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ECOLOGICAL STANDARDS OF ORTHOPTERA IN HERBACEOUS BIOTOPES IN THE FAR EAST*

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Krasnov (1894) after surveying the herbaceous steppes of the Northern Hemisphere identified the meadow-steppe areas of the Far East as historically "primary" steppes of prairie type. Bey-Bienko (1950, 1953) suggested the role of such areas in the formation of a unique type of orthopteran meadow fauna. This situation determined the routes and points of our studies in the southern Soviet Far East in 1976, 1977 and 1982 (Fig. 1), wherein 385 estimates and faunistic selections of Orthoptera were made. The materials collected permit us to formulate an ecological viewpoint regarding the origin of the fauna of the Far East orthoptera. For this, it is essential to identify on a qualitative basis the major types of habitats and ecological standards of Orthoptera which are a reflection of present distribution of each type on the basis of biotopes characterizing the situation in which a species is formed (Sushkin, 1925; Shtegman, 1936; Shvarts, 1980). We have studied 74 species, and for 13 species published information is available (Pravdin and Chernyakhovskiy, 1975). Considering that the results on the distribution of Orthoptera in the mountains were used to a limited extent, such a group of species can be considered sufficient for our studies.

In the first place, it is essential to consider the distribution of Orthoptera in the herbaceous biotopes of plains and plateaus of the Far East southward and westward of the mountain ranges and more or less slanted towards the valleys of large rivers, lakes, or sea. To understand the trends of distribution in these plains in different zones and subzones, we have drawn profiles from the floodlands of rivers (or lakes) up to the local watersheds, reflecting well the gradient of hydrothermal conditions and change in herbaceous vegetation. Doing so, we have identified highly humid, mainly meadow-marshy floodlands (P); lower meadow terraces above floodlands (I) still with more or less constant saturated humidity; high terraces (II) moistened only by slope flow; and watershed (W) with zonal types of herbaceous or forest-meadow biotopes. It may be noted that, according to Krasnov (1894) and Krasheninnikov (1954), the evolutionary transformations in the course of erosion processes from the initial meadow--marshy biogeocenoses to the flat steppe (or forest) areas take place particularly in such series.

For the present article, we have used the data collected in the profiles laid in the main zonal regions identified by us on the basis of other studies (Liverovskiy and Kolesnikov, 1949; Kolesnikov, 1969). As a result of unique orientation of natural zones acquiring meridional distribution here, and the spurs of ranges penetrating into these zones, the forest and forest-steppe regions alternate with each other in the southern Far East. They are characterized here in order to change over from intracontinental to preoceanic, i.e., in the direction from northwest to southeast (Fig. 1).

1) Eastern Transbaikal mountain forest-steppes on the Shilka River, included only for comparison as the most continental in the beginning of the series.

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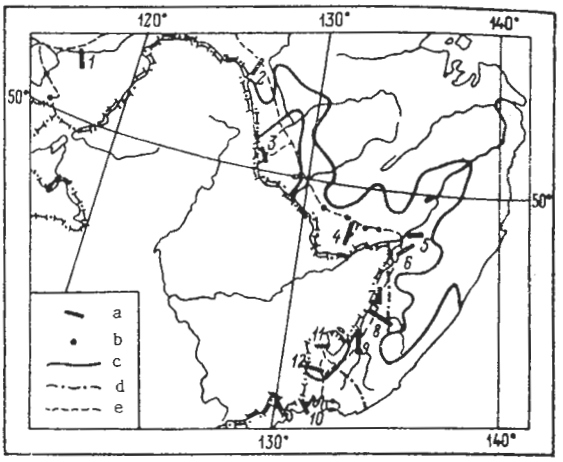

Fig. 1. Location of profiles and additional points of observation. a) Profiles (explanation in text); b) additional points, c) borders of natural zones, d) borders of subzones, e) routes of expedition (c and d after Kolesnikov, 1969).

2) Amur-Zeya erosion-alluvial high plain with southern taiga and forest in which herbaceous, mainly meadow-marshy biotopes are only scattered.

3) Zeya-Bureya alluvial-steppe plain differing from 2) by much lesser continental climate and constant ground humidity.

4) Southern part of the Middle-Amur alluvial plain with more humid climate and coniferous-broadleaved forest near the southern border of large taiga, among which are tall grass, small reed, at some places steppy, meadows of prairie type and occupying large areas.

5) Amur Valley eastward of the Ussuri Depression with similar meadow vegetation.

6) Foothills of the Khekhtsyr Range with well developed forest.

7-9) Sub-mountainous plains of Sikhote-Alin' along the right bank of the Ussuri with changeover from the middle subzone of coniferous-broadleaved forest toward south where various meadows, including steppe, are particularly common.

10) Warm humid border coastal parts of sporadic lower hills in extreme south of the Maritime Territory, where the natural forest vegetation is concentrated to a great extent; there is reason to consider them the subsequent ones.

11) Lake covered plains of the Khankay humid forest-steppes.

12) Areas of divided plateau adjoining the Khankay Depression in the Razdol'naya River Valley with more dry forest-steppes. The results on abundance of species used below were obtained by the methods of counts per unit time and expressed per hour (Gause, 1930).

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The biotope-ecological standard can be completely presented only after estimating zonal variation in the quantitative distribution of its population over biotopes. For this, we have prepared (Stebaev and Sergeev, 1982) block diagrams of internal biotope populational structure of the area of distribution of the species

(SBD) (Fig. 2A), based on the principle of change of locations (Bey-Bienko, 1930). For ecological assessment of the species, its main part (H) is particularly important; it may fall in different regions for different species. The species is found in large numbers in it and occupies all biotopes from floodlands to watersheds to almost the same degree. The remaining parts are separated from it symmetrically toward north and south: the transitional part (K), in which high population of the species is maintained only in the watershed and floodland landscape; the major part (C), where the species is maintained only in these and southward of the main part-predominantly in humic zones and northward in dry zones; and lastly, the marginal part (L), in which the species occupies only the floodlands concentrated in dry zones in the north and humid zones in the south. Furthermore, the importance of local high population levels adapted to different situations and shown as isolated dots in the diagrams (Fig. 2) increases with increasing distance from the main part. Naturally, parts of SBD may be expressed to different degrees depending on species and biotopic structure of the region. Such diagrams were constructed by us for all species studied within the system of above-listed profiles; e.g., for *Chorthippus montanus* (Fig. 2B). In general, they correspond to the block diagram of biotope-populational structure (Fig. 2A). By comparing the SBD of individual species, we could divide them into 6 groups, each of which can be characterized as a whole, as was done for the group of harmful locusts of the Irtysh region (Stebaev and Kozlovskaya, 1980). The population level is expressed as total abundance of species of this group in one or another location. For each group, we identified a distinct set of the so-called leading forms, which includes species with different SBD, corresponds to the SBD of the entire group most distinctly, and belongs to the most typical living forms and types of general geographical distribution. The leading forms are marked with asterisks in the list of species of each group at the end of this article. The group identified can be characterized briefly as follows.

1) Species typical to the forest-steppe and taiga regions of the northwestern part of the region studied (Fig. 2C).

2) Species concentrated in the regions mentioned, but widely occupying the submontainous range over the entire south of the Far East, although still at low population level (Fig. 2D).

3) Species attaining high population levels; on the one hand in the Transbaikal region and on the other in the zone of coniferous-broadleaved forests in the Ussurian plains (Fig. 2E).

4) Species having developed population structure in the last region, but numerous in the northern regions, and completely absent in Transbaikalia (Fig. 2F).

5) Species covering wide areas in almost all regions, but showing a tendency toward concentration in the biotope structure of their population; on the one hand in the summer-xerothermal intracontinental region of Transbaikalia and on the other in the southernmost forest-steppe regions of the Maritime Territory (Fig. 2G).

6) Species found only in the northern and southern forest-steppe regions and almost absent in all other areas located between them in the Soviet Far East (Fig. 2H).

Thus, we have recorded gradual transition in the series of groups proposed from the species typical of the sufficiently humid and relatively drier, but continental on the basis of climatic conditions, through the species mainly associated with areas of monsoon and fairly humid climate, but in the beginning still cold, subsequently warm, to the species capable of living in continental and as well as maritime conditions with good heat availability in summer.

Even in *C. montanus*, used by us as an example (Fig. 2B), 2 specific properties of this region and rarely expressed in other species are manifested distinctly: certain diffusion, which can be explained by the hydrothermal mildness of conditions associated with the summer monsoon climate, which reduces the environmental differences in different biotopes of one region as well as between regions to some extent; as a result, the characteristic parts for the block SBD with the absence of

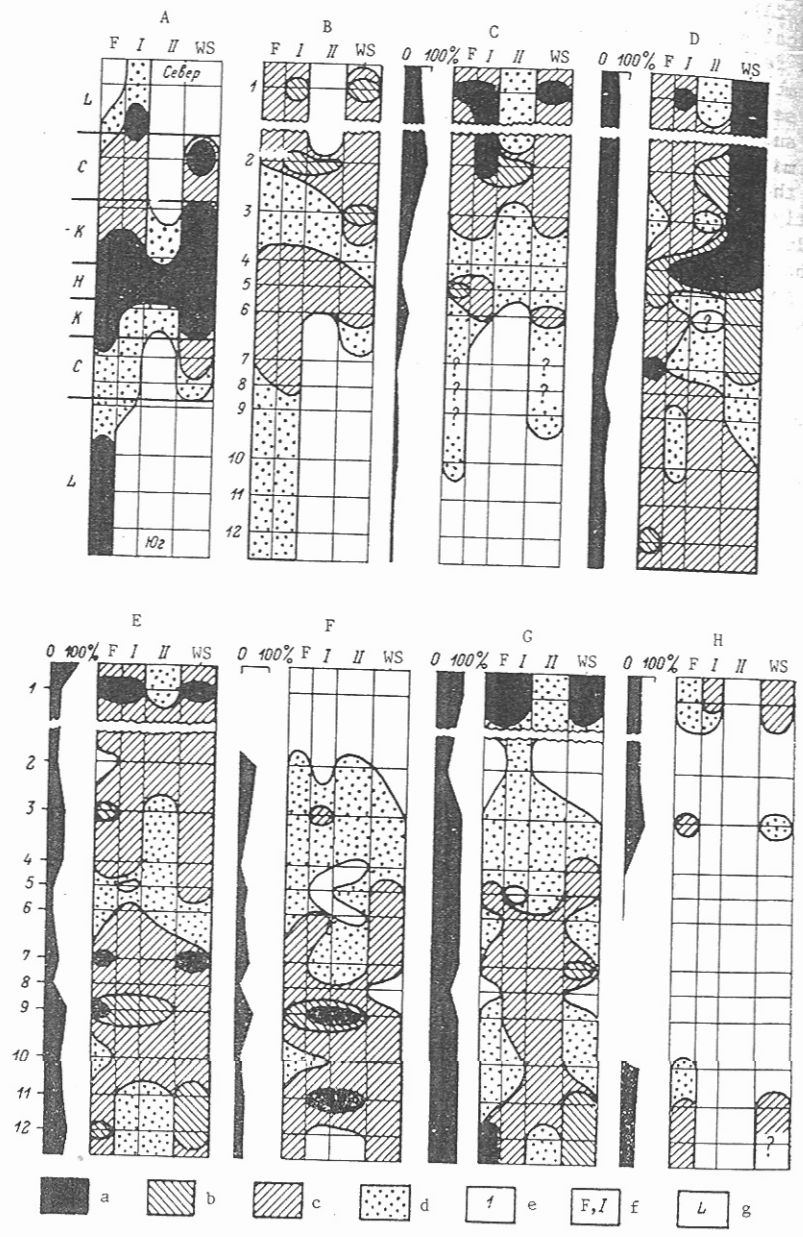

Fig. 2. Diagrams of biotope-population structure of areas of distribution. A) Plot diagram of structure of area of distribution; B) Diagram of structure of area of distribution of *Chorthippus montanus* (Charp.); and C-H) diagram of the isolated group of species. a-d) population levels of Orthoptera (a - highest, d - lowest); e) profiles characterized in the text and shown in Fig. 1; f) types of biotopes (F - floodland, I - first terrace above floodland, II - high terraces and slopes of watersheds, and ws - watershed); g) parts of biotope-populational structure of area of distribution (H - main, K - transitional, C - major, L - marginal). 1-12) Profiles (explanation in text). The part of the number of species of the group distributed in region of each profile at the time of studies is shown to the left of C-H.

species in local conditions appears as parts with very low population density; and 2) roughly speaking, division of SBD, into 2 regions, northern and southern, between which the low population belt is located, each of which in isolation shows elements typical of entire block diagram. This can be explained by the fact that the southern as well as the northern regions studied by us are independently associated with forest-steppe regions located intracontinentally, and also that there are regions between these areas which differ by lower heat availability; for example, the region of Khekhtsyr Range. Of course, the quantitative side of SBD for the group of species may depend not only on the abundance of the species but also their number. The latter is shown in Fig. 2, a group spread in the region of each profile was found during these studies. These diagrams show that species variability has a significant effect on SBD of the group.

Considering these circumstances, we may examine the specificity of utilization of different parts of profiles by the above listed groups of species in the series of regions characterized above. Here are used the additional data on morphological adaptations of Orthoptera (Stebaev and Omel'chenko, 1981; Storozhenko, 1982; Gorokhov, 1983) and their total geographical distribution (Sergeev, 1981, 1984).

Group 1. The main part of the SBD of species of the 1st group, characterized by the inhabitation of all biotopes is in the Amur-Zeya taiga (Fig. 2C, 2) is that in which the highest population levels are found on the terraces. The major part with the watershed-valley isolation of populations is manifested well toward the northwest and southwest. The floodlands are abundantly occupied in the Transbaikal Region (1), which is generally more arid. The peripheral centers of the high population level are formed particularly under these conditions. The SBD breaks in the middle Amur plain (4). Elements of the secondary main part of the SBD are seen directly behind it in the Amur Valley and near the Khekhtsir Range. However, in distinction from the northwestern part of the entire region of study, it does not form fully, which coincides with the beginning of strong reduction in the number of species. In warmer regions, species of this group penetrate into the plains to form strongly isolated small populations (Fig. 2C, 7-10). The relatively cold-loving nature of species of this group thus shown is also confirmed by the nature of their geographical distribution: more than half of the species are forest, forest-steppe, as well as polyzonal transpalearctics. Among the species of this group there are many morphologically adapted to constant existence in the sedge-grass cover, predominantly Tettrioptera *brachyptera, Chrysochraon dispar, Gomphocerus rufus* and *Chorthippus albomarginatus.**

Group 2 differs in that the main part of SBD of total species is in climatically much less continental, but still quite cold, regions of the middle Amur plain (Fig. 2D, 4). Here high population levels are observed over the entire profile from the floodlands to watersheds; in distinction from the previous group, the watershed biotopes are better used toward its north than the floodlands. The belt of population depression in comparison with the Group 1 is shifted southward to the region of the Khekhtsir Range (6). The second region of SBD spreads to all southern regions, however, its characteristic parts are manifested only slightly, in spite of significant reduction in the number of species. Based on the biotopic position of the high population centers of this region of SBD it can be concluded that in distinction from the northern subregion, utilization of floodland is more complete here. Adaptation to watershed in the north and floodlands in the south testifies to the relative heat- and moisture-loving nature of these species. In general, such change in the biotopic position of the most dense populations is a good manifestation of the principal of change of locations toward north as well as south, which is usually characteristic of species in relation to these zones. This is also reflected in the changed nature of the geographical distribution, i.e., mainly the predominance of southern forest species. The significant role of less differentiated forms, typical of the broad grassy glades of deciduous forests is also illustrative. Leading forms are *Gampsocleis sedakovi, Primnoa primnoa, Eirenephillus longipennis* and *Chorthippus montanus.*

*Complete list of species given at the end of this article.

Group 3, in spite of insignificant change in the number of species from one region to another, is distinguished by some "haziness" in the northwestern region of SBD, whereas its southeastern region is well differentiated into a system of biotopic populations (Fig. 2E). The main part of SBD is in the southernmost part of the Ussurian plain (9). It is bordered by the transitional parts of SBD. However, the separation of dense populations in the watersheds and the floodlands, typical of the major part of block SBD, is quite distinctly manifested in the warmest forest-steppe region (11, 12); as regards the northwestern regions, the typical elements of SBD are expressed here much more poorly. The most important main part for the determination of the ecological standard of a species within the limits of the territory investigated has not been found. All this permits us to characterize the species of this group as a whole as somewhat more moisture-loving than the species of the previous group, but undoubtedly more heat loving. This is also reflected in the total geographical distribution. Species associated predominantly with the steppe and forest-steppe zones are predominant. The presence of forms with well expressed morphological geobiontic characters in this group is insignificant. The leading forms are *Phaneroptera falcata, Podismopsis ussuriensis, Arcyptera fusca, Chorthippus aethalinus* and *Celes skalozubovi*.

Group 4. All parts of the diagram of population structure in the Group 4 appear strongly reduced in the northwest (Fig. 2F, 1-4). After the zone of depression they are, on the contrary, well expressed, especially in comparison with the previous group. The main part of SBD is in the south of the Ussuri Plain (9) and Khankay forest-steppe (11). As regards the plateau in the Nagornaya River basin and lower hills of the extreme south of the Maritime Territory, in spite of the maintenance of a fairly large number of species of the group here, their overall population density decreases, and even a gap between the floodland and watershed populations, typical of the major part, is observed as the forest-steppe plateau (12). Considering that similar SBD is also observed in the Ussuri Plain (6, 7), it can be concluded that the main property of the species of Group 4 is the moisture-loving nature combined with naturally higher heat-loving nature in comparison with the previous groups. They are generally most typical of the monsoon regions of the Southern Far East. This is also reflected in that, with the exception of *Podismopsis genicularis*, all species of this group are southern forest dwellers along the Pacific Ocean. This is also evident from the increase in the proportion of the Orthoptera in comparison with the previous group, having phytobiontic characters, i.e., associations with dense, including grassy stands, as well as appearance of forms such as troglobionts. The leading forms are: *Gampsocleis ussuriensis, Zubovskaya parvula, Atlanticus bruneri, Diestrammena unicolor, Primnoa ussuriensis* and *Shirakiacris shirakii*.

Group 5 is again characterized by fairly complete inhabitation of all biotopes and regions. The Taiga regions are least occupied in abundance as well as in number of species (Fig. 2G, 2). The main distinguishing feature of the group is that, on the one hand, the maximum population levels of its species are found in the most Maritime parts of the regions, and on the other hand in the most intracontinental regions of Transbaikal territory. Nowhere could the main parts of SBD be identified. This is related to a distinct separation of the valley and watershed population. At the same time, it must be noted that the species typical of the northwestern region play a subordinate role in the southeast, and those which are unknown in the Transbaikal region are predominant here. All this leads to the conclusion that Orthoptera of this group are drought loving, but a part is more cold loving, and another heat loving. The former are polyzonal transpalearctic, and the latter southern forest species along the Pacific Ocean. The leading forms are *Omocestus haemorrhoidalis* and *Oedaleus infernalis*.

Sharply expressed gaps in population are distinct in the 6th group of species. Such Orthoptera were found in the Transbaikal region, Zeya-Bureya, and Khankay forest-steppes (Fig. 2, 3, 1, 3, 11-12). Here we find major and marginal parts of SBD, which indicates that the optimum regions for these species could be on strongly steppe-like territories. Therefore, this group contains only various steppe Orthoptera, having as a rule clearly expressed geobiontic properties. The leading forms are: *Pararcyptera microptera* and *Sphingonotus mongolicus*.

All this permits us to divide the studied plains and partly lower hill territory

in the south of the Far East of the USSR into the following ecological-geographical regions significant for Orthoptera.

1. The Amur Region (2-6) was already identified earlier (Sergeev, 1978). It is characterized by wide distribution of Orthoptera of groups 1 and 2, which have SBD here similar to the block diagram. As regards all remaining groups, the species set here is quite complete although the overall level of abundance is small. Two unique parts should be distinguished in this region: 1) the high taiga plain separating the Amur Region from the Transbaikal area, and 2) one separating this region from the remaining regions near the separation of Ussuri into Amur. The former region is distinguished by a particularly wide distribution of species of Group 1 over the biotopic profiles, and the latter has species typical of Group 2. In general, the Amur region can be characterized as cold in relation to Orthoptera. It is noteworthy that the species typical of this region are forest and forest-steppe transpalearctics. The most typical of this region are *Chorthippus albomarginatus* and *C. montanus*.

2. The Ussuri Region covers the entire foothill plain along Ussuri from slightly southward of the mouths of the 4 rivers up to the northern limits of the Khankay Depression. It is further continued up to the extreme south of the Far East (7-10). An incomplete number of species of Groups 1 and 2 penetrate into it, their population decreasing in the process and becoming confined to only a few biotopes. Members of Groups 3 and 4, and to a slightly lesser degree, Group 5 have the largest number of species and play the most important role in the degree of biotopic differentiation of populations. Orthoptera of Group 5 are practically absent. The southern forest species along the Pacific Ocean are predominant in this region. Most typical of it are *Atlanticus brunneri*, *Primnoa* species, and others.

3. The Khankay Region includes the Khankay Depression and higher and drier plateau in the Razdol'naya River basin (11-12). Species of Group 1 have not been found at all on its territory, and those of Group 2 are represented poorly, but not so much in the number of species as their population strength. The role of Orthoptera of Groups 3 and 4 is also less important, but it is expressed not as a reduction in the number of species or their abundance, but in that their SBD are represented only by the major part, i.e., species of the valley and watershed populations are separated here, and this usually happens near the southern border of the area of distribution. This group is a typical element of this region, but separation of populations is typical even for it, approximately of the type observed near the borders of the extensively humid regions for the species. Besides, such species are few, especially against the background of the number of Orthoptera typical of the previous region. *Oxya chinensis* and *Euchorthippus unicolor* are the typical dwellers of the Khankay region.

Thus, the most variable and abundant habitats are observed in the south of the Ussuri Region. The poorest in this respect is in the southeast of the Amur Region.

The ecological-geographical regions described reflect the limitations for spread of species, whereas individual biotopes, on the contrary, act as conduits not only within a single region but also from one region into another. Usually floodlands and low floodland play a particularly large role as conduits for mesohydrophils along the humid parts of these biotopes (in south) and for xerophils along dry parts (in the north) (Stebaev and Sergeev, 1982). Their importance as channels of spread has limited manifestation in the plains studied by us (Sergeev, 1978) and is well expressed only in the penetration of Orthoptera of the Group 1 into the regions of sufficient heat availability, and the Orthoptera of Group 6 in regions of less heat supply. The particularly characteristic species for the local fauna of the Groups 1 and, to a lesser extent, 5 are most widely spread along the low and high places, i.e., well drained and better insulated places as a result of surface relief. The importance of watersheds in species spread is manifested only in the Group 3, and that too in the Amur Region.

All this provides a basis for ecological-geographical identification of communities in relation to the origin of Orthoptera population in the herbaceous biogeo-

cenoses of the Far East, appearing as a result of development of erosion proc... among different types of forests of this territory.

On the whole, the Orthoptera of Groups 2, 3 and 4 include the largest n... of species zonally associated with the southern border of the forest zone, and ... dionally limited to the Pacific Ocean sectors of Eurasia with their monsoon cli... Here they occupy all types of local herbaceous biotopes from marshy and prairi... meadows to steppe. Species of these groups form complete systems of biotope po... tion structure with the main, major and marginal parts on the entire territory ... the Zeya-Bureya Plain to the Khankay Depression. All this means that species o... these 3 groups can form communities of Orthoptera in local herbaceous ecosystem... without any significant participation of the members of steppe faunas which co... have been assumed.

Therefore, the hypothesis of Bey-Bienko (1953) concerning formation of a ... complex of Orthoptera in the Far East, occupying the herbaceous biogenocenosis, is fully confirmed from the biotopic-ecological viewpoint, based on the quantitati... distribution of these insects. It is important that, as far as can be inferred b... our data the middle and southern parts of the Ussuri Plain, and within it the ar... of the river valley slopes, is the main region of development of this complex. ... presence of relatively xerothermal species in this complex, generally widespread ... southern Siberia and included in the typical steppe communities, in this complex ... particularly noteworthy. This serves as an additional confirmation of the contri... tion of the nemorose complexes to the formation of the steppe fauna (Sergeev, 19... and this contribution was most probably particularly significant in the past.

SPECIES COMPOSITIONS OF GROUPS

Group 1

Decticus nigrescens (Serg. Tarb.)
Sphagniana ussuriana (Uv.)
Bicolorana bicolor (Phil.)
Tetrix tenuicornis (Sahlb.)
Metrioptera brachyptera (L.)*
Melanoplus frigidus (Boh.)
Chrysochraon dispar (Germ.)*
Stenobothrus lineatus (Panz.)
Omocestus viridulus (L.)
Gomphocerus rugus (L.)*
Aeropus kudia Caud.
A. sibiricus (L.)
Chorthippus intermedius (B.-Bien.)
Ch. albomarginatus (Deg.)*
Stethophyma grossum (L.)
Psophus stridulus (L.)

Group 2

Gampsocleis sedakovi F. d. W.*
Conocephalus chinensis (Redt.)
Teleogryllus infernalis (Sauss.)
Primnoa primnoa F. d. W.*
Eirenephilus longipennis (Shir.)*
Euthystira brachyptera (Ocsk.)
Chorthippus montanus (Charp.)
C. fallax (Zub.)
Mecostethus alliaceus (Germ.)
Epacromius pulverulentus (F. d. W.)

Group 3

Phaneroptera falcata (Poda)*
Tettigonia viridissima L.
Metrioptera engelhardti Uv.
Conocephalus discolor Thnb.
Ruspolia nitidula (Scop.)
Dianemobius fascipes (Walk.)
Tetrix subulata (L.)
T. japonica (I. Bol.)
Calliptamus abbreviatus Ikonn.
Mongolotettix japonicus (I. Bol.)
Podismopsis ussuriensis Ikonn.*
Arcyptera fusca (Pall.)*
Chorthippus aethalinus (Zub.)*
C. hammarstroemi (Mir.)
C. schmidti (Ikonn.)
C. dorsatus (Zett.)
Stethophyma tsherskii Ikonn.
Aiolopus thalassinus (F.)
Celes skalozubovi Adel.*

Group 4

Ducetia chinensis (Br.-W.)
Elimaea fallax B.-Bien.
Tettigonia ussuriana Uv.
Atlanticus brunneri (Pylm.)*
Paratlanticus ussuriensis (Uv.)
Anatlanticus uvarovi (Mir.)*
Gampsocleis ussuriensis Adel.*
Uvarovites inflatus (Uv.)*
Metripptera bonneti (I. Bol.)
Conocephalus japonicus (Redt.)
C. percaudatus B. Bienko
Tachycines boldyrevi Uv.
Diestrammena unicolor Br.-W.*
Nigrogryllus sibiricus (Chop.)
Pteronemobius nitidus (I. Bol.)
Dianemobius csikii (I. Bol.)
D. taprobanensis (Walk.)
Oecanthus longicaudus Mats.
Xya japonica Haan
Clinotettix ussuriensis B.-Bien.
Oxya chinensis (Thnb.), sensu Hollis
Zubovskaya parvula (Ikonn.)*
Anapodisma miramae Dov.-Zap.
Primnoa primoides (Ikonn.)
P. robusta L. Mistsh.
P. assimilis L. Mistsh.
P. tristis L. Mistsh.
P. ussuriensis (Serg. Tarb.)*
P. litoralis (Serg. Tarb.)
Miramella solitaria (Ikonn.)
Ognevia sergii Ikonn.
Shirakiacris shirakii (I. Bol.)*
Podismopsis genicularis (Shir.)

Group 5

Omocestus haemorrhoidalis (Charp.)*
Chorthippus biguttulus (L.)
Euchorthippus unicolor (Ikonn.)
Oedaleus infernalis Sauss.*

Group 6

Paracantha onos (Pall.)
Haplotropis brunneriana Sauss.
Pararcyptera microptera (F. d. W.)*
Bryodema tuberculatum (L.)
Sphingonotus mongolicus Sauss.*

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