On the Zoogeographical Features of the Coleopterous Fauna of the Deserts of Turkmen S. S. R.

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I. General observations

There have been repeated attempts of zoogeographical description of the desert fauna of Middle Asia and of Turkmen S.S.R. in particular.

These attemps were made for the greater part on the basis of the vertebrate fauna, mostly only of the ornithofauna, while the invertebrates includ-

ing insects were almost completely ignored.

The paper by M. A. Menzbier (1914) is the best known among these attempts; although he stressed the geological antiquity of the eremian landscape, he considers the desert fauna of Middle Asia¹ as comparatively young since, according to him, it is a result of the migrations of the species from the other desert centres — the Sahara and especially the Central Asia (Mongolia and Western China) and did not originate before the Quarternary time. Many of the ornithological papers published later are based on the views propounded by Menzbier. Such are, for instance, the chapters devoted to Middle Asia in the well known book of B. K. Stegman (1936) and, during the last decade — the zoogeographical chapters of the monographs

¹⁾ Middle Asia (Средня Азия) — the term used in Soviet geographical and biological literature to designate the territory including Turkmen, Uzbek, Tadjik and Kirghis S. S. R. (formerly — Turkestan); Southern Kasakhstan and North Afghanistan (Northern Hindukush range) are often considered as parts of Middle Asia. The term "Middle Asia" is used in opposition to "Central Asia" (Центральная Азия), which includes the Mongol Peoples' Republic and the Western provinces of China (Sinkiang, Tsinghai, Tibet and western parts of Kansu and Inner Mongolia).

of G. P. Dementiev (1952) and A. K. Rustamov (1954) on the birds of Turkmenia. All these works tend to minimize the originality of the Turkmenian ornithofauna.

According to the above mentioned authors this fauna is a geologically young one and was formed at the Post-Plionebe time out of elements, heterogeneous in their origin: Mediterranean (or North-African) and Central-Asiatic species in desert regions; Mountain-Asiatic, Sino-Himalayan, Mediterranean and European species—in Kopet-Dagh and other mountainous regions.

Such a point of view finds its support in the works of certain botanist-geographers, such as M. V. Kultiasov, who insisted on the geological youth of the Middle-Asiatic desert flora and considered that "The formation of the great diversity of Antophyta is due to the turbulent processes of the progressive speciation during the recent time" (Kultiasov, 1948).

There have also been expressed quite opposite opinions regarding the great peculiarity of the fauna of Turkmen S.S.R. and the whole Middle Asia based on the presence of the very significant and apparently old endemism in this fauna. At the top of the list we must mention the numerous papers of A. P. Semenov-Tian-Shanskij, crowned by his well-known work on the zoogeographical divisions of the Palaeartic region (1936). Many other entomologists as well as herpetologists and theriologists expressed similar opinions. V. G. Heptner (1945) deserves special mention for formulating the idea of the existence of two independent centres of development of the desert fauna: Turanian, where mainly the fauna of sandy deserts developped, and Western-Asiatic or Irano-Afghanian, which was for the most part the centre of development of mountain-desert fauna.

The greater part of botanists, who have studied the deserts and mountains of Middle Asia and Turkmenistan in particular, noted the antiquity and originality of the flora of these regions. For example, M. Iljin (1946) pointed out that, if the modern phytocoenological appearance of the desert vegatation of Middle Asia is the result of the complicated reorganisation processes during the Post-Pleistocene time, the florogenetical structure of this vegetation is the consequence of a long and complicated process of its successive evolution from the Cretaceous period to the present time.

In this respect the data of B. A. Fedorovitsh (1946) are extremely valuable proving that by the results of pollen analysis are obvious not only in the Pleistocene but during the entire Pliocene time there has been a vegetation in Turkmenia closely related to the present Haloxylon-association and including such characteristic plant genera as Haloxylon, Ephedra, Calligonum Eremosparton etc.

The idea of the comparative youth of the desert fauna of Middle Asia is eagerly supported by ornithologists, G. P. Dementiev for instance (1959 etc.).

The conclusions, however, made mainly on the basis of the study of birds, cannot, unconditionnally, be applied to the entire fauna. Moreover, the laws of the geographical distributions of birds may differ strongly from those of the majority of other groups of land animals and plants. In this connection one may remind the reader of the fact that in Talysh (East Transcaucasia), so rich in endemics and relicts in nearly all groups of animals and plants, there are no endemic forms of birds.

The present paper is an attempt at a zoogeographical description of the Coleopterous fauna of the deserts of Turkmen S.S.R. (some data from other orders of Insects are included). Such an attempt seems to be all the more expedient as the opinions regarding Middle Asia in the above mentioned paper of Semenov-Tian-Shanskij (1936) require revision on account of the

abundant material accumulated during the last decades.

The entomological fauna of Turkmen S.S.R. is known at present time better than the fauna of any other Middle-Asiatic republic. Even before the Great October Revolution some extremely rich and interesting faunistical material of Coleoptera has been accumulated regarding Turkmenistan (formerly Transcaspian region). After the October Revolution the work of entomologists in this republic became still more intensive and successful. The exclusively faunistical direction of work gave way to deeper investigations in which great attention was given to the study of ecology of the separate species and their groups, their interrelation and their relation to vegetation and soil, and their significance for man.

Thus, some most interesting collections and ecological data were brought together during the thirties by K. V. Arnoldi, V. B. Popov and other members of the expeditions to the Turkmen S.S.R. (under the guidance of Aka-

demician E. N. Pavlovsky).

Still more abundant material was collected by expeditions of the Zoological Institute, Academy of Science, U.S.S.R., working in Turkmenia (mostly in the western districts of republic) at 1951—1953 and the separate workers of this Institute continued this investigation during the following years. It is also necessary to mention the extremely valuable data accumulated by J. P. Vlasov, E. L. Shestoperov, P. P. Bogush, and during last years by a group of entomologists working in the Academy of Science of Turkmen S.S.R.

The study of these immense materials is very far from completion but they served as the basis of a number of published papers in which is described a great quantity of genera and species of insects new to science, and some dozens of undescribed species are still waiting for description. However many families of insects are known so well, that they may be considered to present the sufficiently reliable material for analysis. These groups were used as a basis for the present paper.

Three families of Coleoptera have been subjected to a most detailed analysis: Scarabaeidae (Kryzhanovskij & Medvedev, 1960), Carabidae,

and Tenebrionidae. Important and interesting data were obtained in Histeridae, Buprestidae, Meloidae, Cerambycidae, Chrysomelidae, Curculionidae, and some others. Some data were given on Apoidea (V. B. Popov, 1948, 1949, 1952, 1955 etc.) Formicoidea, Orthoptera and Blattoidea (Beyblenko, 1950a, 1950b, 1951; Bey-Bienko & Mistshenko, 1951) and other groups of insects. The author is sincerely grateful to all colleagues, who participated in collecting and studying this material and communicated to him the highly valuable data.

The author's work was facilitated by his participitation in three expeditions to Turkmen S.S.R. and several expeditions to other Middle-Asiatic republics; moreover he visited a number of regions of diverse natural conditions and fauna. The series of interesting observations was made during these expeditions and important material was accumulated for comparison. Besides, the author had an opportunity to study the collections of beetles from different regions of Middle Asia and had to determine some of these collections. This circumstance promoted further accumulation of data.

It is necessary to consider the suitability of Coleoptera for zoogeographical investigations before discussing the available material. Some authors are inclined to answer this question negatively. For example, the well-known American entomologist and zoogeographer Ph. Darlington Jr. in his interesting book on the principles of zoogeography (1957) examined only the vertebrates, pointing out that insufficient knowledge of insects ought to prevent their use for the solution of zoogeographical problems. This point of view is supported by other authors. But it is necessary to notice that Darlington has published himself some excellent works on the laws of the geographical distribution of insects. At the same time the zoogeographical papers of such an eminent author as C. Lindroth (1945—1949, 1958 etc.) are based for the most part on entomological material, chiefly on the data of distribution of Coleoptera. A. P. Semenov-Tian-Shanskij (1936 etc.) and many other explorers were successful in using the data of distribution of Coleoptera for zoogeographical purposes.

The knowledge of coleopterous fauna of the world, Middle Asia and adjacent countries in particular, is still far from being complete, but this group of animals is a splendid object for zoogeographical investigations. Both the abundance of species and individuals and the extreme diversity of ecology of beetles and their larvae make them independent of any single biotical or abiotical factor. There is a considerable number of extremely polyphagous species, and a multitude of monophagous and oligophagous species among Coleoptera being closely connected with their food-plants or with a definite type of animal food. Among Coleoptera we meet consumers of all organs of living plants and all kinds of dead vegetable substances; predators and parasitoids, destroying other insects and other invertebrates; specialized inhabitants of burrows and nests of vertebrates, ants and termites. Some species of beetles are adapted to live under various conditions, but the great

majority of them is strictly attached to definite landscapes, soils and plant associations. Among *Coleoptera* there are extremely xerophilous species as well as species inhabiting water or living near to water. Many beetles are good flyers or may at least be transferred passively on air currents and in this way can overcome serious barriers; on the other hand a great number of species is wingless so that their possibilities of dispersion are restricted.

The extreme diversity of the types of range of *Coleoptera* is due to the above mentioned circumstances. As well as species, distributed nearly cosmopolitan or inhabiting extensive areas, there are still more numerous strictly localized species. The last ones are particularly numerous in the mountainous regions, but they are known also among the inhabitants of the plains.

As examples of first category in the fauna of Turkmen S.S.R. (besides cosmopolitan distributed species, being dispersed by man) the following species deserve mention: Eretes sticticus F. (subtropical and tropical regions of both hemispheres), Zuphium olens Rossi (Mediterranean region, great part of Africa and the entire South-Western, Middle and South Asia to Vietnam and South China), Cicindela melancholica F. (Mediterranean region, South-Western and Middle Asia, nearly entire Africa, except tropical rain forest, Madagascar) etc. As examples of the second category the following may be mentioned: some species of the Tenebrionid genera Lasiostola and Calyptopsis, restricted to the definit vertical zones of the separate districts of Kopet-Dagh mountains; Tenebrionid Meladiesia miritarsis Rtt. and Carabia Carabus (Axinocarabus) miles Sem. known only from Badghyz; the chafer Achranoxia varentzovi Sem. found only at few points of sandy deserts of Western Turkmenia, etc.

It is quite obvious that the species of the second category are of special value for detailed zoogeographical investigations, but nevertheless the widely distributed species should not be ignored.

The striking feature in the insect distribution in Turkmenistan is that the fauna of mountainous and plain districts of the republic are quite different. Although the low-mountainous desert zone of Kopet-Dagh and Badghyz connected these fauna to some extent, but the differences are so great that the mountains and plains of Turkmenistan should be investigated separately and even in opposition.

The insect fauna of the plain districts of Turkmenistan is not a homogenous one. The distinct sharply delimited faunistic complexes of insects inhabit on the one hand the sandy deserts, on the other — the deserts with solid soils (loamy deserts, rocky deserts and salines), on the third finally the irrigated cultured lands and tugays¹). The fauna of last two formations over-

¹⁾ Tugays — the moist, often swampy brushwoods along the large rivers of Middle Asia, they include, besides the reed and other giant grasses, also the trees and bushes from the genera *Populus*, *Salix*, *Eleagnus*, *Tamarix*, *Halimodendron* etc.

step the limits of this paper. The visible differences should be traced between the desert fauna of Western, Eastern and less investigated Northern Turkmenistan.

II. The fauna of sandy deserts

The sandy desert fauna of Turkmenistan is an especially distinctive one. Not only the abundance of endemic species should be mentioned here, but there is the multitude of genera being endemic for the sandy deserts of Middle Asia and Kasakhstan (sometimes only of Turkmenistan). Several among them are reaching the desert regions of East Caucasus, Iran, Afghanistan and Western China (Sinkiang), but they are fully absent in the deserts both of North Africa and Mongolia.

It is necessary to mention here a number of Coleopterous genera: Discoptera (Carabidae); Ammostyphrus (Histeridae); Thinorycter, Ochranoxia, Achranoxia, Chioneosoma, Dasytrogus, Leucoserica, Trigonocnemis, Pristadoretus, Eremadoretus, Eutyctus (Scarabaeidae); Petria, Cnecosochara (Alleculidae); Ammozoum, Sphenaria, Leptosphaena, Dengitha, Habrobates, Earophanta, Sternodes, Argyrophana, Diesia, Sympiezocnemis, Remipedella, Tagona, Aphaleria, Udebra, Weisea etc. (Tenebrionidae); Rhampholyssa, Lydulus, Semenovilia (Meloidae); Turkmenigena (Cerambycidae); Aphilenia, Nyctiphantus (Chrysomelidae); Mesostylus and allied genera, Brachycleonus, Leucochromus (Curculionidae) etc. The representatives of other insect groups should be added to this list, e.g. Anisogamia, Mononychoblatta (Blattoidea), Ammoxenulus (Tettigonioidea), Bufonacridella Strumiger, Thrinchus (Acridoidea), Eremaphanta, Pararophites (Apoidea), some genera of Hymenoptera parasitica and many others.

Several above-mentioned genera have doubtless affinities with the inhabitants of the desert regions of West Asia, North (and even South) Africa and the South-Western parts of North America. E. g. the longicorn beetle *Turkmenigena* belongs to the tropical tribe *Oemini*; the bees *Eremaphanta* have their allied genera in South Africa and South-Western North America.

The second, more significant part of the above mentioned genera could be considered as the derivatives of the ancient Mediterranean groups, adapted to life in the sandy desert. E. g. the Scarabaeids *Chionesoma* and *Dasytrogus* are probably the highly specialized derivatives of the widely distributed mainly Mediterranean genera *Rhizotrogus* and *Amphimallon*. Blister-beetle *Semenovilia* originates doubtless from an ancient form, allied to *Mylabris*.

The third group of genera have Central-Asiatic affinities. E. g. Discoptera (Carabidae) is related to some Central Asiatic species of Cymindis; the Tenebrionid Tagona has affinities with the less specialized Central-Asiatic genera of the tribe Blaptini; the Chrysomelid Nyctiphantus is related to the genus Theone, distributed in Kasakhstan and the mountains of Middle Asia.

Sometimes the affinities should be traced with the allied Middle-Asiatic not exclusively psammophilous genera living but in other landscapes. E. g. the Tenebrionid genus Diesia is closely related to the widely distributed genus Trigonoscelis including both the psammobionts and the inhabitants of loamy and salt deserts; and to the less specialized Kasakhstano-Mongolian genus Sternoplax. The very peculiar monotypic Tenebrionid genus Aphaleria living in the moist layer of sand is the psammophilous derivative of the genus Dissonomus as G. S. Medvedev showed recently (1959). The tettigoniid grasshoppers Ammoxenulus are related to Bergiola; the species of the last genus inhabit mainly the rocky deserts, but some of them are living in the sand desert (Bey-Bienko, 1951).

All such affinities are doubtless very ancient in any case from the Neogene and in certain cases (*Eremaphanta*, *Thrinchus* etc.) probably from the Paleogene. But still so ancient affinities could not be traced with certainty in some cases, e. g. for the very peculiar and taxonomically isolated Tenebrionid genus *Remipedella*.

Many of the above-mentioned genera are monotypic or including only few species; some other groups, as the tribe *Mesostylini* (L. Arnoldi, 1960) or the genus *Chioneosoma* are but rich in species and show intensive adaptive radiation.

Thus the voluminous list of endemics of generic level testifies with conviction to the antiquity (probably from the Paleogene) of the independent existence of Middle-Asiatic (Turanian) centre of evolution of desert fauna, sandy desert fauna in particular, and to the intensity of the autochthonous speciation in this centre. These genera are as significant from the zoogeographical point of view, as such generally known representatives of vertebrate fauna of Middle-Asiatic sandy deserts like the ground-squirrel Spermophilopsis leptodactylus, the jerboas Paradipus and Eremodipus, the shrew Diplomesodon and the gecko Crossobamon.

The second group in the insect fauna of the Turkmenian sandy deserts consist of endemic species which inhabit the sandy areas of Middle Asia (or its separate regions), but belong to the more widely distributed genera. It is possible to distinguish at least three subgroups in this numerous group.

The first of these subgroups includes the psammophilous species belonging to the genera with a range of distribution either limited to Middle Asia or having a further range as far as Iran, East Transcaucasia and sometimes even Central Asia. These genera inhabit not only sandy regions, but other biotops too. The species of this subgroup may also be considered as an autochthonous element, but are probably not so ancient and must have begun living in the sands at a later date. There are referred some species to this subgroup, as the Tenebrionids from the genera Trigonoscelis (T. gigas Rtt., T. sublaevicollis Rtt.), Cyphogenia (C. limbata Fisch.-Waldh.), Microdera (M. minax Rtt.), Scarabaeid Cyriopertha massageta Kirsch, Acridoid Diexis and some others. The psammophilous species of Phryno-

cephalus and Eremias (Lacertilia) may be considered among Vertebrata as

species of this category.

The second, most numerous subgroup consists of more or less specialized inhabitants of sandy areas, belonging to the genera, widely distributed in Mediterranean region or in the entire Palaearctic region, and sometimes having nearly world-wide distribution. The Carabid-beetles Calosoma (Caminara) deserticola Sem. (it is probably only a subspecies of C. imbricatum Klug distributed throughout the arid districts of Africa, Arabia and South Iran) and Scarites bucida Pall. are examples of this subgroup. This subgroup includes also the numerous species of the Buprestid genera Sphenoptera and Chrysobothris, living in the stems and branches of psammophilous bushes: some dung-beetles of the genera Onthophagus and Aphodius; the rhinocerosbeetles Oryctes (Eremorytes) ata SEM. & MEDV. and Phyllognathus hauseri Rtt., Histeridae of the genera Saprinus, Chalcionellus, Pholioxenus (e.g. Chalcionellus hauseri RTT., connected strictly with the stems of gigantic Orobanchaceae Cystanche flava, in which it preys on syrphid larvae; or Pholioxenus orichalceus RCHDT., inhabiting the burrows of rodents in the sandy soil), psammophilous species of Meloidae (Mylabris — M. elegantissima Zubk., M. amoenula Mén. etc., and Lytta — L. coccinea Mén., L. deserti Sem.), numerous Tenebrionidae (some representatives of Blaps, Ocnera triangularis Faust, Dichillus reitteri Sem. etc.); Cerambycidae (some species of Phytoecia and the highly specialized Prionus komarovi Dohrn, closely related to North-African species of the last genus); Chrysomelidae (numerous Cryptocephalus) etc. Of other orders the following genera deserve mention: the cockroaches Arenivaga, many bees (Halictus, Nomia, Megachile, Anthophora etc.) sphecoid-wasps (Bembex, Stizus, Ammophila, Sphex etc.), ants Messor excursionis Rusz., Monomorium barbatulum Mayr, M. gracillimum F. Sm. and the highly specialized pale yellow Cataglyphis pallida MAYR.

The third subgroup of this group consists of endemic species of sandy areas of Middle Asia (its southern parts in particular) belonging to the genera inhabiting, besides Middle Asia, the subtropical and tropical deserts of Africa, South-Western Asia and Western Indostan. They may be concerned as the recent derivatives of the fauna of tropical arid regions. The number of species of this subgroup is not so great as of the precedent one, but the subgroup in question includes some extremely characteristic species. Few of these species may be listed, e.g. the gigantic ground-beetle Anthia (Pachymorpha) mannerheimi Chaud. — the single representative in the fauna of U.S.S.R. of the subfamily Anthinae, including many species in the deserts and savannahs of Africa and several species in South-Western Asia and Indostan. The chafers *Pharaonus* are also significant; two species of this genus are frequent in the sandy areas of Turkmenistan on the flowers of Calligonum, the other species are living in Transcaucasia, Iran and North-East Africa: the genus *Pharaonus* is the desert derivative of the immense genus Popillia, inhabiting the forests and savannahs of tropical Africa, South and East Asia. Some genera of Scarabaeidae have a similar distribution, as Dynamopus isolated in the system and forming a seperate tribe (one species — D. athleta Sem. — in sandy deserts of Middle Asia and others species in Iran and the South Sahara), or Coptognathus (C. attila Mén. living in sandy deserts of Turanian lowland and other species inhabiting North Africa southwards to Sudan and the middle course of the Niger). Both Middle-Asiatic species of Phonapate — Ph. chan Sem. and Ph. deserti Sem. — may be referred to this subgroup; they are feeding in the stems of psammophilous bushes; the other species of the genus are known from the Sahara and the African savannahs.

The Histeridae Philothis probably may be drawn together with the last subgroup. They are the extremely specialized inhabitants of the deep layers of sand; five species are known from Middle Asia (four of them being found in Turkmenistan) and some others from North-Eastern and North-Western Africa. The acridoid grasshoppers Hyalorrhipis have a similar range of distribution, they are sand-dwellers with specialized structure of legs and wonderful "sandy" protective coloration; two species of this genus are living in Middle Asia (one of them is restricted to its southern parts) and the rest—in Iran, southernmost Europe and in particular in North Africa and Arabia.

One little group is closely resembling the preceding group, its second and third subgroups in particular. It includes the widely distributed psammophilous species common to Middle Asia and other desert regions of Asia and Africa. As its representatives the following can be mentioned. Calosoma (Campalita) algiricum Géh. (Carabidae), distributed in the deserts of North Africa, Iraq, Iran and Turkmenistan; the Scarabaeids Brenskea varentzovi Sem. and Eremazus cribratus Muls., known from the Sahara to Turanian lowland; and the large Buprestid Capnodis excisa Mén., feeding on Calligonum and distributed from Sinai and Arabian peninsula to Aral Sea.

The last and most heterogenous group among the sand beetles of Turkmenistan is formed by the species, distributed not only in sandy areas, but also in other types of deserts or even in other landscapes and geographical zones. The species are most numerous in this group, living mostly in the sections with solid soils but penetrated also in sands, the anchored sands in particular. Some widely distributed species belong to this group, e.g. Scarabaeus sacer L., Gymnopleurus coriarius HBCT., Aphodius lugens CREUTZ., Coccinella undecimpunctata L., Mylabris crocata Pall.

III. The fauna of desert plains with solid soils

Endemics of Middle Asia are of less importance in the fauna of solid soils of desert districts as in the sands and the endemism here being of specific level mainly, that is probably more recent. As to the genera, the most part of them having wide ranges, included frequently South-Western Asia and North Africa. There are numerous species whose ranges of distri-

bution extend far from the limits of Middle Asia. Many species, living on the plains with solid soils are found also in the lower mountainous-desert zone of Kopet-Dagh and other mountainous regions of Turkmen S.S.R.

The comparatively poor fauna of the strongly salted districts has some very characteristic components. Some of these species are connected with the saline vegetation, e.g. Chrysomelid genus Ischyronota, many weevils of the genera Bothynoderes, Conorrhynchus, Entimetopus etc. The others the predators and detritophagous forms — are living in the soil or on its surface. The Carabids are especially numerous among them, belonging to the genera widely distributed in the Mediterranean region and Middle Asia, e. g. Cicindela (C. lunulata F. distributed on the salt-marshes and the shores of seas and salt-lakes from the Atlantic coast of Europa and North-Africa to North China, C. deserticola Fald. etc.), Dyschirius, Clivina (C. ypsilon Dej.), Pogonus, Chlaenius, [Ch. (Chlaenites) spoliatus Rossi, Ch. (Trichochlaenius) steveni Quens.], Anisodactylus (A. pseudoaeneus Dej.), Brachinus (B. hamatus Fisch.-Waldh., B. cruciatus Quens.) etc. Some of these genera are specific saline-inhabitants, as Daptus and Dichirotrichus. The large tiger-beetle Megacephala euphratica Dej. is of particular interest, being distributed from South Spain and Morocco to South Daghestan, Uzbek S.S.R. and Afghanistan; it is the single Palaearctic representative of the tribe Megacephalini, inhabiting all tropical regions of the world; this species is digging on the salt-marshes deep vertical burrows in which it conceales itself by day and goes out for prey at night.

The Tenebrionidae are also numerous on the saline soils, but only few of them are specific halophilous forms, e. g. the species of the genus Paranemia and probably the recently described Trigonoscelis (Pseudeuthriptera) uzboica Bog. & Kryzh. Some other species of this family are not exclusively halophilous, but are prevalent on the salted soils, such as the species of the genus Scleropatrum, Arthrodosis intermedius Rtt. and Zophosis scabriuscula Mén.

The innumerable Tenebrionids are especially characteristic for the loamy deserts and stony-deserts (hammadas), e. g. the species of the genera Arthrodosis, Microdera, Calyptopsis, Colposcelis, Zophosis, Adesmia, some Trigonoscelis (T. muricata Pall., T. punctipleuris Rtt.), Ocnera (including Trachyderma), Pimelia cephalotes Pall., Blaps, Gonocephalum, some Lobodera, Belopus, Hedyphanes etc. The weevils of the genera Conorrhynchus, Bothynoderes, Megamecus, Phacephorus are also very numerous (in the spring in particular); the common Ammocleonus aschabadensis Fst. and the more rare Georginus bellus Sem. are characteristic for the sections with very poor vegetation. Some species of Carabidae are concealing themselves by day light in the cracks of the soil; by night they are coming out of their shelters and fly often to the light; e. g. Siagona europaea Dej., species of Cymbionotum and Apotomus, Scarites (Distichus) planus Bon., some species

of Pterostichus of the subgenera Poecilus and Angoleus, Amara [A. (Celia) saxicola Zimm. and A. (Phanerodonta) murgabica Tschit. in particular], Glycia ornata Klug, and peculiar Bedeliolus vigil Sem., endemic for South Turkmenistan and North Iran. The chafers are relatively scanty represented here (Madotrogus glabricollis Rtt. is characteristic for loamy desert), but very numerous are dung-beetles of the genera Hybosorus (H. illigeri Reiche) Aphodius, Onthophagus, Gymnopleurus, Chironitis etc. Buprestidae are numerous here also, the species of Sphenoptera in particular, but especially characteristic are some large Buprestids, e.g. Julodis variolaris Pall. a widely distributed Middle-Asiatic and Kasakhstanian species; J. iris Cast., an inhabitant of South-Western Asia with its northern border in Turkmenistan; and Lampetis argentata Mnnh., the single representative of the immense genus Lampetis in the fauna of U.S.S.R.; other Lampetis are living in the tropical regions of the both hemispheres.

The small species of Buprestidae, Chrysomelidae, Bruchidae, Curculionidae, some Meloidae and other phytophagous beetles are rather numerous on the sections with more rich vegetation.

Of great interest is the small but very peculiar biological group of Coleoptera, living on the Umbelliferous genus Ferula, which originates from the mesophilous tertiary ancestors. This group includes the weevils Lixus desertorum Gebl., the Buprestids Anthaxia anatolica Chevr., A. lucidiceps Gory and some species of Acmaeodera living in the stems of Ferula. The longicorn beetle Plocaederes scapularis Fisch. is also a member of this group, its larvae are living in the lower parts of the stem and in the roots of Ferula; the species is widely distributed in deserts and mountains of Kasakhstan, Middle Asia, Iran and Afghanistan — everywhere when the species of Ferula are growing. It is undoubtely the autochthoneous species of this region, but closely related with tropical fauna in its origin; all other of *Plocaederes* (more than 50) are living in tropical Africa and Asia and only two of them crossed the borders of tropical zone in North Africa. Finally, the both species of endemic and probably autochthoneous Middle-Asiatic phytophagous Carabid genus Machozetus (Dioctes) — M. lehmanni Mén. and M. concinnus Dohrn — are feeding on the seeds of Ferula and supplying with these seeds the burrows of their larvae.

The insect population of the *Tamarix*-brushwoods is still more peculiar, but this formations is not a typically desert one and the analysis of its fauna is beyond the limits of our investigation.

If one tries to analyse the range of species, inhabiting the landscape in question, greater dependence (greater than in sands) of the sizes of these ranges to the ability of a species to dispersion draws our attention. The species with reduced wings, e.g. many *Tenebrionidae* and some weevils, having rather limited ranges in most cases. Some of them are endemic to the comparatively small regions of Turkmenistan, e.g. the above mentioned

Trigonoscelis uzboica Bog. & Kryzh. found only at two points on Western Uzboi, or Calyptopsis incerta Fst., Arthrodosis orientalis Rtt. and Leptodes zubkovi Sem., characteristic for the Western parts of the republic and absent in its Eastern districts. On the other hand the ranges of forms with strong flight activity are frequently very wide, e. g. Cicindela melancholica F., C. lunulata F. and Zuphium olens Rossi; or such species as Siagona europaea Bon., Cymbionotum semelederi Chaud., Scarites (Distichus) planus Bon., Zuphium testaceum Klug, Hybosorus illigeri Reiche, Gonocephalum setulosum Fald., Opatroides punctulatus Brullé etc. The ranges of the listed species include the Mediterranean region (or its Eastern part at any rate), all South-Western and Middle Asia, the Western Indostan and more or less considerable regions of tropical Africa.

This rule has rather numerous exceptions, e. g. the flightless but widely distributed Tenebrionids Pimelia cephalotes Pall., Adesmia servillei Sol. (fagergreeni Baudi) and Mesostena puncticollis Sol. The first named species is distributed through West, Central and South Kasakhstan, Middle Asia and North Iran; the second one inhabits Iraq, Iran, Afghanistan, Western Pakistan and South Turkmenistan (it is restricted here by the vast, nearly barren plains, so called "takyrs"); the third one is known from North-East Africa, Arabian peninsula, Iraq, Iran and few points of South Turkmenistan. It is noteworthy that the first two species form series of very distinct subspecies. Among good flyers, on the contrary, some species have restricted ranges, the fact which in a series of cases is probably stipulated by the corresponding distribution of their food plants (e. g. in some Buprestids of genera Sphenoptera and Acmaeodera, Chrysomelid Cryptocephalus etc.); and in some other cases, as in Carabids Amara (Phanerodonta) murgabica TSCHIT. and Bedeliolus vigil SEM., may be caused by the adaptation to very peculiar environmental conditions.

The fauna of the examined types of Turkmenian deserts — loamy deserts, stony deserts and salines — as a whole includes a great number of endemic species from all considered families of *Coleoptera*. The specific endemism and the generic one in particular are but more feeble as in sandy deserts; and the species are numerous here, distributed beyond the borders of Middle Asia in South-West Asia, in arid districts of Mediterranean region and still in tropical regions of Africa and Asia.

Many of the genera represented here are characteristic and in some cases endemic for the region, including the southern parts of Middle Asia, Iran, Afghanistan and partly Eastern Transcaucasia. There may be mentioned for example the Carabid Bedeliolus, tenebrionids Arthrodosis, Calyptopsis, weevils Ammocleonus and Georginus. Such genera probably should be considered as autochthonous forms, but not originated in the Turanian sandy desert centre, but in other centre in which developed the fauna of loamy deserts and often of mountainous deserts.

IV. The fauna of mountainous-desert zone

The effect of the above mentioned centre is noticeable to a greater extent in the fauna of lower mountainous-desert zone of the Kopet-Dagh Mts. and of Badghys plateau. The great number of species is represented in this fauna, living on the lowland districts of Turkmenistan, but nearly all characteristic inhabitants of sandy deserts and many species living on the salt-marshes and takyrs are absent on foot-hills. But numerous species and some genera are added, characteristic for the desert low mountains of South Middle Asia, North Iran and North Afghanistan, and many of them are endemic for Kopet-Dagh and other parts of Turkmeno-Khorassanian mountain system.

Only from the examined families of Coleoptera the following shall be mentioned as such endemics: Carabids Taphoxenus (Stenolepta) transcaspica Sem., T. (Pseudotaphoxenus) turanicus Zn. in litt., Scarabaeids Lethrus cicatricosus Rtt., L. spinimanus B. Jak., L. turcomanicus Sem., Hemictenius tekkensis Rtt., Rhizotrogus (Xanthotrogus) sieversi Rtt., Potosia persica RTT. and Tenebrionids of the genera Tentyria (T. robustoides RTT.), Gnathosia (G. skobelewi Starck, G. hydrobiiformis Rtt. etc.), Pachyscelis (P. gemmans Baudi), Stalagmoptera (S. ruginota Rtt.), Lasiostola (L. elongata Kr., L. nitens Rtt., L. ashkhabadensis Bog. & Kryzh., L. nephelidis Rtt. etc.), Prosodes (P. solskyi Fst., P. jakowlewi Sem., P. cribrella Baudi etc.), Dendarus (D. vagabundus RTT.), Zophohelops (Z. lazarus RTT. and 3—4 still undescribed species). There may be added to this list of endemic species the Staphylinid Physetops giganteus Sem., Buprestid Capnodis jacobsoni Richt., Meloid Mylabris karakalensis Kryzh., weevils Alexiola romadinae Zasl. and Baris kryzhanovskii Zasl., many acridoid grasshoppers, e. g. the species of Mizonocara, Melanotmethis fuscipennis Uv., large and clumsy Saxetania cultricollis Sauss. and S. paramonovi Dirsch etc. Some of the above mentioned species stretched slightly from the foothills to lowlands, but they were never be found in any distance from the mountains or hills.

The investigations of last years proved that some species formerly reputed as endemic of Kopet-Dagh are really distributed more wider. The large and outstanding Carabid Calosoma (Caminara) reitteri Roeschke was considered to the recent time as endemic of the Turkmenistan mountains and was very rare in the collections. It was ascertained during the last some years, this species is common on the foothills of Kopet-Dagh and Badghys, but its activity season is restricted to a short period of early spring (not later than middle of April); moreover it was found in two remote localities of Kasakhstan (on the east of Turgai and in Tshu-Ili mountains); probably it is widely distributed in the ephemer-plant formations of Middle Asia, but retains imperceptible because of the peculiarities of its phenology. These data make to treat with some caution to the other species reputed as endemic of the region in question, but they can not refute the fact of numerosity here of the real endemics.

There may be mentioned some more species characteristic of the mountainous-desert zone of Kopet-Dagh, but not restricted to the Turkmeno-Khorassanian mountains, e. g. Scarabaeids Amphicoma analis Sols.— an inhabitant of the foot-hills with ephemeral vegetataion of South Middle Asia, North-East Iran and North Afghanistan, and Aethiessa bagdadensis Burm. from the mountainous-desert zone of Western Kopet-Dagh, Iran and Iraq; the large Buprestid Capnodis anthracina Fisch.-Waldh. known from the lower mountains of Turkmen and Tadjik S.S.R. and North-East Iran (it is apparently feeding on Atraphaxis); Tenebrionids Pimeliocnera darwini Fst. and Lobodera remota Rtt. not rare in the lower parts of Kopet-Dagh and inhabiting the most part of Iran to Luristan and Kerman.

The majority of the listed species have affinities in the fauna of the mountains — the lower mountains and foot-hills in particular — of Middle Asia, North Iran and North Afghanistan; only few of them have related species in the fauna of Middle-Asiatic lowlands and in South-Western Asia, the affinities with Africa are almost absent.

The above mentioned examples definitely testify to the great originality of the fauna of Kopet-Dagh mountainous-desert zone. This fauna is probably also the result of autochthonous speciation but of quite another origin than the sandy desert fauna. It is bound more closely with the fauna of other low-mountainous districts of South Middle Asia, North Iran and North Afghanistan.

This fauna may be considered as the derivative of an independent mountainous desert centre, for which I suggest the name "Irano-Bactrian centre". The term "Irano-Afghanian centre", suggested by V. G. HETTNER (1945) and by other authors, seems to be less suitable so far as the significance of the Middle-Asiatic parts of this centre is not reflected in the last term.

V. Some peculiarities of the fauna of myrmecophilous Coleoptera of Turkmen S.S.R.

It seems to be expedient to attempt an analysis of zoogeographic affinities of some components of the highly original sinusia of myrmecophilous *Coleptera* in Middle Asia as yet hardly investigated. Their range of distribution is usually more or less correlated with the range of their hostants.

The majority of better known Turkmenian myrmecophilous beetle species are living on the solid soils, only few species, moreover less specialized ones, inhabit the sandy areas.

¹) Bactria — the ancient region of Middle Asia is situated on the northern slopes of the Hindukush range and on the middle course of the Oxus (Amu-Daria). Different regions of contemporary Tadjik, Uzbek and Turkmen S.S.R. and northern Afghanistan were included in Bactria during different historical epochs.

We have seen among these myrmecophilous *Coleoptera* first of all some species undoubtelly related to tropical ones; the ants they live with have tropical affinities too.

For example Paussus turcicus Friv. — the single representative in the fauna of U.S.S.R. of the tropical family Paussidae; it lives in the nests of Pheidole pallidula Mayr — also the only species found in our fauna of the widely distributed genus for the main part tropical. It is interesting that the majority of other Paussidae are connected with the species of Pheidole. Commatocerus turkmenicus Kryh. was discovered recently (Kryhanovskij, 1957) at the foothills of Kopet-Dagh, and is the representative of the genus previously known only in tropical Africa (Ethiopia, Congo). It was found in a nest of the ant Acantholepis frauenfeldi Mayr, belonging to the genus distributed mainly in Ethiopian realm. The biology of another derivative from tropics. Eremoxenus chan Sem. found only in South Turkmenistan is still unknown; it is the single representative of the tropical family Brenthidae in the fauna of U.S.S.R.; there are reason sto suppose this species being myrmecophilous, because its other relatives of the tribe Amorphocephalini are so.

Some genera of myrmecophilous Tenebrionids have other types of distribution. The range of several of these genera is limited to Middle Asia and adjacent parts of Iran and East Transcaucasia, for example Platamodes with the single species P. dentipes Mén. living mainly in the nests of Messor, or Oogaster, who's Middle-Asiatic species O. lehmanni Mén. was found in the nests of Cataglyphis and Messor. The genus Reitterella Sem. with 2 or 3 poorly known species was found only in Turkmenistan. Two species are known in the genus Microblemma — M. simplex Sem. living in the nests of Cataglyphis setipes turcomanica Em. in Turkmenistan and recently described M. afghanica Kasz. from Afghanistan.

G. S. Medvedev found at the most recent time on the Kuhitang range (East Turkmenistan) in the nest of *Tetramorium* still one quite separate blind genus *Kuhitangia* G. Medv. in litt., probably from the family *Colydiidae*.

Several species of the large Mediterranean genus *Thorictes* (fam. *Thorictidae*) are living in the Southern parts of Middle Asia. They are the specialized commensalists of *Cataglyphis* and other ants.

There are some less specialized myrmecophiles among the *Tenebrionidae*, for example *Scleron carinatum* Baudi, living in Turkmenistan in the nests of very different genera of ants; the genus *Scleron* has a number of species and is distributed throughout tropical and subtropical regions of Eastern hemisphere. The species of *Dichillus* may also be considered here; some of them for instance. *D. tenebrosus* Rtt. and sand-dwelling *D. reitteri* Sem. can not be reputed as really myrmecophilous species because they are living (probably as scavengers) both in the nests of very different ants and in the rodent burrows. Other *Dichillus* are evidently the more specialized

inhabitants of ant-nests, as D. schusteri Rtt. known from few localities in

Kopet-Dagh in the nests of Pheidole pallidula.

The myrmecophilous Staphylinidae and Pselaphidae of Middle Asia are nearly unknown. However it is clear from above mentioned examples, that the myrmecophilous Coleoptera of Turkmenistan show the high specific and generic endemism and undoubted relations with tropical fauna. On the other hand, the widely distributed Palaearctic myrmecophilous groups of beetles are but slightly represented here or fully absent.

VI. The differences between the fauna of Coleoptera of different regions of Turkmen S.S.R.

We shall discuss now the peculiarities of the insect fauna of different desert regions of Turkmenistan, first of all the difference between the fauna of its western and eastern parts.

We have some cases among the inhabitants of all types of deserts when in the West of the republic are living species replaced in the East by other closely related forms (species or sometimes subspecies). Such cases are especially numerous among the relatively well known *Tenebrionidae*; there is no doubt that one can meet such pairs also in other families of Insects.

For example Argyrophana caspia Sem., Dengitha crystallina Sem., Sternodes caspicus caspicus Fisch.-Waldh. and Discoptera komarovi tschitscherini Sem. are living in the sandy deserts of Western Turkmenistan. Argyrophana deserti Sem., Dengitha lutea Rtt., Sternodes caspicus eous Sem & Bog. and Discoptera komarovi komarovi Sem. replaced them in Eastern and especially in South-Eastern parts of Kara-Kum desert. Arthrodosis orientalis Faust and Calyptopsis incerta Faust are characteristic for the loamy deserts of Western Turkmenistan and are replaced by A. schusteri Rtt. and C. clypeata Fst. in Eastern districts of the republic; it is interesting in the last case, that the range of both paires of species is covered by each another in Central Turkmenistan, in the environments of Ashkhabad in particular.

Similar pairs of species are known in other families. For instance, the psammophilous Scarabaeid Achranoxia varentzovi Sem. is found in Western Kara-Kum, and very similar A. koenigi Ret. living in the North, centre and South-East of this desert. The weevil Mesostylus hauseri Ret. widely distributed in the sandy deserts of south Middle Asia, is replaced by the

closely related M. uzboicus L. Arn. in Western Kara-Kum.

Still more convincing cases of geographical vicarism are known among the inhabitants of mountainous-desert zone. Several small species of the genus Lasiostola (Tenebrionidae) are living on foot-hills of Kopet-Dagh; L. nitens Rtt. is characteristic for the Western Kopet-Dagh (one subspecies living on its Northern slopes near Kasandjik and Kizyl-Arvat and the second one — in the valley of river Sumbar); L. ashkhabadensis Bog. & Kryzh.

(L. minima auct., nec Mén.) replaces the preceding species in the environments of Ashkhabad; L. nephelidis Rtt. inhabits Eastern Kopet-Dagh and Badghyz. The species of Tentyria and Zophohelops show the similar regularities of its distribution.

There are other more essential distinctions between the fauna of West and East Turkmenistan, besides the geographical vicarism of the related species. Some characteristic species of Tenebrionidae are known only from the Western parts of the republic, e.g. Trigonoscelis pseudoechinata Bog. (T. echinata auct., nec Fisch.-Waldh.), T. (Pseudeuthriptera) uzboica Bog. & Kryzh., T. (Ps.) steinbergi Bog. & Kryzh., Microdera fausti Kr. and probably Colposcelis longicollis Zoubk. (old data on the finding of the last species in Eastern Turkmenistan are not confirmed by the more recent investigations). On the other hand Urielina nitida Baudi, Meladiesia miritarsis Rtt., Carabus (Axinocarabus) miles Sem., the Chafers Cyphonoxia (C. glazunovi Sem., C. brenskei Rtt.) etc. are found only in East and South-East Turkmenistan.

Still more peculiar is the poorly known fauna of the Kuhitang range on the extreme East of the republic; there are some endemics and many forms are common with the low mountains of South Uzbekistan and Tadjikistan.

It may be stressed however that many species reputed formerly as the endemics of South-East Kara-Kum and mostly described from the well studied Repetek, were found later in other parts of Turkmenistan.

Finally, we shall examine some peculiarity of the feebly known insect fauna of Northern Turkmenistan. Several species found here are extremely characteristic for Northern (Kasakhstanian) deserts but are fully absent in South Middle Asia, e. g. the Tenebrionids Lasiostola pubescens Pall. and Sternoplax deplanata Kryn. There are some endemics in this region, e. g. Mylabris kuzini Kryzh. described recently from the sandy deserts of Tashaus region. The detailed description of North-Turkmenian insect fauna is still impossible because of the insufficient data.

VII. Conclusions

- 1. In zoogeographical literature one usually finds the conception of the relatively small originality of the Turkmenistan's desert fauna which is generally considered of recent formation. It is believed to date from the Post-Pliocene time and supposed to have come there as a result of migration of the Mediterranean and Central-Asiatic faunistic elements. This opinion is based mainly on the investigations of bird fauna and is not confirmed by the data on many other groups of animals, on *Coleoptera* in particular.
- 2. The insect fauna of the deserts of Turkmenistan and the other Middle-Asiatic republics includes a great number of highly specialized endemics, not only the species but also the genera and sometimes of a

higher taxonomic level. Besides this endemic nucleus, there are in this fauna migrants from the other centres (Central-Asiatic, South-Western-Asiatic, Saharo-Sindhian etc.) and the relation could be traced to the fauna of tropical arid regions, with the Ethiopian realm in particular.

The abundance of endemic genera confirms the antiquity of this Middle-Asiatic (Turanian) centre of evolution of sandy desert fauna and the inten-

sity of autochthonous speciation in this centre.

3. The insect fauna of lowlands of South Turkmenistan with the solid soils (loamy deserts, salt deserts and hammadas) is very different from the fauna of sandy deserts. It includes a great number of endemic species, but the generic endemism is comparatively insignificant and many extremely widely distributed forms are present here.

The insect fauna of mountainous-desert zone of Kopet-Dagh and Badghys is closely related, but the specific endemism is still more expressed and there is a close relationship to the fauna of other low-mountainous regions

of Middle Asia, Iran and North Afghanistan.

This fauna may be considered as the derivative of the centre of evolution of mountainous-desert fauna, existing on the above mentioned territories. Heptner (1945) named this centre Irano-Afghanian and the author of this paper proposes the name "Irano-Bactrian".

4. There are differences between the insect fauna of the desert districts of different parts of Turkmenistan which can be used as a reliable basis for the more detailed zoogeographical delineation.

Summary

The opinion is repeatedly expressed in zoogeographical literature about the small originality of the Turkmenistan's desert fauna, which is believed to be of the Post-Pliocene age and originated as a result of migration of Mediterranean and Central-Asiatic elements. This opinion is not confirmed by the data on Coleoptera. The insect fauna of Turkmen deserts has a large endemic nucleus including many genera and a great number of species. Particularly great is the abundance of endemics in the sandy desert fauna, which confirms the antiquity of Turanian centre of evolution of sandy deserts and the intensity of autochthonous speciation in this centre. The lowlands with solid soils (hammadas, loamy and salt deserts) have the fauna very different from that of sandy deserts: the generic endemism is insignificant here, but the number of endemic species is great. Still more endemics have the mountainous-desert fauna of Kopet-Dagh and Badghyz; it is closely related to the fauna of other low-mountainous regions of Middle Asia, Iran and North Afghanistan and many be considered as the derivative of another centre of evolution, for which the name "Irano-Bactrian" is proposed. The differences between the insect fauna of different parts of Turkmenistan can be used as a basis for the more detailed zoogeographic delineation.

Zusammenfassung

In der zoogeographischen Literatur wird häufig die Ansicht vertreten, daß die Turkmenische Wüstenfauna im späten Pliocän als Ergebnis der Einwanderung mediterraner und zentralasiatischer Elemente entstanden sei und wenig Originalität besitze. Diese Ansicht wird durch coleopterologische Untersuchungen nicht bestätigt. Die

Insektenfauna des Turkmenischen Wüstengebietes besitzt einen großen endemischen Kern, der mehrere Gattungen und eine große Anzahl von Arten umfaßt. Besonders groß ist die Fülle von Endemismen in der Sandwüstenfauna, die damit das Alter des Turanischen Entwicklungszentrums der Sandwüsten und die Intensität der autochthonen Entwicklung in diesem Zentrum bestätigen. Die Ebenen mit festem Boden (Hammadas, Lehm- und Salzwüsten) besitzen eine von der der Sandwüsten völlig verschiedene Fauna. Hier sind Endemismen von Gattungen unbedeu tend, aber die Zahl der endemischen Arten ist beträchtlich. Noch mehr Endemismen besitzt die Gebirgswüstenfauna des Kopet-Dagh und Badghyz. Sie ist eng verwandt mit der Fauna anderer Gebirgsregionen Mittelasiens, Irans und Nordafghanistans und läßt sich von einem anderen Entwicklungszentrum ableiten, für das die Bezeichnung "Irano-Bactrisches Zentrum" vorgeschlagen wird. Die Unterschiede zwischen der Insektenfauna der verschiedenen Teile Turkmenistans lassen sich als Grundlage für genauere zoogeographische Abgrenzungen verwenden.

Резюме

В зоогеографической литературе широко распространено мнение, что фауна пустынь Туркменистана мало свое образна и представляет постплиоценовое образование, сложившееся путем миграции из Средиземноморья и Центральной Азии. Данные по жесткокрылым не подтверждают этого мнения. В энтомофауне пустынь Туркменистана имеется мощное эндемичное ядро, включающее многие роды и очень большое количество видов. Наибольшее количество эндемиков отмечено в фауне песчаных пустынь, что говорит о древности туранского очага развития этих пустынь и об интенсивности автохтонного формообразования в этом очаге. Пустынные равнины с плотными почвами (глинистые, каменистые и солончаковые) имеют фауну, сильно отличающуюся от песчаных пустынь, с незначительным родовым эндемизмом, но с большим числом эндемичных видов. Еще больше эндемиков в горно-пустынной фауне Копет-Дага и Бадхыза, которая тесно связана с фаунами других низкогорных районов Средней Азии, Сев. Ирана и Сев. Афганистана и является производным другого очага формирования фауны, для которого предлагается название ирано-бактрийского центра. Различия между энтомофаунами различных районов Туркменистана могут служить основой для детального зоогеографического районирования.

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