revealed 3 distinct mountain speciation centers (Middle Asian, Tibetan, and Anatolian). The Macaronesian center, owing to its geographical isolation from the Mediterranean one (island effect), is considered a mere speciation center. Because of the high degree of endemism and small total number of species, some faunistic centers (Stenopean, South Japanese, Tibetan, Himalayan, and Middle Asian) are also regarded as only speciation, but not diversity centers.

The substantial difference in the pattern of faunistic centers results largely from different taxon ranks (genera or species), rather than from different methods applied (range superposition or cluster analysis). Analysis of distribution at the species level produces a more detailed pattern; this is probably true for all groups of insects. For example, De Lattin (1967) in his analysis of the fauna of Lepidoptera Rhopalocera at the species level, revealed 14 arboreal and 8 desert centers (Ausbreitungszentren) in the Palaearctic Kingdom (Fig. 8).

It is noteworthy that the faunistic centers revealed in three independent studies (Figs. 6–8) generally coincide. The Iranian (Irano-Afghan), Turanian, Gobi, and Himalayan (Nepalese) faunistic centers are revealed in all cases and have about the same outline for numerous groups of animals. The boundaries between other faunistic centers of the Palaearctic Kingdom are less distinct and more dependent on the distribution specificity of the groups studied. Such "complex centers" are Mediterranean (Mediterranean proper + Macaronesian), Sahara-Arabian (Sahara + Arabian), and Manchurian (Stenopean + South Japanese).

Thus, our analysis of the antlion fauna exemplifies a new methodological approach to a particular case of zoogeographical regionalization. In this approach, the elementary faunas and faunistic centers are established on the basis of a faunistic analysis of general biogeographical subdivisions, rather than on a traditional study of ranges and geobotanical or landscape-related subdivisions.

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