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Distribution and Biological Diversity of the Melanopline Grasshoppers (Orthoptera: Acrididae: Catantopinae) in the Holarctic Kingdom¹

Michael G. SERGEEV

Department of General Biology Novosibirsk State University 2, Pirogova St., Novosibirsk 630090 RUSSIA

and

Institute for Systematics and Ecology of Animals SB RAS 11, Frunze St., Novosibirsk 630091 RUSSIA

ABSTRACT

General patterns of distribution of the Melanoplini grasshoppers are described for the Holarctic Kingdom. Taxonomic composition of Melanoplini and history of their studies are discussed. This group is considered as a tribe consisting of the subtribes Podismina, Bradynotina, Miramellina, Melanoplina, Dactylotina, and Dichroplina. Main centres of diversity and endemism are evaluated. Distribution patterns of the Melanoplini in Eurasia and North America are compared.

Key words: grasshoppers, diversity, distribution, Melanoplini, Eurasia, North America.

INTRODUCTION

The tribe Melanoplini (s. 1.) is one of the most important groups of grasshoppers It includes both dangerous pests and rare species. This tribe is

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an example of a few acridid taxa mainly distributed in the Holarctic Kingdom. Some genera and species are widely distributed. However, the majority of the melanopline grasshoppers are those whose form limit possibilities for spreading. Many are brachypterous or apterous and, as a result, have very small distribution ranges. Therefore, this tribe of grasshoppers is very interesting and important for biogeographical, evolutionary and ecological studies. The aim of this paper is to describe the general patterns of distribution and biological diversity of the Melanoplini (s. l.) in the Holarctic Kingdom.

GENERAL TAXONOMIC NOTES

The taxonomic structure of the tribe Melanoplini is not determined definitely. In this paper I intend to understand the acridid tribe Melanoplini Scudder, 1897 (=Podismini Jacobson, 1905) in general sense and follow mainly the revisions of Mistshenko (1952), Rehn and Randell (1963) and Storozhenko (1993).

The history of taxonomic and biogeographical studies of this group is complicated. It is reviewed briefly by Storozhenko (1993). Usually orthopterists recognize this group as a member of the Catantopinae or Catantopidae but sometimes it is included in other grasshopper families (or subfamilies), e.g. Oedipodidae (Yin, 1984).

Dovnar-Zapolskij (1932) recognized this group as the tribe Podismini, revised its Palaearctic forms and erected 10 new genera. His study was continued by Tinkham (1936 et al.) and Chang (1940). Chang described taxonomy and distribution of these grasshoppers in China. He noted the possible relationship of the Old World Podismae and the New World Melanopli and emphasized that the insular distribution of this group might be associated with glaciations.

Mistshenko (1952) suggested using the tribal rank (Podismini) for these grasshoppers and described their main traits and general distribution. This point of view was particularly supported by Harz (1975), Galvagni (1986), and Sergeev (1986, 1993). Harz (1975) described the general distribution of the Podismini in Europe. Galvagni (1986 et al.) revised the group *Miramella*

Dovnar-Zapolskij and established some new taxa. Distribution patterns of these grasshoppers in North and Central Asia were analyzed by Sergeev (1986, 1993, 1995). Dirsh (1975) considered this group as the subfamily Podisminae and included it in the family Catantopidae. However, Yin (1984) recognized it as the member of the family Oedipodidae.

Rehn and Randell (1963) proposed to erect the supertribe Melanoplini for the following tribes: Podismini (consisting of the Podismae, Miramellae, Bradynotae, and Primnoae groups), Melanoplini (s. str.), and Dactylotini (including *Dichroplus* Stål and its relatives). Later, an independent status of the tribe Dichroplini was proposed by Liebermann (1968). Vickery (1977, 1989). Vickery and Kevan (1983) considered this group as the subfamily Melanoplinae containing two tribes-Melanoplini (s. str.) (Dactylotina, Melanoplina) and Podismini (Podismina, Bradynotina, Miramellina). They used both morphological and karyotypic traits. Later the general biogeography and possible history of the North American Melanoplini were also discussed (Vickery, 1989).

Willemse (1921) erected the family Tonkinacridae containing many genera of the Melanoplini. Herrera (1982) included the Spanish *Podisma* Berthold and their relatives in the subfamily Catantopinae (Catantopidae).

Storozhenko (1993) described the general taxonomic situation with this group and considered it as the tribe Melanoplini of the subfamily Catantopinae (s. 1.). He also described some new taxa and established new synonymy.

Here I suggest using the name Melanoplini for the single tribe that consists of the subtribes Podismina, Bradynotina, Miramellina, Melanoplina, Dactylotina, and Dichroplina. Therefore, the name Podismini of many European orthopterists is evidently the junior synonym for the Melanoplini

I recognize Melanoplus (Bohemanella) frigidus (Boheman) as the member of the genus Melanoplus Stål which includes many quite various forms. Perhaps, somebody might prefer to exclude this Holarctic species from the genus. Why then can we not discuss dividing this genus into several small genera ⁹ This is because Vickery (1977; Vickery, Scudder, 1987) and Rentz (1978) emphasized that this genus should be revised.

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GENERAL DISTRIBUTION IN THE WORLD

The general distribution of the Melanoplini was described by Mistshenko (1952). He emphasized that a lot of the Melanoplini is distributed in North and South America, and partly in East Asia. This tribe is absent in Africa, Australia, and in South-West Asia.

A few genera and species are distributed both in North and South America or in North America and Eurasia. Four genera (*Paroxya* Scudder, *Dichroplus*, *Pedies* Rehn, *Baeacris* Rowell et Carbonell) include North American and South American forms. The only species that occurs both in North America and in Eurasia is *Melanoplus frigidus*. Most of the genera and species are limited by a continent or usually by its part. Many melanopline grasshoppers are mountain endemics.

This tribe includes some insular endemics too. Endemic genera inhabit Japan and South Kuril Islands (*Parapodisma* L. Mistshenko, *Callopodisma* Kano), Taiwan (*Niitakacris* Tinkham), the Canary Islands (*Arminda* Krauss, *Chopardminda* Morales Agacino), the Galapagos Islands (*Desmopleura* Scudder), and Curacao (in West Indies) (*Radacris* Ronderos et Sanchez). Two endemic species of *Paroxya* occur in the Bahamas (*P. bermudensis* Rehn) and the Bermuda Islands (*P. dissimilis* Morse).

The genera and species are distributed among three continents comparatively equally:

	Eurasia	North America	South America
Genera	42	47	42
Species	215-220	399-410	235-250

However, the main centre of Melanoplini diversity is associated with North America. All subtribes are represented there. On the contrary, South America is inhabited primarily by representatives of the subtribe Dichroplina. The Podismina and Miramellina grasshoppers are dominant among Eurasian Melanoplini.

DISTRIBUTION IN THE PALAEARCTIC REGION

The Palaearctic Melanoplini are mainly short-winged or apterous herbivorous grasshoppers. Only a few forms are widely distributed. Among them are *Podisma pedestris* (Linnaeus) (boreal forest, forest-steppe, steppe life zones from Europe up to East Siberia, the Caucasus and Dzungarian Alatau, mountains of Europe), *Zubovskya koeppeni* (Zubovsky) (the boreal life zone from the Enisej River and Altai to the Pacific coast), *Ognevia* (Eirenephilus) debilis Ikonnikov (from Altai in the southern Siberia up to the Far East), and *Primnoa primnoa* (Fischer de Waldheim) (from Tuva in the southern Siberia up to the Kunashir Island). Several forms are good flyers (especially species of *Ognevia* Ikonnikov).

Other genera and species are mainly limited by essentially small ranges. We can observe two main areas of melanopline diversity in the Palaeartic, the first is connected with the southern mountains of Europe (mainly around the Mediterranean), the second is in the Far East and East Asia (fig. 1).

The South European area includes at least 9 local centres of diversity and endemism:

- 1. The mountains of the Iberian Peninsula (endemic species of Cophopodisma Dovnar-Zapolskij and Podisma);
- 2. The mountains of the Italian Peninsula (*Italopodisma* Harz);
- 3. The Alps, mainly their southern ranges (Kisella Harz, Nadigella Galvagni, Italopodisma, Chortopodisma Ramme, Epipodisma Ramme, Pseudoprumna Dovnar-Zapolskij);
- 4. The Balkan area, including local plains and plateaus (Odontopodisma Dovnar-Zapolskij, Galvagniella Harz);
- 5. The Carpathian area (Kisella, Capraiuscola Galvagni, Zubovskya banatica Kis);
- 6. The Greek mountains (Oropodisma Uvarov, Peripodisma F Willemse);
- The mountains of Anatolia (Rammepodisma Weidner);
- The Caucasus (Pachypodisma Dovnar-Zapolskij, Podisma and Micropodisma Dovnar-Zapolskij);
 - 9. The Canary Islands (Arminda, Chopardminda). The East Asian area of

melanopline diversity is chiefly limited by the boundaries of the deciduous forest life zone of the temperate and subtropic types and some mountains of East and South-East Asia. Overall, the entire area is under of influence of monsoons.

It includes 9 main centres of diversity and endemism:

- The Manchurian area (local endemics of Primnoa Fischer de Waldheim, Ognevia, Miramella, Anapodisma Dovnar-Zapolskij, Zubovskya Dovnar-Zapolskij);
- 11. The Japan and South Kuril Islands (Callopodisma, Parapodisma, Podisma);
- 12. The Central Chinese area (Sinopodisma Chang, Qinlingacris Yin),
- 13. Taiwan (Niitakacris, Sinopodisma);
- 14. South-East China (Sinopodisma, Tonkinacris Carl, Paratonkinacris You, Li et Bi, Podismodes Ramme);
- 15. The Yunnan centre (Anepipodisma Huang, Curvipennis Huang, Qinshuiacris Yin, Sinopodisma, Yunnanacris Chang);
- 16. The Assam area (Indopodisma Dovnar-Zapolskij, Rhinopodisma L. Mistshenko);
- 17. South-East Tibet and Hengduanshan (Kingdonella Uvarov, Eokingdonella Yin);
- 18. The Karokoram region (Dicranophyma Uvarov).

An additional centre of diversity in the South Siberian Mountains probably deserves an independent status. A few endemic species of *Zubovskya* (including undescribed ones) occur in this area. Besides that, the monotypic genus *Cophoprumna* Dovnar-Zapolskij was described from Transbaikalia (Dauria). Its taxonomic status should be revised. It seems to be the synonym of *Primnoa*. Unfortunately, its types were lost.

It is interesting that the complicated arid and subarid environment of Central Asia, while being very favorable for many Orthoptera, is not suitable for the Melanoplini. However, absence of the Melanoplini in the mountains of Tien Shan and Pamiro-Allay is especially enigmatic, because there are a lot of suitable habitats. Perhaps this is a result of evolutionary competition with the ecologically similar Conophymatini grasshoppers (Uvarov, 1929).

A few species are known from frontiers of this territory. Podisma pedestris

occurs in Dzungarian Alatau. The grasshoppers of *Kingdonella* and *Eokingdonella* are distributed along the southeastern ranges of the Tibetan Plateau, the Sino-Tibetan Mountains, and the Himalayas. Several species of *Dicranophyma* are described from the Karakoram region, near the boundary between the Pamirs and the Himalayas. All of them colonize montane meadows on the high altitudes only.

DISTRIBUTION IN THE NEARCTIC REGION

The general patterns of melanopline distribution in the Nearctic Region were described by Vickery (1989 et al.). The following centres of diversity and endemism can be proposed here:

- 1. The Rocky Mountain area occupies the central part of the Rocky Mountains. Several genera (Argiacris Hebard, Asemoplus Scudder, Booneacris Rehn et Randell, Buckellacris Rehn et Rehn, Prumnacris Rehn et Rehn, Melanoplus, Nisquallia Rehn) are typical for the territory. All of them include endemic species.
- 2. The Appalachian centre is limited by the southeastern parts of Canada and the northeastern parts of the USA. The genus *Appalachia* Rehn et Rehn is associated with this area. Besides that, a few local species of *Melanoplus* occur there.
- The Californian area is characterized by the distribution of the Mediterranean type ecosystems. Several endemic genera (Agnastokasia Gurney et Rentz, Karokia Rehn, Hebardacris Rehn, Hypsalonia Gurney et Eades) and many endemic species (especially of Melanoplus) occur there.
- 4. The Sonoran region occupies arid territories of North America. This area is settled by many melanopline genera (more than 25) and species (mainly from the genus *Melanoplus*). Among typical local forms are *Agroecotettix* Bruner, *Campylacantha* Scudder, *Oedaleonotus* Scudder, *Paraidemona* Brunner, *Sinaloa* Scudder.
- 5. The Gulf Coastal centre is associated with the southeastern parts of the USA. Some genera (Aptenopedes Scudder, Eotettix Scudder, Gymnoscirtetes Scudder, Dendrotettix Packard, Paroxya) prefer this

area. Many endemic species of Melanoplus occur there.

All North American centres include many endemic genera and species. Probably each of them should be divided into a set of connected centres of diversity and endemism.

However, between these areas, the territory (mainly the prairian one) is inhabited by many Melanoplini with comparatively wide distribution (a large number of Melanoplus, Phoetaliotes nebrascensis (Thomas), Hypochlora alba (Dodge), Hesperotettix viridis (Thomas)). This is not evidently connected with flight capacity. This group includes both good flyers (some Melanoplus) and flightless forms (e.g. Phoetaliotes Scudder), many of which penetrate into arid and subarid territories.

CONCLUSIONS

The general distribution of the Melanoplini in the Palaearctic and in the Nearctic regions is similar. In each case, the main centres of diversity and endemism are associated with mountain areas near the western and eastern coastal regions of each continent. Each region is colonized by many endemics with small ranges. These patterns show evident spatial evolutionary trends common for this grasshopper tribe.

However, some essential differences can be noticed. In North America, there are many forms adapted for arid and subarid environment. On the contrary, the xerophilous melanoplines are almost absent from Eurasia. As a result, a specific centre of diversity and endemism is in the arid areas of the Neartic region.

Another (but well known) distinctive feature of Melanopline grasshoppers is connected with regional dominance of different subtribes. In North America, the representatives of the Melanoplina (often good flyers and graminivorous forms) are dominated and abundant. Almost all Eurasian Melanoplini are of the subtribes Podismina and Miramellina, usually flightless and herbivorous.

Some authors attempted to discuss possible history of the Melanoplini. Uvarov (1929) proposed that this group originated in the temperate part of East Asia (so called the Angara fauna). Dirsh (1975) speculated that these

grasshoppers probably originated from the Catantopinae (s. str.) stock comparatively recently and probably in the Old World. Recently evolutionary history of the Melanoplini was discussed by Vickery (1987, 1989).

Unfortunately, our data is not enough for solving all historical problems and known points of view are controversial. Two general evolutionary events of the Melanoplini history should be estimated as only comparatively reliable. The first is that almost all the North American and Eurasian stems of the Melanoplini developed in isolation from each other for a long time. Probably this is true for different centres of diversity and endemism in each continent. The second event is that present distribution and recent speciation of the Melanoplini is the evident result of Pleistocene glaciations and postglacial changes (Chang, 1940; Dirsh, 1975; La Greca, Messina, 1979; Vickery, 1987, 1989).

Therefore, the general distribution and particular evolutionary trends of the Melanoplini should be compared more accurately on the basis of ecological and geographical knowledge. This comparison will allow us to learn the main evolutionary and ecological trends of these grasshoppers and to understand the general situation of an acridid evolutionary biogeography.

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