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Zoogeographic relationships between true bugs (Heteroptera) in the fauna of relict forest-steppes of the middle taiga subzone of Yakutia and the steppes of southern East Siberia

Зоогеографические связи полужесткокрылых (Heteroptera) реликтовых степей среднетаежной подзоны Якутии и степей юга Восточной Сибири

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KEY WORDS: True bugs, Heteroptera, Central Yakutia, extrazonal steppe, East Siberia, fauna, zoogeography.
КЛЮЧЕВЫЕ СЛОВА: Полужесткокрылые, Heteroptera, Центральная Якутия, экстразональные степи, Восточная Сибирь, фауна, зоогеография.

ABSTRACT. This paper presents a comparative chorological analysis of the steppe complex of true bugs (Heteroptera) in three regions: the south of East Siberia, relict steppes of the middle taiga subzone, and mountain steppes of North-East Yakutia. The study reveals the presence of ancient connections between the entomofauna of the last two territories and the steppe biota of the south of East Siberia, which aligns with botanical data indicating the Dauro-Mongolian roots of relic steppe phytocenoses in the middle taiga subzone of Yakutia. The analysis includes 52 species from 13 families, with Euroasian steppe (25), Eastern steppe (17), Desert-Steppe (2), Central-Asian montane Eastern steppe (4), and North-East Siberia subendemic (2) distributional ranges. In North-East Yakutia, the steppe true bug fauna is found to be less diverse, consisting of 33 species, including 11 Euroasian steppe, 7 Eastern steppe, 1 Desert-Steppe, 14 mountain-steppe species with disjunctive Altai-Sayan-Khangai-Eastern steppe and North-East Siberian ranges, as well as local endemic ranges. Overall, the steppe complex of relic steppe phytocenoses in the middle taiga subzone and northeastern Yakutia is considered an impoverished derivative of the steppes and forest-steppes of southern East Siberia. It also reveals evidence of ancient faunogenetic relations with the desert biota of Central Asia. The findings provide valuable insights into the historical biogeography of the studied regions.

РЕЗЮМЕ: Проведен сравнительный хорологический анализ степного комплекса полужесткокрылых юга Восточной Сибири, реликтовых степей среднетаежной подзоны и горных степей Северо-Востока Якутии. Показано наличие древних связей энтомофауны рассматриваемой территории со степной биотой юга Восточной Сибири, согласующиеся с ботаническими данными о дауро-монгольских корнях реликтовых степных фитоценозов среднетаежной подзоны Якутии. В среднетаежной подзоне Якутии распространено 52 вида из 13 семейств, из них 25 евразиатских и 17 восточных степных, пустынно-степных — 2, горно-центральноазиатско-восточносстепных — 4 и субэндемиков Северо-Востока Сибири — 2. Обедненная фауна степных клопов Северо-Востока Якутии состоит из 33 видов — 11 евразиатских и 7 восточных степных, а также горностепных видов с дизъюнктивными алтае-саяно-хангайскими восточностепными и северо-восточносибирскими ареалами и локальными эндемичными ареалами. Таким образом, степной комплекс полужесткокрылых реликтовых степных фитоценозов среднетаежной подзоны и северо-восточной Якутии является обедненной производной степей и лесостепей юга Восточной Сибири и обнаруживает следы древних фауногенетических связей с пустынной биотой Центральной Азии.

Introduction

One of the striking features of the Yakutian taiga biota is the presence of extrazonal forest-steppes [Abolin, 1929; Sheludyakova, 1938; Karavaev 1945, 1958; Karavaev, Skryabin, 1971; Ivanova, 1971a, b, 1981; Zakharova, 2005; Zakharova *et al*., 2010; Troeva *et al*., 2012, etc.], which are mostly confined to the Central Yakut Plain and

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the mountain basins of the Yana and Indigirka Rivers (Fig 1). These landscapes have been identified by Academician Gerasimov [1952] as modern remnants of late glacial phenomena near the coldest region of the World. Their location in the northern part of the sharply continental sector of Eurasia [Isachenko, 1979] is associated with the borders of the arid Daurian-Yakutian-Chukchi-Alaska arc [Galanin, Belikovich, 2012] — Fig. 2.

The main factors contributing to the preservation of these steppes in northeast Asia are a sharply continental semi-arid climate with high temperatures in summer and very low in winter, a deficit of precipitation comparable to the Lower Volga region, in conditions of the preservation of a powerful underground ice complex. According to Gavrilova [1973], in Central Yakutia, the duration of sunshine due to summer hours is approaching the southern regions of the Volga region; summer temperatures reach +38 °C, the average July temperature reaches +18 °C, and in winter drops to –50…–60 °C; annual precipitation is low — only 250–300 mm and similar to steppe and semi-desert regions; the "dryness index" according to Budyko [1956] for Yakutsk is only 1.40, which is also close to climatic indicators in the steppe regions. Shashko (1961) noted that the summer climate of Central Yakutia in structure resembles the climate of the steppes, and in terms of absolute and relative air humidity it differs little from the steppe regions of Kazakhstan. Also, Berman [2008] showed that the heat supply of

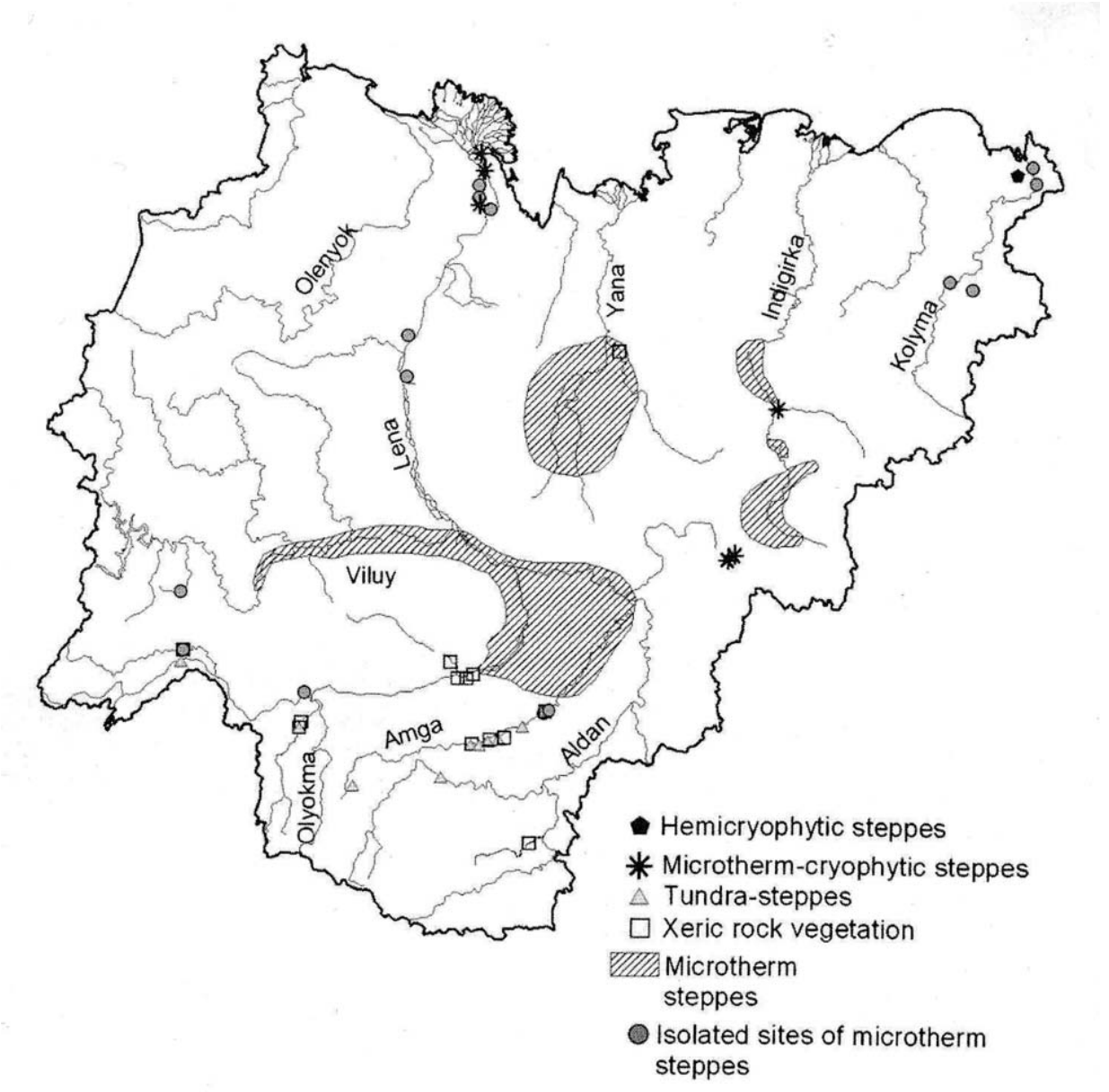

Fig. 1. Distribution of steppe vegetation in Yakutia (after Troeva & Cherosov [2012], modified).
Рис. 1. Распространение степной растительности в Якутии (по: Troeva & Cherosov [2012], с изменениями).

steppe slopes in the valleys of large rivers in North-East Siberia is very high (It > 2000 °C) and is comparable to the heat supply of the mountain steppes of Altai; the surface layer of soil in steppe stations is very heated and very dry (4–6% at a depth of 10 cm).

Thus, relatively high summer temperatures combined with low precipitation have a beneficial effect on the development of steppe vegetation and steppe insect fauna in this harshest region of Siberia.

The distribution of steppe insects alien in the northern boreal landscapes of Yakutia was already recognized during the early stages of entomological research. Miram [1929] for the first time indicated steppe orhtopterans *Metrioptera montana* (Kollar, 1833), *Arcyptera fusca albogeniculata* (Ikonnikov, 1911), *Gomphocerus variegatus* (Fischer von Waldheim, 1846), and *Bryodemella tuberculatum dilitum* (Stoll, 1813), which are typically distributed in Transbaikalia and Mongolia, in Central Yakutia. Subsequent studies have revealed a significant representation of the southern extrazonal steppe element in the local fauna [Emelyanov, 1976; Korotyaev, 1977; Korotyaev, Ter-Minassian, 1977; Danzig, 1974; Medvedev, Ammosov, 1974; Narchuk, Fedoseeva, 1980; Tanasijchuk, 1986; Antonova, Berman, 1988; Vinokurov, 1988; Bagachanova, 1990; Berman, 1974, 2001; Pesenko, Davydova, 2004; Ermakova *et al*., 2009; Labina, Evdokarova, 2009; Ermakova, 2017], setting Yakutia's insect fauna apart from the neighboring northern regions of East Siberia and the Far East. Although some of the abovementioned works have discussed the origin and formation of modern Yakutian insect fauna, it remains inadequately explored. This paper aims to address the taxonomic composition of the extrazonal steppe element in the true bug fauna within the middle taiga zone of Yakutia, exploring its chorology and zoogeographical relations with the fauna of steppes and forest-steppes in the south of East Siberia.

Material and methods

In East Siberia, large island areas of steppes and forest-steppes are located north of the Sayan Mountains, in the southern taiga — Abakan, Achinsk, Krasnoyarsk and Kansky on the Yenisei (for ease of analysis, these "islands" are given under the general name of the Minusinsk depression in a broad sense), Tulunsky and Irkutsk-Balagansky in the Baikal region. In the relict form, forest-steppes have been preserved far in the north in Central Yakutia and in the northeast in the mountain basins of the Yana and Indigirka Rivers and in the upper reaches of the Kolyma River. The northern Mongolian, or Central Asian, steppes enter Tuva, the south of Buryatia and the Trans-Baikal Territory in small ledges.

The horological analysis of the heteropteran fauna of the steppe complex of Yakutia, Khakassia and the south of the Krasnoyarsk Territory, Cis-Baikalia and Transbaikalia was carried out on the basis of materials obtained in the course of many years of field research in the relict steppes of Yakutia, the col-

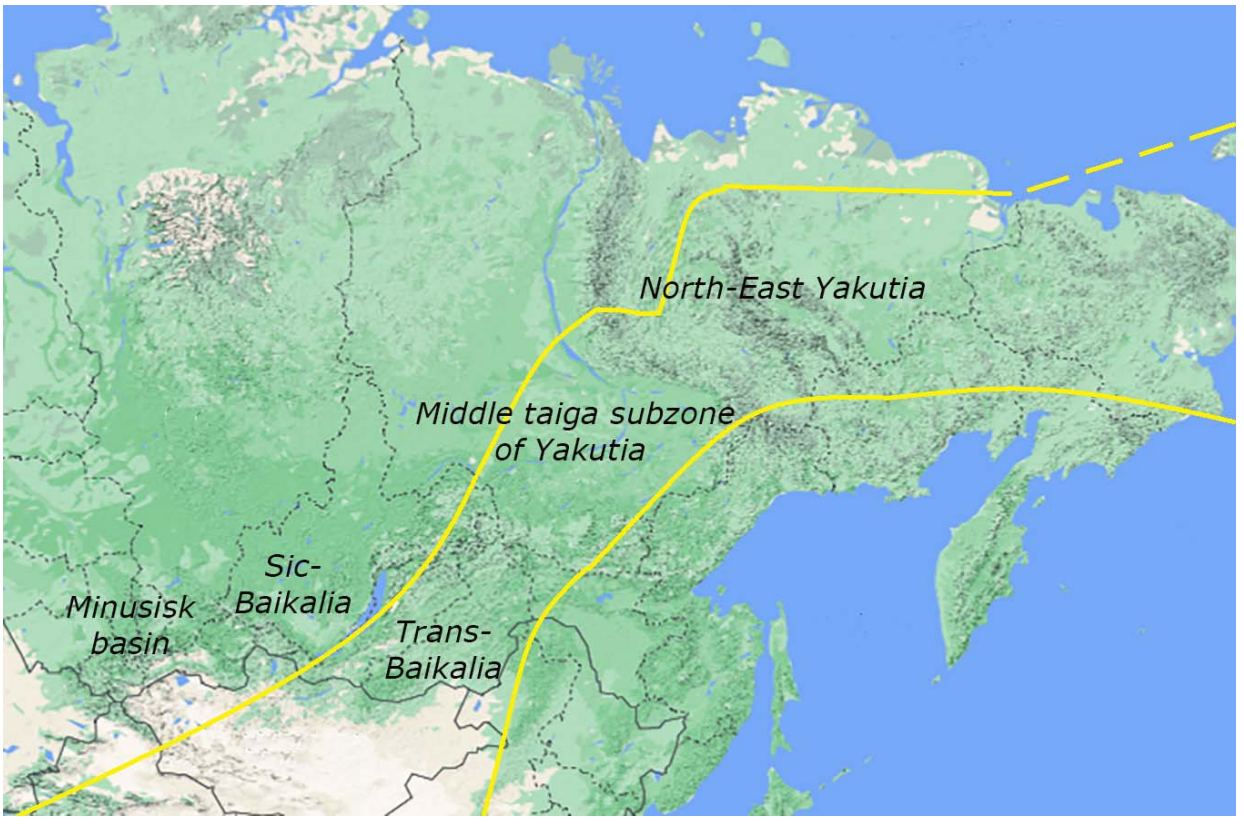

Fig. 2. Asian part of the arid Daurian-Yakutian-Chukotian-Alaskan arc (after Galanin & Belikovich [2012], modified).
Рис. 2. Азиатская часть аридной даурско-якутско-чукотско-аляскинской дуги (по: Галанин, Беликович [2012], с изменениями).

lections of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg, further as ZIN RAS), the Institute of Animal Systematics and Ecology of the Siberian Branch of the Russian Academy of Sciences (Novosibirsk), and the Institute of Biological Problems of Cryolithozone of the Siberian Branch of the Russian Academy of Sciences (Yakutsk) were studied. The paper uses data on the distribution of these insects in the steppe zone contained in the extensive faunistic and taxonomic literature on heteropterans in Siberia and neighboring Mongolia by domestic and foreign authors — V.F. Oshanin, V.E. Yakovlev, A.N. Kiritshenko, I.M. Kerzhner, C.A. Kulik, V.P. Petrova, V.B. Golub, J. Salhberg, O.M. Reuter, G. Horváth, E. Wagner, L. Hoberlandt and many others dating from the second half of the 19th century to the present day. It is not possible to list these publications in a journal paper, but references to them can be found in the monograph by Vinokurov *et al.* [2010].

The names of taxa of the ranks of families, genera and species are given according to the Catalogue of the Heteroptera of the Palaearctic Region [Aukema, Rieger, 1995–2006]. To identify species, keys for heteropteran fauna of Russia and Ukraine [Kerzhner, Jaczevsky, 1964; Putshkov V.G., 1960, 1969, 1974, 1986; Kerzhner, 1962; Seidenstűcker, 1952; Vinokurov, 1988; Putshkov P.V., 1987; Vinokurov, Kanyukova, 1995], numerous taxonomic and faunistic articles on the former USSR and Mongolia by A.N. Kiritshenko, I.M. Kerzhner, V.B. Golub, V.F. Konstantinov, V.G. Putshkov, P.V. Putshkov, G.P. Chernova, N.N. Vinokurov and others. The accuracy of the identification of the true bug species within the steppe complex of Yakutia was confirmed through a comparison of the specimens being identified with samples preserved at the ZIN RAS. These species are biotopically associated with the warmest xerophytic habitats, including treeless slopes with southern exposures, meadow steppes, and dry meadows typical of the steppe zone [Kerzhner, 1962, 1964; V.G. Putshkov, 1960–1986; Seidenstücker, 1962, etc.; personal observations].

The typology of species ranges of the steppe complex of the territory under consideration is based on the works of A.F. Emelyanov [1974], K.B. Gorodkov [1984] and O.L. Kryzhanovsky [2002] on the zoogeography of Palearctic insects, as well as on their own research [Vinokurov, 1988, 1996, 2020]. The diversity of the ranges of these species fit into 14 types, and the limits of their geographical distribution in the Palearctic are presented in Table. 1.

To compare the steppe components of the true bugs faunas of the middle taiga subzone and North-Eastern Yakutia with three regions of the south of Eastern Siberia — the Minusinsk Basin, the Cis-Baikalia and Transbaikalia, a cluster analysis was carried out using the Chekanovsky-Sørensen coefficient of faunal similarity (DICE). When constructing dendrograms, statistical processing of the material was performed by the unweighted pair-group method using arithmetic averages (UPGMA) of the PAST program (PAlaentological STatistics, ver. 1.75) [Hammer *et al*., 2006].

Steppe vegetation of Yakutia's middle taiga subzone: a brief review

The middle taiga subzone of Yakutia is delineated by the basin of the left bank of the Vilyui River to the north, the mountain chains of the Verkhoyanskiy Range to the east, and coincides with the administrative border of the Republic Sakha (Yakutia) to the south. Large areas of island forest-steppes in the Central Yakutian plain are confined to the valleys of the Lena and Amga Rivers, the Lena-Amga interfluve, and along the Vilyui River. A forest-steppe enclave exists above the town of Olekminsk on the left bank of the Lena River, acting as a connecting link between the Sic-Baikalia and Central Yakutia forest-

Table 1. Geographical distribution patterns of steppe bugs in East Siberia.
Таблица 1. Типы ареалов степных клопов Восточной Сибири.

Type of distributon	Patterns of distribution
Holarctic steppe	Species widely distributed in Eurasian steppe zone and in Nearctic
Eurasian steppe	Species widely distributed in Eurasian steppe zone and in relic steppe of Yakutia
Eastern steppe (Dauro-Mongolian)	Dauro-Mongolian steppe species distributed in Mongolia, south of East Siberia and in relic steppe of Yakutia
Western steppe (Sic-Black See-Kazakhstanian)	Species distributed in European and Kazakhstan steppe
Western steppe & Central Yakutian	Species distributed in European and Kazakhstan steppe and disjunctive area in Central Yakutia
Desert/Semi-desert–Steppe	Species distributed in deserts, semi-deserts and Eurasian steppe zone and disjunctive area in Central Yakutia
Kazakhstano-Eastern steppe	Species distributed in Kazakhstan and south of East Siberia and Mongolia
Kazakhstano-Mongolian	Species are distributed in Kazakhstan and Mongolia, in the east they go to the south of Buryatia and Transbaikalia
Kazakhstanian & Yakutian	Species distributed in Kazakhstan steppe and disjunctive area in Central Yakutia
Mountain Central Asian-Eastern steppe	Species with main area in Central Asia, mountain of South Siberia and disjunctive area in Central and North-East Yakutia
Altae-Sayano-Khangayan subendemics	Species are distributed within the Altai-Sayan-Khangai mountainous country
Altae-Sayano-Khangayan-North East Siberian (disjunctive)	Species are distributed within the Altai-Sayan-Khangai mountainous country and are found with a large gap in the mountain steppes of North-Eastern Yakutia
South Siberian montane & North-East Yakutian (disjunctive)	Species with disjunctive distribution in South Siberia mountain and North-East Asian mountain steppe
North-Eastern mountain steppe (endemics)	Species with local endemic distribution in mountain steppe of North-Eastern Asia

Fig. 3. A fragment of a four-grass steppe (*Cleistegenes squarrosa*, *Koeleria cristata*, *Stipa krylovii*, and *Festuca lenesis*) in the lower slope of the Lena River, Tuymaada valley. Photo by N.K. Sosina.
Рис. 3. Фрагмент четырехзлаковой степи из *Cleistegenes squarrosa, Koeleria cristata, Stipa krylovii* и *Festuca lenesis* в нижней части склона р. Лена, долина Туймаада. Фото Н.К. Сосиной.

Fig. 4. Feather-grass steppe with *Stipa capillata* on the slope of the Lena River in the Tuymaada valley. Photo by N.K. Sosina.
Рис. 4. Ковыльная степь со *Stipa capillata* на склоне р. Лена в долине Туймаада. Фото Н.К. Сосиной.

steppes. These phytocenoses are linked with Dauro-Mongolian steppes due to their origin; and the region harbors a diverse flora with over 250 known species, including steppe and mountain-steppe species as well as desert natives with ancient Mediterranean, Central Asian and Turanian roots. Impoverished variants of Transbaikalian four-grass steppes, comprising *Cleistogenes squarrosa*, *Koeleria cristata*, *Stipa krylovii*, and *Festuca lenensis* (Fig. 3) have been described in the Middle Lena valley near Yakutsk [Karavaev, 1945, 1958; Karavaev, Skryabin, 1971;

Fig. 5. Thermokarst alas depression in the Leno-Amga interfluve, Central Yakutia. Photo by A.P. Isaev.
Рис. 5. Аласная котловина на Лено-Амгинском междуречье, Центральная Якутия. Фото А.П. Исаева.

Fig. 6. Petrophytic steppe slope (dominant *Artemisia frigida*) on the Lena River, Erkeeni valley. Photo by N.K. Sosina.
Рис. 6. Петрофитный степной склон (доминант *Artemisia frigida*), р. Лена, долина Эркээни. Фото Н.К. Сосиной.

Ivanova, 1971a, b, 1981]. According to the geobotanical classification [Gogoleva, 1996], steppe communities of Central Yakutia, like those of Transbaikalia, belong to the classes *Caricetea duriusculae* Mirk. and *Cleistogenetea squarrosae* Mirk. *et al*.

Southern slopes and high floodplain terraces of river valleys host true bunchgrass steppes consisting of *Stipa krylovii*, *Agropyron cristatum*, *Elytrigia villosa* with an addition of *Artemisia jacutica*, *Veronica incana*, *Delphinium graniflorum*, *Phlox sibirica* (Fig. 4). On deforested slopes of river valleys and alases, steppe communities dominated by *Psathyrostachys caespitosa* prevail, sometimes with *Artemisia commutata* as a subdominant. Grass-grass-grass steppes of *Festuca lenensis* with richer herbs are much more common and are considered secondary digressive phytocenoses due to anthropogenic factors, leading to the reduction of native plant communities. In degraded landscapes, communities of *Koeleria cristata* with impoverished motley grass can be found, often accompanied by ruderal species.

Meadow steppes dominated by *Festuca lenensis,* characterized by high alpha-diversity and dense vegetation cover, thrive in more humidified conditions such us depressions of high overflow terraces, meso- and xerotic belts of alases, etc. The floristic diversity of these steppes includes xerophytes and mesoxerophytes *Pulsatilla flavescens*, *Carex pediformis*, *Bromopsis pumpelliana*, *B. korotkiji*, *Agrostis trinii*, *Lichnus sibirica*, *Diantus versicolor*, etc. In the taiga-alas landscapes of the Lena-Amga interfluves, distinct relict forest-steppe “charans” can be observed, resembling the appearance of West Siberian birch “spikes”. These “charans” feature groves of birch *Betula pendula* and undergrowth of steppe grasses *Festuca lenensis* and *Poa botryoides* with xerophilous grasses (Fig. 5).

Petrophytic steppes, confined to limestone rocks, grow on slopes of southern exposures of river valleys. They form communities of couch grass (*Elytrigia jacutorum*) and petrophytic variants *Stipa krylovii* and *Psathyrostachys caespitosa* with participation of petrophytic herbs *Artemisia santolinifolia*, *Youngia teniufolia*, *Patrinia rupestris*, *Orostachis spinosa*, etc (Figs. 6, 7).

Results

Analysis of a large number of literature sources [Vinokurov *et al*., 2010; Babichev, Vinokurov, 2011; Kuzhuget, Vinokurov, 2016; Kuzuget, 2017, 2019; Babichev, Kuzhuget, 2019; Sofronova, Sofronov, 2018; Korotyaev *et al*., 2022, etc.] revealed that the steppe complex of East Siberian heteropterans comprises 115 species belonging to 15 families (Table 2). It should be noted that the desert-steppe fauna of Tuva isolated by the Western Sayan is not discussed in this paper.

Fig. 7. Petrophytic steppes with participation *Krascheninnikovia lenensis* (Kumin.) on Cambrian limestones in the Lena valley, the vicinity of the Olekminsk town. Photo by N.K. Sosina.
Рис. 7. Петрофитные степи с участием *Krascheninnikovia lenensis* (Kumin.) на кембрийских известняках в долине Лены, окрестности г. Олекминск. Фото Н.К. Сосиной.

Table 2. Taxonomic and chorological composition Heteropteran steppe faunogenetic complex in south of East Siberia and Yakutia.
Таблица 2. Таксономический и хорологический состав полужесткокрылых степного фауногенетического комплекса на юге Восточной Сибири и в Якутии.

Family, species	Minusinsk basin	Sic-Baikalia	Trans-Baikalia	Middle taiga subzone of Yakutia	North-East Yakutia	Type of area
1	*2*	*3*	*4*	*5*	*6*	*7*
Nabidae						
Nabis punctatus mimoferus Hsiao, 1964	+	+	+	+	+	Eurasian steppe
Nabis nigrovittatus J. Sahlberg, 1878*	+	+	+	+	+	Holarctic steppe
Anthocoridae						
Orius sibiricus Wagner, 1952	+	+	+	+	+	Eurasian steppe
Orius agilis (Flor, 1860)		+	+	+		Eurasian steppe
Xylocoris modestus Kerzhner et Elov, 1976				+		Kazakhstanian &Yakutian
Xylocoris tesquorum Kerzhner et Elov, 1976		+	+			Eurasian steppe
Xylocoris thomsoni (Reuter, 1883)		+		+		Eurasian steppe
Miridae						
Dicyphus orientalis sibiricus Kerzhner, 1979		+	+	+		CAsM-Eastern steppe
Orthops mutans (Stål, 1858)		+	+			Eastern steppe
Polymerus ammosovi Vinokurov, 1995				+	+	Endemic of NE Siberia
Leptopterna albescens Reuter, 1891	+	+	+	+	+	Eurasian steppe
Notostira sibirica Golub, 1978	+	+	+	+		Eastern steppe
Trigonotylus longitarsus Golub, 1989	+	+	+			Eastern steppe
Trigonotylus major Zheng, 1985			+			Eastern steppe
Anapus kirschbaumi Stål, 1858	+	+	+			Kazakhastanian-Eastern steppe
Anapus longicornis Jakovlev, 1882	+	+	+			Eurasian steppe
Anapus rugicollis (Jakovlev, 1877)	+	+	+			Eurasian steppe
Myrmecophyes alboornatus (Stål, 1858)	+	+	+	+		Eurasian steppe
Piezocranum simulans Horváth, 1877				+		Eurasian steppe
Orthotylus algens Vinokurov, 1982				+	+	Subendemic of NE Yakutia
Orthotylus lenensis Lindberg, 1928		+		+	+	CAsM-Eastern steppe
Orthotylus parvulus Reuter, 1879			+			Eurasian steppe
Orthotylus turanicus Reuter, 1883		+	+	+		CAsM-Eastern steppe
Orthotylus oshanini Reuter, 1883	+		+	+		Eurasian steppe
Omphalonotus planus Kulik, 1965			+			Eastern steppe
Chlamydatus allii V.G. Putshkov, 1959			+			Eurasian steppe
Conostethus hungaricus Wagner, 1941		+	+			Eurasian steppe
Criocoris sibiricus Kerzhner, 1984			+		+	CAsM-Eastern steppe
Dacota nigritarsis (Jakovlev, 1882)	+					Western steppe
Excentricoris pictipes (Reuter, 1878)	+	+	+	+	+	Eastern steppe
Macrotylus dimidiatus Jakovlev, 1889	+	+	+	+	+	Eastern steppe
Macrotylus mundulus (Stål, 1858)	+	+	+	+	+	Eastern steppe
Macrotylus zinovievi Kerzhner, 1984			+			Eastern steppe
Phaeochiton caraganae (Kerzhner, 1864)	+	+	+			Eurasian steppe
Psallopsis neglecta Konstantinov, 1997			+			Eurasian steppe
Psallus anticus (Reuter, 1876)				+	+	Eurasian steppe
Sacculifer picticeps Kerzhner, 1959						Eurasian steppe
Salicarus fulvicornis Jakovlev, 1889			+			Eastern steppe
Tingidae						
Acalypta cooleyi Drake, 1917		+	+	+	+	Eastern steppe

Table 2 (*continued*).

1	*2*	*3*	*4*	*5*	*6*	*7*
Agramma mongolicum Golub, 1990	+		+			Altae-Sayano-Khangayan
Derephysia foliacea abbreviata Golub, 1995				+	+	Subendemic of NE Siberia
Dictyla minuta Golub, 1976	+		+			Altae-Sayano-Khangayan
Dictyla platyoma (Fieber, 1861)	+	+	+	+	+	Eurasian steppe
Dictyonota dlabolai Hoberlandt, 1974	+		+			Eastern steppe
Elasmotropis distans (Jakovlev, 1903)			+			Altae-Sayano-Khangayan
Kalama aridula Jakovlev, 1902			+			Desert-Steppe
Kalama vinokurovi Golub, 1979					+	Mongolian & NE Siberian
Lasiacantha haplophylli Golub, 1977		+	+	+		Eastern steppe
Lasiacantha kaszabi Hoberlandt, 1977	+		+	+		Eastern steppe
Sphaerista paradoxa (Jakovlev, 1880)		+	+			Eurasian steppe
Tingis bianchii Golub, 1977				+		Eastern steppe
Tingis pauperata (Puton, 1879)	+	+	+	+		Eurasian steppe
Tingis platynota Golub, 1976			+			Altae-Sayano-Khangayan
Tingis scutigerula Golub, 1977				+		Eastern steppe
Reduviidae						
Empicoris gracilentus (Jakovlev, 1907)			+	+		Eurasian steppe
Coranus contrarius Reuter, 1881	+					Western steppe
Coranus hammarstroemi Reuter, 1891	+	+	+			Eastern steppe
Coranus cf. *laticeps* Wagner, 1952				+		? Eastern steppe
Berytidae						
Neides propinquus Horváth, 1901	+	+	+	+		Eastern steppe
Piesmatidae						
Parapiesma longicranum Hsiao et Jing, 1979			+			Eastern steppe
Lygaeidae						
Lygaeosoma sibiricum Seidenstücker, 1962	+	+	+	+		Eurasian steppe
Lygaeus hanseni Jakovlev, 1883	+	+	+			Kazakhstano-Mongolian
Geocoris arenarius (Jakovlev, 1867)		+	+	+		Eurasian steppe
Geocoris mongolicus Horváth, 1901	+	+	+	+		Eastern steppe
Bianchiella adelungi Reuter, 1907			+			Eastern steppe
Crophius bermani Vinokurov, 1975					+	Endemic of NE Siberia
Camptotelus lineolatus (Schilling, 1829).	+	+	+	+	+	Eurasian steppe
Jakowleffia setulosa (Jakovlev, 1874)			+			Eurasian steppe
Ischnocoris claripes Muminov, 1967				+	+	CAsM & Central-NE Yakutia
Emblethis brachynotus Horváth, 1897	+	+	+	+	+	Eurasian steppe
Emblethis denticollis Horváth, 1878	+		+			Eurasian steppe
Diomphalus annulicornis Jakovlev, 1890			+			Eastern steppe
Pionosomus trichopterus frigidus (Vinokurov, 1979)					+	Endemic of NE Siberia
Pionosomus monochrous Jakovlev, 1889	+	+	+	+		Eastern steppe
Pionosomus opacellus (Horváth, 1895)	+			+		Eurasian steppe
Pionosomus trichopterus frigidus (Vinokurov, 1979)					+	Endemic of NE Siberia
Parapolycrates hannesi Kerzhner et Vinokurov, 2007			+			Altae-Sayano-Khangayan
Trapezonotus subtilis Jakovlev, 1889		+	+			Altae-Sayano-Khangayan
Hadrocnemis diversipes (Kiritshenko, 1922)			+	+		Desert-Steppe
Lamprodema rufipes Reuter, 1891	+	+	+			Eastern steppe
Naphiellus irroratus (Jakovlev, 1889)		+	+			Eastern steppe
Pyrrhocoridae						
Pyrrhocoris fuscopunctatus Stål, 1858		+	+			Altae-Sayano-Khangayan
Coreidae						
Enoplops sibiricus Jakovlev, 1889	+	+	+	+		Eastern steppe
Spathocera albomaculata Jakovlev, 1889		+	+			Eastern steppe

Table 2 (*continued*).

1	*2*	*3*	*4*	*5*	*6*	*7*
Alydidae						
Megalotomus ornaticeps (Stål, 1858)	+	+	+	+		Eastern steppe
Rhopalidae						
Corizus tetraspilus Horváth, 1917	+	+	+			Eastern steppe
Rhopalus distinctus (Signoret, 1859)	+	+	+	+		Eurasian steppe
Stictopleurus sericeus (Horváth, 1896)*		+	+	+	+	Eurasian steppe
Stictopleurus viridicatus (Uhler, 1872)*	+	+	+	+	+	Holarctic steppe
Chorosoma macilentum Stål, 1858	+	+	+			Eastern steppe
Myrmus calcaratus Reuter, 1891	+					Eurasian steppe
Myrmus glabellus Horváth, 1901	+					Kazakhstano-Eastern steppe
Cydnidae						
Adomerus notatus (Jakovlev, 1882)	+	+	+	+		Eastern steppe
Scutelleridae						
Phimodera carinata Reuter, 1879			+			Altae-Sayano-Khangayan
Phimodera fumosa Fieber, 1863	+		+			Desert-Steppe
Phimodera kiborthi Jakovlev, 1889	+				+	South & NE Siberia montane
Phimodera laevilinea Stål, 1873	+	+	+	+	+	Eastern steppe
Phimodera nigra Reuter, 1879			+			Eastern steppe
Phimodera sibirica Kerzhner, 1976	+	+	+		+	CAsM-Eastern steppe
Irochrotus sibiricus Kerzhner, 1976	+	+	+	+	+	Eastern steppe
Odontoscelis byrrhus Seidenstücker, 1972	+	+	+			Kazakhstano-Eastern steppe
Eurygaster dilaticollis Dorhn, 1860		+	+			Kazakhstano-Eastern steppe
Pentatomidae						
Aelia frigida Kiritshenko, 1930					+	South & NE Siberian montane
Aelia sibirica Reuter, 1884	+	+	+	+		Eurasian steppe
Anteminia eurynota remota Horváth, 1907 *					+	CAsM & NE Siberia
Antheminia lindbergi Tamanini, 1962		+	+			Eastern steppe
Carpocoris coreanus Distant, 1899	+	+	+	+	+	Desert-Steppe
Peribalus inclusus (Dohrn, 1860)	+	+	+	+	+	Eurasian steppe
Sciocoris abbreviatus (Reuter, 1879)	+	+	+			Kazakhstano-Eastern steppe
Sciocoris placidus Jakovlev, 1903		+	+			Eastern steppe
Asaroticus ogloblini Kiritshenko, 1926		+	+			Eastern steppe
Sternodontus binodulus Jakovlev, 1893	+			+		Kazakhstanian & Yakutian
Sternodontus similis (Stål, 1854)	+	+	+			Eastern steppe
Capnoda nigroaenea Jakovlev, 1887					+	South & NE Siberian montane
Всего:	56	57	87	52	33	

* Palearctic component of two Holarctic species is the Eurasian steppe.
Abbreviations: CAsM — Central Asian montane, NE — North Eastern.

The data presented in Table 3 indicate that six of 15 families – Miridae (23–29%), Lygaeidae (16–20%), Tingidae (11–15%), Rhopalidae (up to 11%), Scutelleridae (up to 12%) and Pentatomidae (11–15%) — dominate the steppe heteropteran complex. The remaining eight small families have only a single steppe species each, resulting in their low overall participation in this complex.

The highest diversity of steppe bugs in the south of East Siberia is observed in the steppes of Trans-Baikalia, where 87 species from 15 families are found in the northeastern extension of the Mongolian steppes. In comparison, the fauna of forest-steppes to the west of Lake Baikal in Sic-Baikalia and Minusinsk Basin is notably poorer, with 57 species from 14 families, and 56 species from 13 families, respectively. The differences in species richness can be attributed to two factors: firstly, the insufficient study of the forest-steppe and steppe fauna of the region, and secondly, the presence of Lake Baikal as a zoogeographical barrier for some steppe species that are more prevalent in the eastern regions.

The relict steppe complex of true bugs in the middle taiga subzone of Yakutia is slightly less diverse than the fauna of Minusinsk Basin and Sic-Baikal region. It comprises 52 species from 39 genera and 13 families, accounting for 16% of the total list of terrestrial bugs in the studied area, with 28 and 34 common species shared with Minusinsk Basin and Sic-Baikalia region, respectively. Notably, three families show a high

Table 3. The ratio of Heteropteran families of the steppe faunogenetic complex in south of East Siberia and Yakutia.
Таблица 3. Соотношение семейств полужесткокрылых степного фауногенетического комплекса на юге Восточной Сибири и в Якутии.

Family	Minusinsk basin		Sic-Baikalia		Trans-Baikalia		Middle taiga subzone of Yakutia		North-East Yakutia	
	n	**%**	**n**	**%**	n	%	n	%	n	%
Nabidae	2	3.6	2	3,5	2	2.3	2	3.8	2	6.1
Anthocoridae	1	1.8	1	1,8	3	3.4	3	5.8	1	3.0
Miridae	**13**	**23.2**	**13**	**22.8**	**24**	**27.6**	**15**	**28.8**	**8**	**24.2**
Tingidae	**6**	**10.7**	5	8.8	**12**	**14.9**	**8**	**15.4**	**4**	**12.1**
Reduviidae	2	3.6	1	1.8	1	1.1	2	3.8	–	–
Piesmatidae	–	–	–	–	1	1.1	–	-	–	–
Berytidae	1	1.8	1	1,8	1	1.1	1	1.9	1	3.0
Lygaeidae	**9**	**16.1**	**11**	**19,3**	**15**	**18.4**	**9**	**17.3**	***6***	**18.2**
Pyrrhocoridae	–	–	1	1.8	1	1.1	–	-	–	–
Coreidae	2	1.8	2	3.5	2	2.3	1	1.9	–	–
Alydidae	1	1.8	1	1,8	1	1,1	1	1.9	–	–
Rhopalidae	**6**	**10.7**	5	8,8	5	5,7	3	5.8	2	6.1
Cydnidae	1	1.8	1	1,8	1	1.1	1	1.9	–	–
Scutelleridae	**7**	**12.5**	5	8.8	8	9.2	2	3.8	**4**	**12.1**
Pentatomidae	**6**	**10.7**	**8**	**14.0**	8	9.2	4	**7.7**	**5**	**15.2**
Total:	56	100	57	100	87	100	52	100	33	100

presence of steppe species: Miridae with 15 species (28.8%), Lygaeidae with nine species (17.3%), and Tingidae with eight species (15.4%). In terms of these indicators, the heteropterofauna of the forest-steppe of middle taiga Yakutia is comparable to that of the Baikal region.

The mountain steppe fauna in North-East Yakutia, located in the area of the cold pole of the Northern Hemisphere, is strongly impoverished and includes 33 species from nine families. The leading families in this region are Miridae with eight species (24.2%), Lygaeidae with five species (18.2%), Tingidae with four species (12.2%), Scutelleridae with four species (12.1%), and Pentatomidae with five species (15.2%).

The entire diversity of species ranges within the steppe complex of East Siberia, with the exception of Tuva, is limited to 13 types, among which in all regions Euroasian and Holarctic steppe species (31–45%) and Eastern steppe species (20–44%) prevail. The participation of the remaining species, including Western steppe, Desert-Steppe, Kazakhstano-Eastern steppe, Kazakhstano-Mongolian, Mountain-Central Asian-Eastern steppe, Altai-Sayan-Khangai subendemics and Altai-Sayan-Khangai and Northeast Siberian is modest and varies from one to seven per region.

In the middle taiga subzone of Yakutia, the steppe faunistic complex is represented by six groups (Fig. 8).

1. Euroasian and Holarctis steppe (24 species, 45%), with majority being Palaearctic species, and a few being Holarctic species: *Nabis nigrovittatus* (Fig. 9a), *N. punctatus*, *Orius agilis*, *O. sibiricus*, *Xylocoris thomsoni*, *Leptopterna albescens* (Fig. 9b), *Myrmecophyes alboornatus*, *Piezocranum simulans*, *Orthotylus oshanini*, *Psallus anticus*, *Sacculifer picticeps*, *Dictyla platyoma*, *Tingis pauperata*, *Empicoris gracilentus*, *Lygaeosoma sibiricum* (Fig. 9i), *Geocoris arenarius*, *Camptotelus lineolatus*, *Emblethis brachynotus*, *Pionosomus opacellus*, *Rhopalus distinctus* (Fig. 10c), *Stictopleurus sericeus* (Fig. 10d), *S. viridicatus*, *Aelia sibirica* (Fig. 10j), *Peribalus inclusus* (Fig. 10l).

2. Eastern steppe (18 species, 34%) — *Notostira sibirica* (Fig. 9c), *Macrotylus mundulus* (Fig. 9d), *Excentricoris pictipes*, *Lasiacantha haplophylli* (Fig. 9f), *L. kaszabi, Tingis bianchii* (Fig. 9g), *T. scutigerula*, *Acalypta cooleyi*, *Coranus* cf. *laticeps*, *Neides propinquus* (Fig. 9h), *Geocoris mongolicus* (Fig. 9j), *Pionosomus monochrous* (Fig. 9k), *Enoplops sibiricus* (Fig. 10a), *Megalonotus ornaticeps* (Fig. 10b), *Adomerus notatus* (Fig. 10e), *Irochrotus sibiricus* (Fig. 10f), *Phimodera laevilinea*.

3. Kazakhstanian & Yakutian disjunctive: *Xylocoris modestus* and *Sternodontus binodulus* (Fig. 10h) with a large gap from the main range in Kazakhstan are found in the middle taiga subzone of Yakutia (*S. binodulus* is also found in Khakassia).

4. Desert-Steppe is a very rare type of the Turanian-Steppe and East Siberian range represented by two species *Hadrocnemis diversipes* and *Carpocoris coreanus* (Fig. 10k).

5. Central Asian montane-Eastern steppe. Four species in this group have distinct meridional disjunct ranges — the southern part of their range lies in the mountains of Central Asia and South Siberia, while the northern part extends to the middle taiga subzone of Yakutia. (*Dicyphus orientalis sibiricus*, *Orthotylus turanicus*), while in *Orthotylus lenensis* and *Ischnocoris claripes* it reaches even further beyond Verkhoyansk range.

6. Subendemics of North-East Siberia — *Orthotylus algens* and *Derephysia foliacea abbreviata* (Fig. 9e) inhabit petrophytic steppes on the slopes of the Lena River valley.

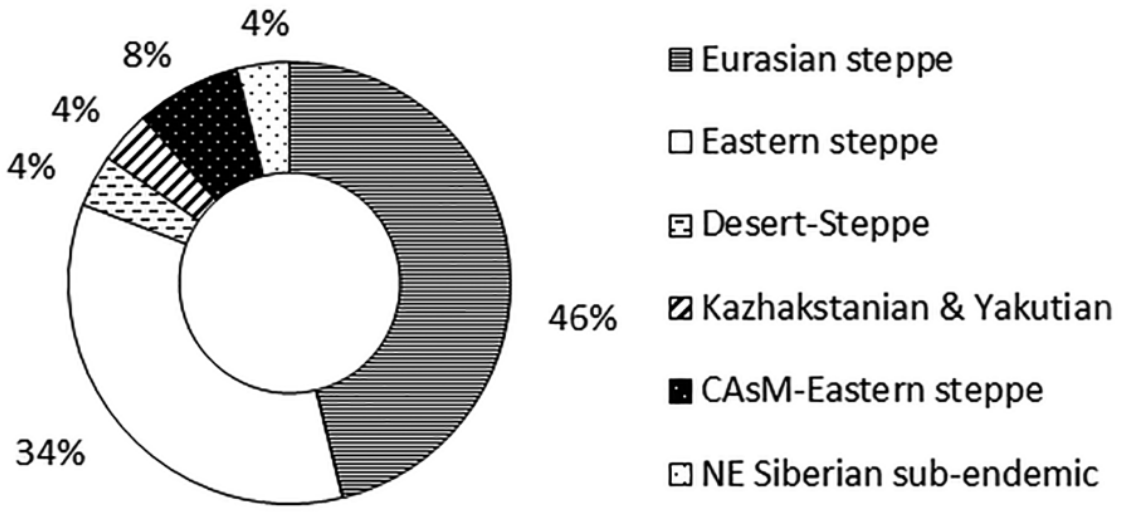

Fig. 8. The relationship of chorological groups within the steppe complex of heteropteran in the middle taiga subzone of Yakutia.
Рис. 8. Соотношения хорологических групп степного комплекса полужесткокрылых среднетаежной подзоны Якутии.

Discussion

As cluster analysis data show, there are close connections between the faunas of the steppes of Southern Siberia and the middle taiga subzone of Yakutia, and the isolation of the mountain-steppe fauna of the North-east has also been revealed (Fig, 11). The inclusion of the fauna of the middle taiga subzone of Yakutia into a single cluster with that of South Siberia is attributed by the significant presence of common Eurasian steppe (24 out of 33 in Yakutia) and Eastern steppe (18 out of 39 in Yakutia) species, along with certain species belonging to the Central Asian montane and Eastern steppe group (Table 3). The steppe complex in Trans-Baikalia and Sic-Baikalia consists of 87 and 57 species from 15 and 14 families, respectively, including families Piesmatidae and Pyrrhocoridae, which are absent in the fauna of Yakutia. Apart from the 33 Eurasian steppe and 39 East steppe species, the complex in these regions includes five Kazakhstano-Eastern steppe species and seven Altai-Sayan-Khangai subendemics. It should be noted that *Xylocoris modestus* and *Sternodontus binodulus* with a disjunctive range between Kazakhstan and Yakutia, are not found in Trans-Baikalia and Sic-Baikalia (in Table 3 they are listed as Kazakhstano-Eastern steppe). Additionally, two steppe subendemics of North-East Siberia, *Orthotylus algens* and *Derephysia foliacea abbreviata*, are also present in the steppe complex.

The complex of heteropterans in subarctic mountain steppes of North-East Siberia comprises 33 species from eight families, with steppe phytocenoses distributed in mountain depressions of Yana, Indigirka, and upper Kolyma Rivers, forming an isolated cluster. Common to both the middle taiga subzone of Yakutia and the North-East are 11 Eurasian steppe, seven Eastern steppe species, along with Desert-Steppe *Carpocoris coreanus* and six Central Asian montane-Eastern Steppe species. Several species serve as indicators of ancient contacts between the mountain biota of North-East Siberia, Central Asia, and the Altai-Sayan-Khangai mountain country. These include Altai-Sayan-Khangai and North-East Siberian species viz., *Kalama vinokurovi*, *Phimodera kiborthi* (Fig. 10g), *Aelia frigida* (Fig. 10i), and *Capnoda nigroaenea*, as well as the Central Asian montane-East steppe species *Dicyphus orientalis sibiricus*, *Orthotylus lenensis,* and *Ischnocoris claripess*, *Ph. sibirica*. In the North-East, under conditions of prolonged isolation, the phenomenon of endemism was noted in many groups of insects [Ustjuzhanin, 1988; Mráĉek, 1989; Yakovlev *et al*., 2020]. Five cryoxerophilic endemics and subendemics were identified among heteropterans: *Polymerus ammosovi*, *Orthotylus algens*, *Derephysia foliacea abbeviata*, *Pionosomus trichopterus frigidus*, and *Crophius bermani* (Fig. 9l). Notably, the last species is the sole representative of the Nearctic genus *Crophius* Stål with 15 species distributed from North to South America [Vinokurov, 1975; Henry *et al*., 2015].

Conclusions

A comparative chorological analysis of relict steppe insects of the middle taiga subzone of Yakutia and the South of East Siberia (Trans-Baikalia and Sic-Baikalia) was conducted using the order Heteroptera as a primer. Cluster analysis was employed, utilizing the faunistic similarity index by Chekanovsky-Sjerensen. The study reveals the presence of ancient connections between the entomofauna of the considered territories and the steppe

biota of the south of East Siberia, supporting botanical data on Dauro-Mongolian roots of relic steppe phytocenoses in the middle taiga subzone of Yakutia.

In the relict steppes and forest-steppes of the middle taiga subzone of Yakutia, the steppe true bug complex is primarily composed of the species widely distributed in the steppe zone, such as Eurasian steppe (24 species), Eastern steppe (18), Desert-Steppe and Kazakhstano-Eastern steppe (2 species each). The mountain element is limited to six species, four of which are Central Asian montane and two are subendemics of North-East Siberia.

In contrast, the steppe true bug fauna in North-East Yakutia is impoverished and consists of 11 Eurasian steppe and seven Eastern steppe species along with one Desert-Steppe species. Notably, the mountain element is highly

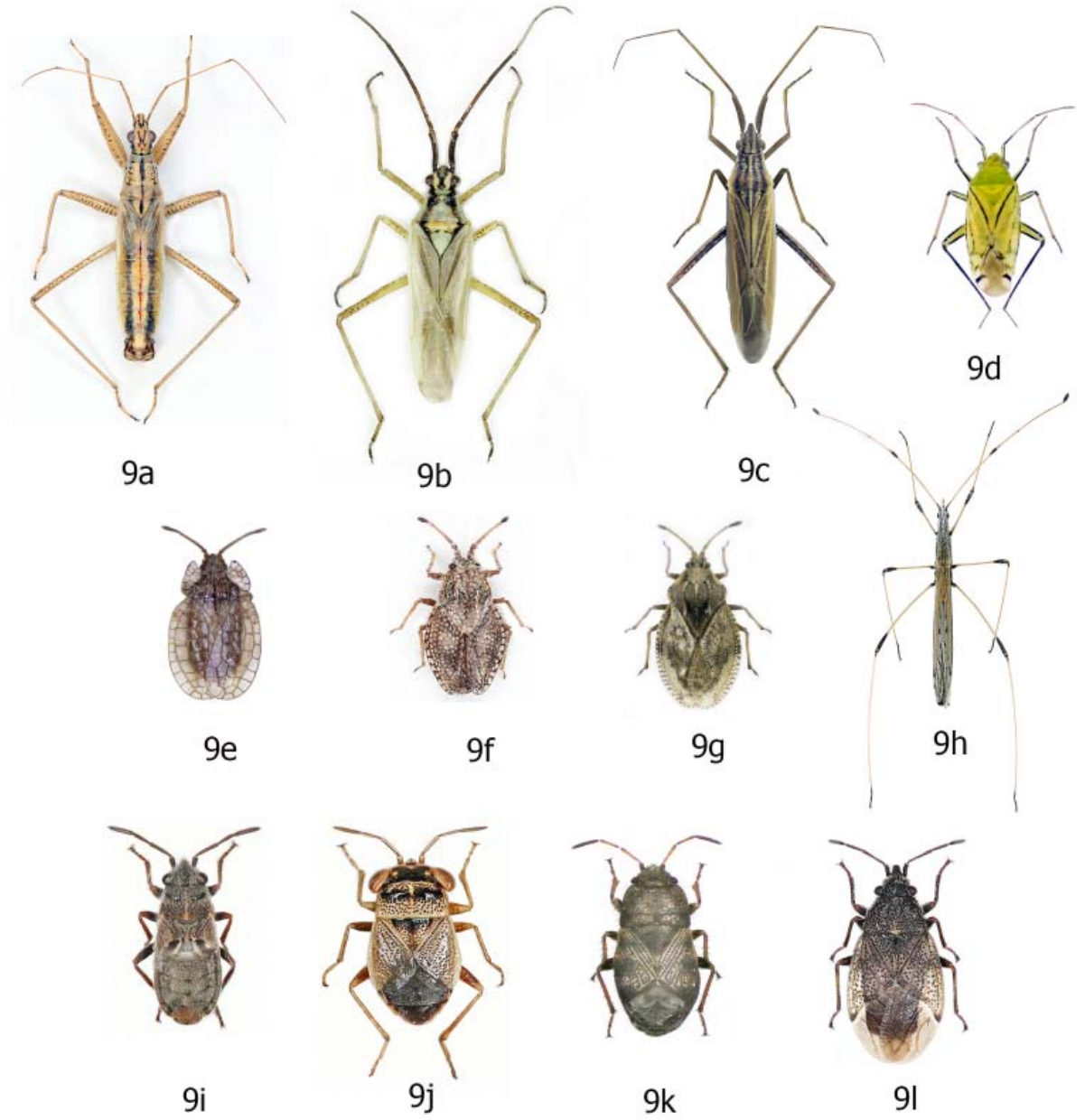

Fig. 9. True bugs of the steppe complex, found in relict forest-steppe phytocenoses of Central and North-East Yakutia. Foto by N.N. Vinokurov.
Рис. 9. Полужесткокрылые степного комплекса реликтовых лесо-степных фитоценозов Центральной и Северо-Восточной Якутии.
a–g — Cimicomorpha: 9a — *Nabis nigrovittatus*, 9b — *Leptopterna albescens*, 9c — *Notostira sibirica*, 9d — *Macrotylus mundulus*, 9e — *Derephysia foliacea abbreviata*, 9f — *Lasiacantha haplophylli*, 9g — *Tingis bianchii*; h–l — Pentatomomorpha: 9h — *Neides propinquus*, 9i — *Lygaeosoma sibiricum*, 9j — *Geocoris mongolicus*, 9k — *Pionosomus monochrous*, 9l — *Crophius bermani*. Фото Н.Н. Винокурова.

presented, comprising 14 species with disjunctive Altai-Sayan-Khangai and Eastern steppe, Altai-Sayan-Khangai and North-East Siberian, as well as several local endemics.

Thus, the analysis of the taxonomic composition of the hetropterans shows that the steppe insect complex in the relic steppe phytocenoses of the middle taiga subzone and northeastern Yakutia is a less diverse derivative of steppes and forest-steppes of southern East Siberia. Additionally, it provides evidence of ancient faunogenetic connections with the desert biota of Central Asia.

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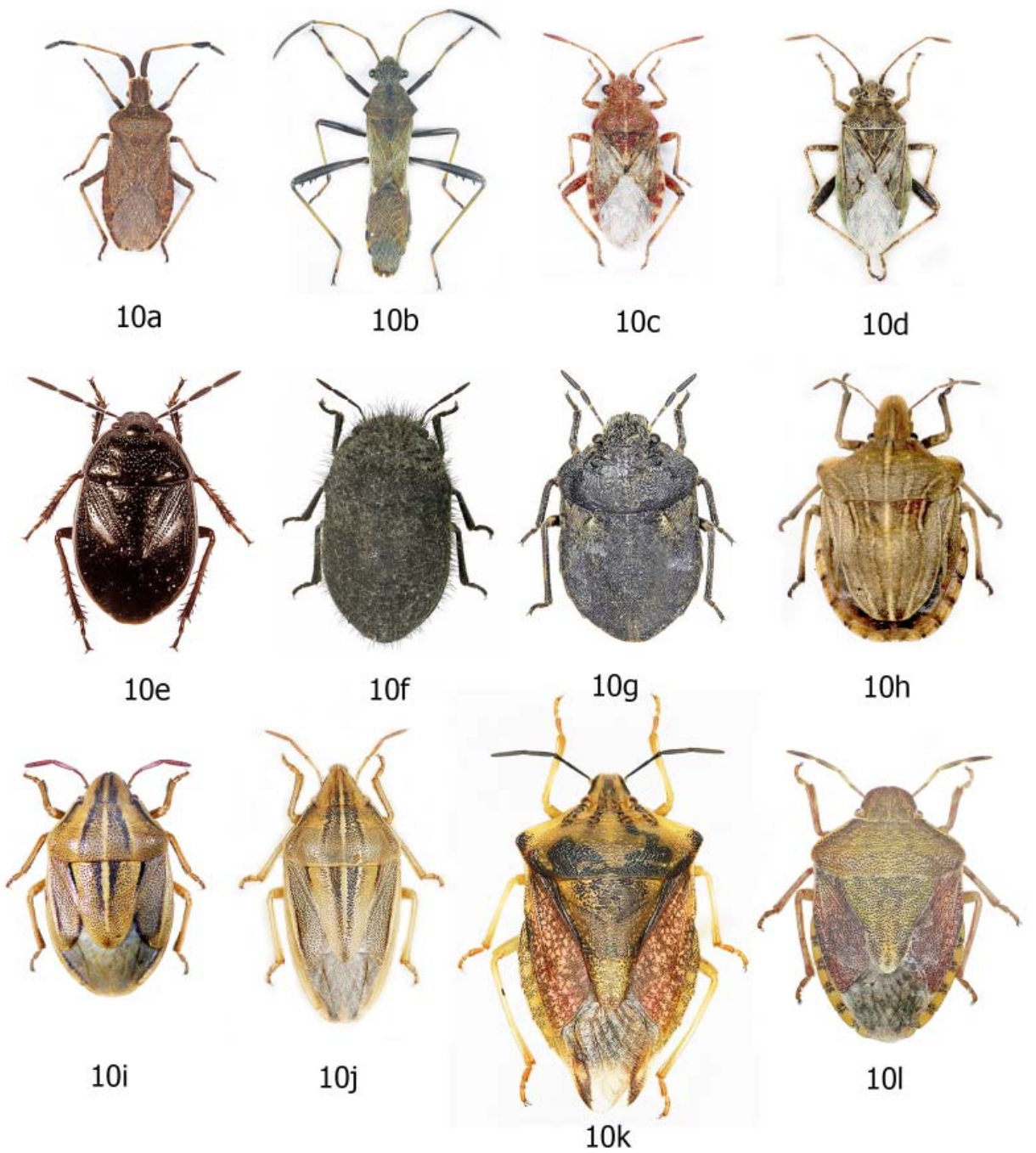

Fig. 10. True bugs of the steppe complex, found in relict forest-steppe phytocenoses of Central and North-East Yakutia. Foto by N.N. Vinokurov.
Рис. 10. Полужесткокрылые степного комплекса реликтовых лесо-степных фитоценозов Центральной и Северо-Восточной Якутии. Pentatomomorpha: 10a — *Enoplops sibiricus,* 10b — *Megalotomus ornaticeps*, 10c — *Rhopalus distinctus*, 10d — *Stictopleurus sericeus*, 11e — *Adomerus notatus*, 10f — *Irochrotus sibiricus*, 10h — *Sternodontus binodulus*, 10i — *Aelia frigida*, 10j — *Aelia sibirica*, 10k — *Carpocoris coreanus*, 10l — *Peribalus inclusus*. Фото Н.Н. Винокурова.

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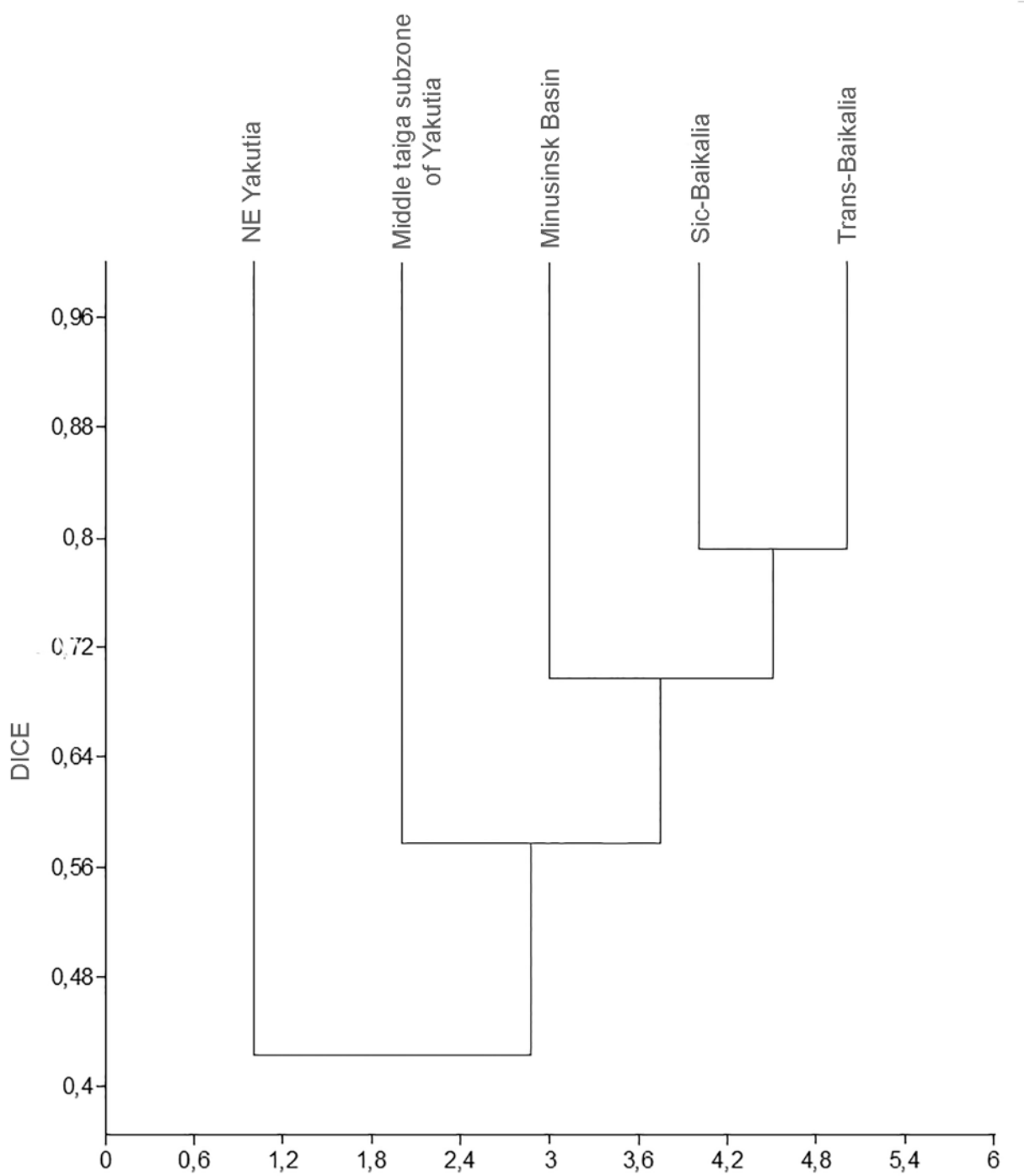

Fig. 11. Dendrogram of the similarity of the steppe faunogenetic complexes of hemipterans in Yakutia, the Minusinsk basin, Cis-Baikalia and Transbaikalia according to the Chekanovsky-Sørensen coefficient (DICE).
Рис. 11. Дендрограмма сходства степных фауногенетических комплексов полужесткокрылых Якутии, Минусинской котловины, Прибайкалья и Забайкалья по коэффициенту Чекановского-Съеренсена (DICE).

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