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APPLIED PROBLEMS OF ARID LANDS DEVELOPMENT

Taxonomic Diversity of Insects from the Relic Steppes of the Mid-Lena River Valley (Central Yakutia)

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Abstract—Data on insects of the central Yakutian steppes preserved in the relic state since the Late Pleistocene are presented. Orthoptera, Homoptera, Heteroptera, Coleoptera, and Diptera are used as examples to demonstrate that, in addition to meadow and meadow-steppe species, these steppes are inhabited by species belonging to an extrazonal steppe fauna–genetic complex comprising five elements: Eurasian, Dauria–Mongolian, Black Sea–Kazakhstan, desert–steppe, and mountain–central Asian. Disjunctive areas are characteristic for these species.

Keywords: insects, Orthoptera, Homoptera, Heteroptera, Coleoptera, Diptera, fauna, steppe, central Yakutia, Siberia.

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A peculiarity of central Yakutian landscapes is relic steppes, which were described by botanists as early as the 1900s (Cajander, 1903; Abolin, 1929; Dolenko, 1913; Drobov, 1914). Steppe sites are situated among massifs of larch taiga and occupy forest-less edges of river valleys on southern slopes, altitudinal river terraces, and thermokarstic alas kettles. In the Late Pleistocene, steppe communities spread throughout the periglacial zone of northern Eurasia (Velichko, 1973), and during the Holocene interglacial pockets were preserved in central Yakutia, in the northeast in Verkhoyanskaya and Oimyakon kettles, and along the upper reaches of the Kolyma River (Karavaev, Skryabin, 1971; Yurtsev, 1981). The main factors facilitating the preservation of these steppes in northeastern Asia are the acutely continental, dry climate with high summer and extremely low winter temperatures, and deficient precipitation comparable to the Lower Trans-Volga Region, under conditions of a powerful underground ice complex (Gavrilova, 1973). D.I. Shashko (1961) remarked noted that the summer climate in central Yakutia resembles that of the steppe in terms of structure; in terms of absolute and relative humidity, it differs little from steppe areas of Kazakhstan.

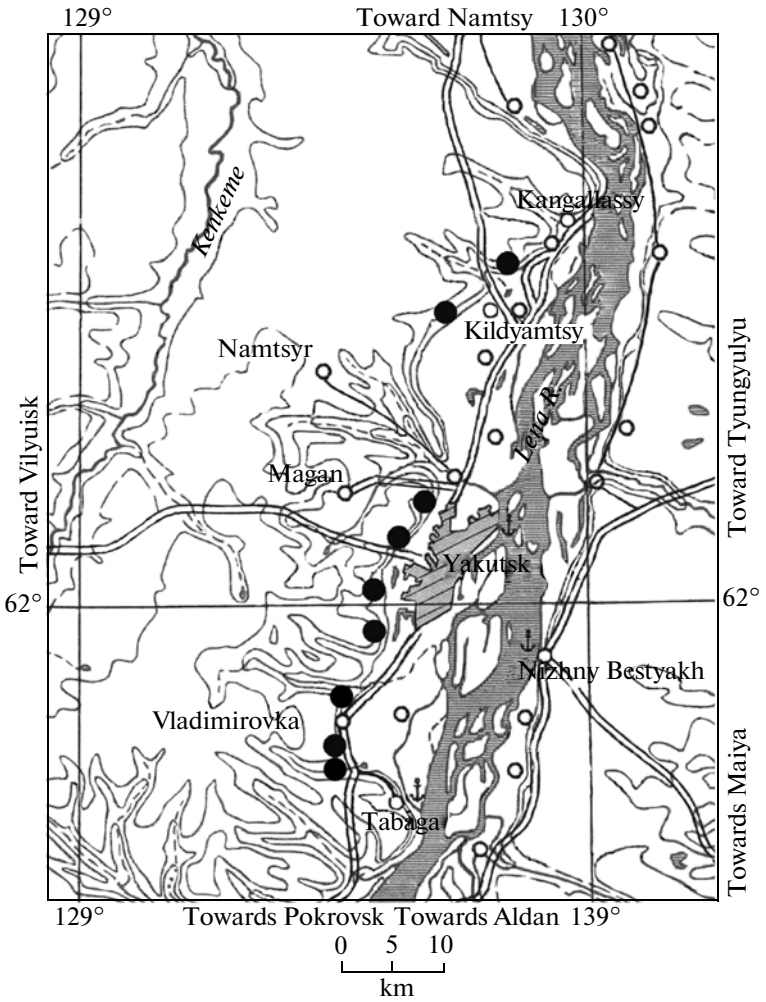
No special research on the entomological fauna of Yakutian steppes has been conducted to date. In the literature, there are disparate data on various insect groups: Orthoptera (Ermakova, 2003), Coccids (Danzig, 1978), leafhoppers (Emeljanov, 1976; Sivtsev and Vinokurov, 2002), Hemipterans (Vinokurov, 1979a, 1979b), Chrysomelids (Medvedev and Ammosov, 1978), weevils (Korotyaev, 1977; Korotyaev and Ter-Minasyan, 1977); and cornflies of the genus *Meromyza* (Narchuk and Fedoseeva, 1980). In these papers, data are presented on the existence of an extrazonal steppe complex of insects in the boreal taiga fauna of this part of eastern Siberia and on disjunctive areas belonging to this complex that had not been observed earlier.

In the present paper, results of studies of insects of true steppes in the middle part of the Lena River valley are described. Studies devoted to the complex investigation of the flora and arthropod populations of steppe landscapes in central Yakutia were carried out at the Institute of Biological Problems of the Cryolithozone, in the Siberian Branch of the Russian Academy of Sciences.

MATERIALS AND METHODS

The studies were conducted at an expanded site of the Lena River valley called "Tuimaada" (61°52′N, 129°31′E and 62°18′N, 129°49′E), 60 km long and a maximum of 14 km wide, in 2007–2009. This report is based on materials collected at ten sites of relic steppes, located on the slopes of the primary bank (figure), as well as data collected in preceding years by the authors.

Due to agricultural development and expansion of the territory of the city of Yakutsk, ecosystems of the Tuimaada valley have long been subject to anthropogenic impact. The natural steppe vegetation has also been transformed. Thus, V.P. Ivanova (1971) pointed



Layout of surveyed sites on the slopes of the Tuimaada valley.

to the disappearance of primary fescue–stipa steppes, which were widespread on superinundated terraces in early the 20th century (Abolin, 1929; Dolenko, 1913). Today they have been replaced by greatly expanded digressive steppes, while stipa, wormwood, and hard-sedge formations of true steppes have remained predominantly on the slopes of the primary bank of the Lena River (Zakharova et al., 2009). The cleistogenic formation described by Ivanova (1971) is also absent, and *Cleistogenes squarrosa* is only a codominant or adulterant in stipa and wormwood formations.

The stipa formation, which is among the most widespread, occupies southern, eastern, and western expositions on the valley's slopes. Typical are forbs (*Stipa capillata*, *Pulsatilla flavescens*, *Artemisia commutata*, *Chamaerhodos erecta*, or *Orostachys malacophylla*), wormwood–stipa (*Stipa capillata* and *Artemisia frigida*), and stipa–forbs associations (*Stipa capillata*, *Pulsatilla flavescens,* and *Artemisia frigida*).

Wormwood steppes with predominant *Artemisia frigida* are distributed at the same expositions of slopes as stipa steppes. Most frequently observed are stipa–wormwood (*Artemisia frigida*, *Stipa capillata*, and *Cleistogenes squarrosa*) associations, while cleistogenic stipa–wormwood (*Artemisia frigida*, *Stipa capillata*, and *Cleistogenes squarrosa*), wormwood–hard sedge (*Carex duriuscula* and *Artemisia frigida*), and wormwood–large gramineous (*Artemisia frigida*, *Calamagrostis epigeios*, *Leymus littoralis*, and *Stipa capillata*) associations are rarely seen.

The hard-sedge formation has been described on the slope of the southeastern exposition of the mountain Chochur-Muran, and two plant associations are distinguished here: forbs–gramineous (*Agropyron cristatum*, *Festuca lenensis*, *Stipa capillata*, and *Pulsatilla flavescens*) and hard sedge–graminaceous (*Carex duriuscula*, *Agropyron cristatum*, *Festuca lenensis*, and *Elytrigia repens*).

Insect counts at the grass layer were carried out by collection with entomological nets, with the subsequent reduction of results to 50 wags. Orthoptera were similarly collected during a preset period of time, and the results were reduced to 1 h (Gause, 1930; Pravdin et al., 1972). Grades of dominance are presented

Faunal composition of insects of the Tuimaada valley steppe

Orders	Number of species		Number of genera		Number of families	
	Steppes	Meadows	Steppes	Meadows	Steppes	Meadows
Odonata	12	28	7	11	4	7
Orthoptera	11	27	8	16	2	3
Homoptera	106	140	45	80	9	9
Heteroptera	57	About 130	46	86	11	14
Thysanoptera	12	29	7	16	3	3
Coleoptera	69	About 150	54	77	14	17
Lepidoptera	78	116	59	66	9	10
Hymenoptera	29	–	22	–	11	–
Diptera	97	About 200	45	90	11	18
Total	471	Above 800	293	About 440	65	81

according to Kontkanen (1948). The volume of collected material consisted of approximately 25000 arthropods, of which 24000 specimens were insects.

RESULTS AND DISCUSSION

As the conducted studies have shown, the grass layer of relic steppes of the Lena River valley is inhabited by four groups of arthropods: ticks, spiders, centipedes, and insects. The latter are represented by 12 orders: Collembola, Odonata, Orthoptera, Psocoptera, Thysanoptera, Homoptera, Heteroptera, Coleoptera, Neuroptera, Lepidoptera, Hymenoptera, and Diptera. For dragonflies, which develop in water reservoirs, steppe vegetation sites are hunting territory. In addition, counts include single cases of Trichopterans, which are also not permanent inhabitants of steppe cenoses.

The composition of the steppe entomofauna of the Tuimaada valley has been studied insufficiently. The diversity of Orthoptera, Coleoptera, Heteroptera, and some families of Diptera is revealed rather well. On the whole, there are limited data on such major orders as Hymenoptera and Diptera, while inferior Lepidoptera, Collembola, and some other orders remain unstudied. Thus, at the current stage of research, the insect fauna of steppes in the Tuimaada valley is known to include 471 species of 293 genera, 65 families, and 9 orders (table). Homoptera (106) and Diptera (97) prevail, followed by Lepidoptera (78), Coleoptera (69), Heteroptera (57) and Homoptera (106); the other orders (Odonata, Orthoptera, Thysanoptera, and Hymenoptera) are currently represented by 12–29 species. The real volume of steppe insect fauna, taking into account the erratic examination of taxons, evidently exceeds these numbers. The fauna of some families is more diverse: Chloropidae, 45 (Diptera); Aphididae, 35; Cicadellidae, 42 (Homoptera); Miridae, 19 (Heteroptera); and Carabidae and Curculionidae, 17 species each (Coleoptera). From 6 to 15 species were revealed in the following families: Acrididae, 9 (Orthoptera); Lygaeidae, 9; Pentatomidae and Rhopalidae, 8, (Heteroptera); Thripidae, 8 (Thysanoptera); Chrysomelidae, 7 and Coccinellidae, 6 (Coleoptera); Nymphalidae, 15; Geometridae, 14; Noctuidae, 14; Satyridae, 12; Lycaenidae, 9 and Pieridae, 8 (Lepidoptera); Chamaemyiidae, 9; Ephydridae, 7; and Conopidae, 6 (Diptera). Other families have 1–5 species.

The low taxonomic diversity of steppe insects in the Tuimaada valley, confined to slopes of southern exposition and high levels of super-floodplain terraces, becomes visible when compared with the fauna of true and damp meadows of super-floodplain and inundated terraces. The table below provides comparative data on some well-studied orders. Only 11 species of acridoid katydis and grasshoppers are manifested in steppes, while meadows are occupied by 27 species of Orthoptera, including many mesophils and hygrophils, as well as some eurymesophils. The number of species and genera of Hemipterans is twice as low as in meadows, and mesophils and hygrophils disappear. The same picture of fauna depletion can be traced in orders of damselflies, thrips, coleopterans, lepidopterans, and dipterans. Thus, the examined relic steppes of central Yakutia are largely inhabited by stenoecic specimens of steppe biota, with their main habitat lying far to the south, and xerophil meadow-steppe and meadow species.

According to D.I. Berman (2008), the heat supply in mountainous steppes located in the sub-Arctic zone on southern bank slopes of the Kolyma River's upper reaches is very high and comparable with that of the mountainous steppes of Altai. At a depth of 1 cm, the sum of positive soil temperatures reaches 2500°C; given the longer warm period, this measure should be even higher in central Yakutia (up to 3000°C). This factor, along with the serious siccation of the upper layer of soil, creates an acute temperature–humidity regime; as a result, meso- and hygrophilous species tend to avoid areas of steppe vegetation and are only incidentally registered along their periphery. This can

explain the scarcity of insect fauna of the Yakutian steppes.

The average number of chortoecic insects in all steppe plant associations under survey was 490 specimens/50 wags. This indicator was greatest in stipa–wormwood, heterogramineous–grassland, and grassland–stipa steppes: 1845, 1805, and 1510 specimens/50 wags, respectively. The minimum numbers (172 specimens/50 wags) are typical of the stipa steppe.

In the chortoecic community, four dominant orders are remarkable in terms of season-averaged values of abundance according to Kontkanen's gradient (Kontkanen, 1948). Diptera account for about one-third (23.4%, or 155 specimens/50 wags) of the total numbers of chortoecic insects; Heteroptera (17.9%, 88 specimens/50 wag); Homoptera (16%, 78 specimens/50 wag); Thysanoptera (15.5%, 75 specimens/50 wag). Two orders, Coleoptera (11.1%, 55 specimens/50 wags) and Hymenoptera (8%, 39 specimens/50 wags), pertain to influents. Indicators for all other orders are below 6%.

CHARACTERISTICS OF MAIN ORDERS OF INSECTS

Given below are the characteristics of the five insect orders comprising the core of insect fauna of relic steppes in the Tuimaada valley.

Order Orthoptera

Relic steppes of the Tuimaada valley are inhabited by 11 species from the families Tettigonidae (2) and Acrididae (9). Steppe (7) and forest–steppe (3) species comprise the basic fauna, and one forest-dwelling species has been recorded (*Aeropus sibiricus* L.). According to M.G. Sergeev (1986), most species (6) pertain to the steppe–west Asian fauna–genetic complex (*Montana montana* Koll., *Omocestus haemorrhoidalis* Charp., *Glyptobotrus maritimus jacutus* Storozh., *Aeropedellus variegatus variegates* F.-W., *Euthystira brachyptera* Ocsk., and *Bryodemella tuberculata* F.); two species belong to the forest–steppe–east Palearctic complex (*Chorthippus fallax* Zub. and *Celes skalozubovi* Adel.). The steppe–central Asian, forest–steppe–west Palearctic, and forest–east Palearctic complexes are represented by one species each (*Gampsocleis sedakovi* F.-W., *Chorthippus albomartginatus* De Geer, and *Aeropus sibiricus* L., respectively). Polyzonal trans-Palearcts dominate by type of habitat (64%), followed by north steppe–west Palearctic species (18%); steppe–European-Siberian (9%) and forest–forest-steppe Siberian-Pacific species (9%) are also represented. Most steppe Orthopterans are cereal-dwelling (46%) in terms of the spectrum of life forms and facultative (27%) chortobionts, while other species are undercover geophils, eremobionts, and specialized phytophils (9% each). In terms of food specialization, phytophages prevail, comprising all specimens of the Acrididae family. The family Tettigoniidae is divided into zoophages and phytozoophages, the former being represented by the large grasshopper *G. sedakovi*, and the latter, by the smaller one, *M. montana*. As a rule, communities of Orthopterans dwelling in central Yakutian steppes are comprised of a few species (3–10), most of them being *G. maritimus jacutus*, *G. sedakovi*, *M. montana*, and *B. tuberculata*. *G. maritimus jacutus* dominated in virtually all surveyed steppe communities, with abundance indicators varying in the range of 12.3–80%.

Order Homoptera

In the relic steppes of Yakutia, populations of Homopteran insects are represented by four suborders, which are numerous, especially leafhoppers. Their characteristics by suborder are given below.

Suborder Cicadinea. According to the data collected by Sivtsev and Vinokurov (2002), 43 species from 31 genera and 4 families dwell in the steppes and meadow steppes of the territory in question. The extrazonal steppe element in the studied fauna is very high, up to 34.9%, which is evidence of close genetic bonds with zonal steppes in the Palearctic. Eurasian steppes are represented by 7 species; Dauria–Mongolian, 4; Black Sea–Kazakhstan, 1; and desert–steppe, 1. For central Yakutia, A.F. Emeljanov (1976) described two steppe endemics of the genus *Mongolojassus* Em. Interestingly, they pertain to different groups of species that are not closely related, and *M. jakuticus* Em. was found only on the right shore of the Lena River, while *M. vinokurovi* Em. dwells only on the left shore.

The remaining 28 species of leafhoppers are widely occurring meadow xerophiles and eurymesophils; they occupy meadow steppes and are found on steppe slopes. Horologic analysis showed that they are dominated by trans-Palearcts (27.9%) and species spread throughout the Asian part of the continent (16.3%).

Suborder Coccoidea. According to Danzig (1978), steppe sites are occupied by 12 species of Coccids, of which the steppe fauna–genetic complex is represented by the Eurasian steppe and Dauria–Mongolian elements. Six species pertain to the former; they are related to cereals, mainly fescue. They are two species of the genera *Phenacoccus*, *Metadenopus festucae* Sulc, *Rhodania porifera* Goux, and *Euripersia tomilini* Newstead; one species, *Rhodococcus spiraea* Borh., lives on *Spiraeae media*. The Dauria–Mongolian element includes *Heliococcus pavlovskii* Borh. d. Terez. and *Euripersia herbaceae* Danzig. *Phenacoccus discadenatus* Danzig is a steppe endemic. The remaining three species are widespread dwellers of dry meadows.

Suborder Psyllinea. According to data of the authors and the literature (Loginova, 1961, 1963, and 1966; Klimaszewski 1983; Labina and Evdokarova, 2009), there are 40 known species in the Yakutian fauna. At steppe sites of the Tuimaada valley, the authors collected 6 species, of which *Bactericera cur-*

vatoventris Förster and *B. rossica* Horvath are new for Yakutia.

Suborder Aphidinea. According to the authors, 39 aphid species pertaining to 17 genera of 4 families dwell in the studied steppes. The scope of their trophic relationships is wide and includes mainly background plants belonging to families of Poaceae, Asteraceae, Brassicaceae, Rosaceae, Apiaceae, Scrophulariaceae, etc. Chorological analysis is deemed impossible at the current stage due to insufficient data on the geographic distribution of these species. However, it should be noted that the vast majority of habitats of aphids harvested in steppes are very wide and represented by multiregional, Holarctic, trans-Palearctic, and trans-Eurasian types.

Order Heteroptera

At steppe sites of the Lena River valley, confined to slopes of southern exposition, 57 species from 11 families have been revealed. This is one-fifth of the bug fauna occurring in the middle-taiga subzone of Yakutia. The families Miridae (19), Lygaeidae (9), Rhopalidae (8), and Pentatomidae (8) are most representative. Most Heteroptera collected are phytophages (48 species), trophically related to cereals, legumes, Rosaceae, the goosefoot family, and crucifers, as well as steppe mosses, etc. The carnivore complex includes nine species: four species of the genus *Nabis* (Nabidae), two steppe species of the genus *Orius* (Anthocoridae), *Deraeocorus punctulatus* Fall. (Miridae), *Geocoris arenarius* Jak. (Lygaeidae), and *Zicrona caerulea* L. (Pentatomidae). Dominants of the grass layer are *Lygus gemellatus* H.-S. (in meadow steppes, dwelling on Compositae), *Leptopterna albescens* Reut. (steppe, on cereals), *Dictyla platyoma* Fieb. (meadow steppe, on *Lappula echinata*), *Stenodema virens* L. (meadow, on cereals), and *Aelia klugii* Hahn. (meadow, on cereals). In the ground layer, the steppe polyphage *Lygaeosoma sibirica* Seid prevails.

Hemipterofauna of the studied steppes includes three fauna–genetic complexes: steppe, meadow-steppe, and meadow (Vinokurov, 1979a).

The specific weight of the relic steppe complex in the middle-taiga subzone of Yakutia is surprisingly high and reaches 35.6% (16 species). The main habitat of these bugs lies far to the south in the steppe zone, whereas Yakutian habitats are disjunctive and confined to the dry central Yakutian province and Olekminskii enclave of steppe vegetation in southwestern Yakutia. Holarctic (2), Eurasian steppe (7), Dauria–Mongolian (5), and desert–steppe (2) types of habitats are typical of steppe species.

The meadow-steppe complex contains 11 xerophilous species (24.4%), which are found in steppes, meadow steppes, and steppe meadows in Yakutia. Very broad temperate areas are characteristic for this complex, i.e., trans-Palearctic (6), west-central-Palearctic (4), and trans-Eurasian (2 species).

The meadow complex includes 18 xerophilous and mesophilous species (40%), which as a rule are confined to the fringes of steppe plots, adjacent to moister habitats, i.e., forest edges along narrow valleys and edges of water reservoirs at the foot of slopes. Hygrophilous and eurymesophilous bugs from neighboring meadow and swampy sites go to the steppe's periphery. Species of this complex pertain to boreal and temperate xero- and mesophilous meadow and eurymesophilous meadow–forest species and have broad habitats: Holarctic, 4; trans-Palearctic, 6; west-central-Palearctic, 2; and European–Siberian, 6.

Order Coleoptera

According to the data available to the authors, about 120 steppe and meadow Coleopteran species dwell at steppe sites of the surveyed territory. Carabid beetles (25), Chrysomelid beetles (22), and weevil prevail here; ladybugs (7) and capricorns (7) were also recorded, and other families are represented by 1–5 species. Typical steppe species are Carabids *Pseudotaphoxenus dauricus* F.-W., *Carabus kruberi* F.-W., *Poecilus fortipes* Chaud., and *Microlestes minutulus* Gz.; the blossom beetle *Cteniopinus altaicus* Gebl. (a new species for the Yakutian fauna); the borer *Cylindromorphus pyrethri* Stierlin.; blister beetles *Meloe violacea* L. and *Mylabris aulica* Men.; leaf beetles *Cassida lineola* Creutz., *Cryptocephalus equestris* Gebl., and *Labidostomis imitatrix* Ogi. et. L. Medv.; the hister beetle *Saprinus spernax* Mars.; the antlike flower beetle *Notoxus raddei*; and ladybugs *Adonia amoena* Fald. and *A. variegate* Gz.

In accordance with L.N. Medvedev and Yu.N. Ammosov (1978), the fauna–genetic complex is represented in the Yakutian fauna of leaf beetles by Dauria–Mongolian (8%) and Eurasian steppe (3%) elements.

Order Hymenoptera

The fauna of Hymenoptera in the Tuimaada valley has been studied little, and most data are on the suborder of Symphytans (Kaimuk and Popov, 2003; Popov and Kaimuk, 2007; Popov, 2004 and 2008). During the study, the authors revealed 29 species of 22 genera and 11 families. The basic list consists of bees (13 species); a poorer abundance of wasps (10 species) is observed, and sawflies and ants together account for 6 species.

The family Tenthredinidae. The largest family of sawflies is represented in the richest abundance in moderate and northern latitudes of the Holarctic. There are three species of sawflies: *Allantus cinctus* L., *Dineura viridorsata* Retz., and *Selandria serva* F. Larvae (caterpillars) are leaf-eating phytophages, and imago feed on flower nectar. *Selandria serva* dwelling on cereals is the most characteristic for the steppes.

The family Formicidae. Typical carnivores, they are an inseparable part of insect cenoses, and they are almost always observed in masses. There are three spe-

cies (*Formica gagatoides* Ruzs., *F. picea* Nyl., and *Camponotus saxatilis* Ruzs.) from two genera, and *Formica picea* and *Camponotus saxatilis* are characteristic representatives of steppe landscapes in Yakutia (Dmitrienko and Petrenko, 1976).

Wasps. This taxon is represented by ten species of four families: Pompilidae (*Anoplius viaticus* L. and *Ceropales maculata* F.), Sphecidae (*Ammophila campestris* Latr., *A. pubescens* Curt., *Lestica alata* Panz., and *Tachysphex pompiliformis* Panz.), Mutillidae (*Myrmosa atra* Panz.), Vespidae (*Allodynerus delphinalis* Gir., *Polistes riparius* Sk. Yamane, and *Pseudepipona herrichii* Sauss.). All species are entomophages except *Myrmosa atra*, which is an insect ectoparasite. Vespidae seem to be the most useful of the wasps, because as social insects they have the broadest spectrum of food resources. Specialization of sole fossorials and spider wasps is narrow; as food for larvae, they hunt only on spiders and therefore decrease the number of entomophages.

Bees. The vast superfamily of bees (Apoidea) includes numerous specialized pollinators, broadly represented in steppe biocenoses. This group incorporates 13 species from 5 families (Colletidae, Halictidae, Megachilidae, Apidae, and Andrenidae), of which Halictidae (*Anthidium punctatum* Latr., *Evylaeus jakuticus* Pes. et Dav., *E. subfulvicornis* Blüthg., and *Seladonia leucahenea* Ebm.) and Apidae (*Epeolus cruciger* Panz., *E. variegata* L., *Psithyrus bohemicus* Seidl., and *P. rupestris buyssoni* Vogt.) are the most numerous.

Order Diptera

The Dipteran fauna of steppes and steppe meadows includes specimens of 39 families, out of which 97 species from 45 genera of 11 families were identified. Chloropidae (44 species), Syrphidae (25), Chamaemyiidae (9), and Ephydridae (7) manifest diversity and species richness; other families include 1–3 species.

In terms of biotopical confinement, steppe (35 species, 36%), meadow-steppe (8, 8.3%), and meadow (54, 56.7%) groups are most distinguished. The first two groups are of interest for chorological analysis.

The total diversity of the steppe group of Dipterans can be divided into 16 types. Widespread species (23, 65.7%) are predominant: multiregional polyzonal (1), Holarctic polyzonal (4), trans-Palearctic polyzonal (8), trans-Eurasian temperate (2), Euro-Siberian–central Asian temperate (1), west-central Palearctic (1), and Euro-Siberian temperate (6). These thermophilic species seem to be genetically related to steppe landscapes, as, judging by their numbers, the habitation optimum falls on steppe meadow and steppe sites. A narrower geographic dispersion, comprising 6 types, has been revealed for 12 species: east-Palearctic temperate (1), Siberian–American temperate (1), east Siberian–central Asian temperate (1), Kazakhstan–Mongolian temperate (1), Dauria–Mongolian temperate (5), and east Siberian boreal (3).

Broad habitats are typical of meadow-steppe Dipterans: multiregional polyzonal (1), trans-Eurasian (2), Euro-Siberian–central Asian (2), west-central-Palearctic temperate (1), Euro-Siberian (1), and east Siberian–far eastern temperate (1).

Representatives of the families Chloropidae, Chamaemyiidae, and Ephydridae are numerous in relic steppes and meadow steppes. Among cornflies, the steppe species *Meromyza zachvatkini* Fedos. is frequently found in net collection, up to 100 specimens/50 wags; in grassland–stipa steppe at the bottom of slopes, its abundance may reach 224 specimens/50 wags. The diversity of Chamaemyiidae flies is greatest on steppe slopes, where 7 species are found; at steppe meadows in the Lena River valley and alas hollows of Lena–Amga interfluves, only 3–4 species were collected, predominantly from genus *Chamaemyia*. Specimens of *Ch. subjuncorum* Tanas. (up to 28 specimens/50 wags) and, sometimes, *Ch. aestiva* Tanas (up to 48 specimens/50 wags) are most numerous. Plant-eating meadow species of ephedrids from the genus *Psilopa* (with a large population of *P. stackelbergi* Nartsh., up to 72 specimens/50 wags) are widely represented. Widespread hoverflies from the xerophilous genus *Paragus*—*P. lelejii* Mutin and *P. tibialis* Fall.—are also typical of true steppes.

CONCLUSIONS

A total of 421 insect species has been revealed in relic Pleistocene steppes of the Tuimaada valley; they are incorporated in 285 genera of 76 families from 9 orders. The fauna includes species pertaining to steppe, meadow-steppe, and meadow fauna–genetic complexes. Disjunctive areas are typical of steppe and some meadow-steppe species. In this case, the main section of the habitat is located in the southern arid part of Eurasia; the minor section is located in the north in central Yakutia and in the northeast beyond the Verkhoyanskii range.

According to the results of chorological analysis conducted for various orders of insects, the steppe fauna–genetic complex includes five elements: Eurasian steppe, Dauria–Mongolian, desert–steppe, Black Sea–Kazakhstan, and mountain–central Asian. Analysis of the zoogeographic relationships among the species of the extrazonal element, under conditions of the taiga zone of the steppe complex, shows that the formation of the fauna of the relic steppes in central Yakutia in its modern shape took place over a long period of time; and repeated expansions of the steppe fauna seemingly took place in different periods. For example, the presence of single desert–steppe species spread throughout central Asia and Kazakhstan points to ancient contacts between biotas of the studied region and deserts of the ancient Mediterranean. The last penetration of steppe and

meadow-steppe insects into the ñentral Yakutian plain could possibly have taken place in the Middle Holocene 4000–6000 years ago, in the Xerothermic period.

The presence of a series of relic west-central-Palearctic species is characteristic for the meadow-steppe complex; along with steppe species, they are found in the Cryolithozone of Siberia in areas with better heat supply, i.e., at sites of xerophyte steppe vegetation.

Compared to the population in the bottomland meadows and terraces above the floodplain, the insect fauna of the steppes of the Lena River valley is essentially poor. The high xerophytic degree of steppe and meadow-steppe landscapes, occupying the slopes of southern exposition and the high-level terraces above the floodplain, hinders the colonization of these stations by meso- and hygrophilous components of the local fauna. Therefore, the core of the fauna is comprised of stenoecic steppe species, meadow-steppe and meadow xerophils, while low numbers of mesophilous and hygrophilous insects invade the periphery of these communities and are found in mesophilous microcaverns, which highlights the mosaic nature of the steppe communities.

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