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Habitus Diversity of Ladybirds (Coleoptera, Coccinellidae) in the Steppe Zone of the Southern Urals and the South of Western Siberia

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Abstract—In the ladybird fauna of the steppe zone of the Southern Urals and the south of Western Siberia, five variants, three forms, and two habitus types of adult beetles are distinguished, and their hierarchy is established. The habitus diversity of ladybirds is revealed using a new method of describing each form in a polar system of coordinates whose center coincides with the center of gravity of the insect body. The system of ladybird habitus reflects the main directions of trophic specialization in the family.

Key words: life forms, ladybirds, habitus, the Southern Urals, the south of Western Siberia.

With respect to the development of classification principles, modern systems of life forms are still at the pre-Linnaean stage. The work on the principles of ecosystematics is a prerequisite for progress in developing the general theory of life forms (Lyubarskii, 1992). We understand a life form as an integral hierarchical system of interrelated adaptations accounting for the morphofunctional similarity within a group of organisms living under similar environmental conditions. In this context, studies on the structure of adaptation systems deserve special attention. In our opinion, the main principle of classifying life forms is that the structure of their system must correspond to the structure of the adaptive complex.

The original body constitution of an organism developing under the effects of certain environmental factors, or habitus, is determined by a variety of adaptive morphological structures differing in morphofunctional universality. Among a variety of the morphological criteria determining habitus, the body build (especially monolithic parts of the skeleton) is the most conservative (universal) character, and its sharp change in the course of evolution is related to the emergence of large systematic subdivisions within families (Mordkovich, 1977). In this connection, the study of the habitus diversity of a taxon, chosen for making a concrete system of life forms, is the first and essential step in the work of an ecotaxonomist, and the classification of life forms should apparently be based on habitus types. It is believed that the habitus of ladybirds is relatively uniform and rather specific for the family as a whole (Savoiskaya, 1983). No special research of the habitus diversity of adult beetles in the family has been performed.

METHODS FOR DISTINGUISHING HABITUS TYPES IN LADYBIRDS

In our opinion, the existing approaches to the description of body forms in insects using the systems of morphometric indices are subjective in the choice of these indices and the very principle of description. The methods of geometric morphometry discussed in recent publications (Pavlinov, 1999) do not provide the possibility of making broad intertaxon comparisons, which are necessary in ecosystematics if the homologous structures determining habitus are lacking. Hence, we used in this work a new method of describing the forms of organisms using circular matrices.

Habitus formation is determined by a great number of past and present factors. At the same time, some environmental factors have a system-forming role in biological constructions due to the constancy of their influence on these constructions This primarily concerns the effect of gravitation.

The basic consequence of the influence of gravitation on the organism is that all morphogenetic processes follow the principle of passive stabilization of spatial orientation. The essence of this principle is that all parts of the body are formed strictly in balance with respect to the moment of force relative to its center of gravity. This minimizes energy expenditures for maintaining a stable position of the body in space. We believe that gravitation, due to the constancy of its effect on all biological constructions, is reflected in each of them as a system of masses balanced with respect to the moment of force, and this, in turn, may be a general principle of organization for the existing variety of forms.

The form as a spatial property of matter, in our opinion, can be described only in the system of coordinates whose center coincides with the body's center of gravity. The description of habitus can be made using a multiradial matrix, which is actually a polar coordinate system whose center coincides with the center of gravity.

The method for determining the center of gravity used in this work is a modification of the known method that involves hanging an insect in alignment with the rotation axes (Alexander, 1970). The center of gravity is located in the intersection of the longitudinal body axis and the plumb line. In our method, the body form is described using a circular matrix of forty rays (the number of rays depends on the desired accuracy of description and can be chosen arbitrarily, provided the matrix remains symmetrical). In projecting an insect on the matrix, two requirements should be met: (1) its center of gravity should coincide with the center of the matrix, and (2) the projection plane should be strictly perpendicular to the optical axis of the projector. In Figs. 1–3, matrix rays 2–20 correspond to the dorsal projection, and rays 22–40, to the lateral projection of a beetle. Rays 1 and 21 are common to both projections.

At the next stage, the coordinates of points at which matrix rays intersect the image boundary are determined. The effects of size on the description and comparison of forms is eliminated by setting the scale of a single coordinate. As we studied the habitus diversity of ladybirds using their projections, the latter were brought to the same scale on the basis of their areas, and the value of a single coordinate corresponded to the radius of a circle with the same area as the projection of a beetle.

The area of diversity of ladybird forms (Fig. 1) was obtained by superimposing the projections. Using a cluster analysis, this area was divided into smaller areas corresponding to habitus variants, and the dendrogram with three levels of branching was obtained, which reflected habitus hierarchy. As the coordinated categories of ladybird habitus, we used types, forms, and variants. The study was based on the material collected by V.P. Pekin between 1983 and 1997 in the Southern Urals and in the south of Western Siberia. On the whole, 36 species comprising the faunistic nucleus of ladybirds in this region were processed. Over 500 ladybirds were used for morphological studies.

BRIEF CHARACTERIZATION OF VARIANTS, FORMS, AND TYPES OF LADYBIRD HABITUS AND THEIR SYSTEM

All representatives of the Coccinellidae studied in this work were divided into two habitus types, which coincided with the taxonomic division of the family Coccinellidae into the Epilachninae and Coccinellinae subfamilies. The cause of this coincidence is a striking habitus specificity of representatives of the subfamily Epilachninae, which is manifested in a considerably smaller size of the pronotum relative to the total body size. Ladybirds belonging to the Epilachninae habitus type have a large or medium-sized hemispherical body with a small pronotum tightly attached to the elytra (Fig. 2a).

Within the Coccinellinae habitus type, two groups of ladybirds sharply differing in habitus—"flat" and "hemispherical"—are distinguished. Ladybirds belonging to the hemispherical form have a more rounded and convex body (Fig. 2b). Ladybirds of the flat form are characterized by an elongated medium-sized body with long legs and antennae (Fig. 2c).

Within the flat habitus form, two habitus variants—"oval" and "narrow-bodied"—are distinguished. The main distinguishing feature of the narrow-bodied variant is a flattened, sharply elongated body with parallel sides (Fig. 3a); in the oval variant, the body is flattened but resembling an oval (Fig. 2b).

Among ladybirds of the hemispherical habitus form, the "universal" (Fig. 3c) and "hat-shaped" (Fig. 3d) variants are distinguished by means of cluster analysis. The hat-shaped beetles are characterized by widely stretched sides of the clypeus and epipleuras of the elytra (the form is typical of the Chilocorini). The universal variant comprises the greatest number of ladybird species and is the most typical variant of body form in the family. Its representatives have a convex, hemispherical body with a fairly large pronotum.

Thus, using the method for describing the forms in the polar system of coordinates adjusted to the center of gravity of the insect, we distinguished in ladybirds five habitus variants, three forms, and two types and determined their hierarchy.

CONNECTION BETWEEN THE HABITUS DIVERSITY OF LADYBIRDS AND MAIN DIRECTIONS OF TROPHIC SPECIALIZATION IN THE FAMILY

To create the system of life forms whose hierarchy, in our opinion, should correspond to the general structure of the adaptive system, it is necessary to reveal the connection between the group of adaptations determining the habitus of a beetle and other adaptive complexes that are the components of a life form. In many systems of life forms, higher categories are distinguished according to the parameters (usually morphological) closely related to the type of feeding (Sharova, 1981; Medvedev and Samoderzhenkov, 1986). A fairly comprehensive generalization of the trophic specialization in the family was made by Savoiskaya (1983). This resulted in the classification of ecological groups of ladybirds according to their food and identification of

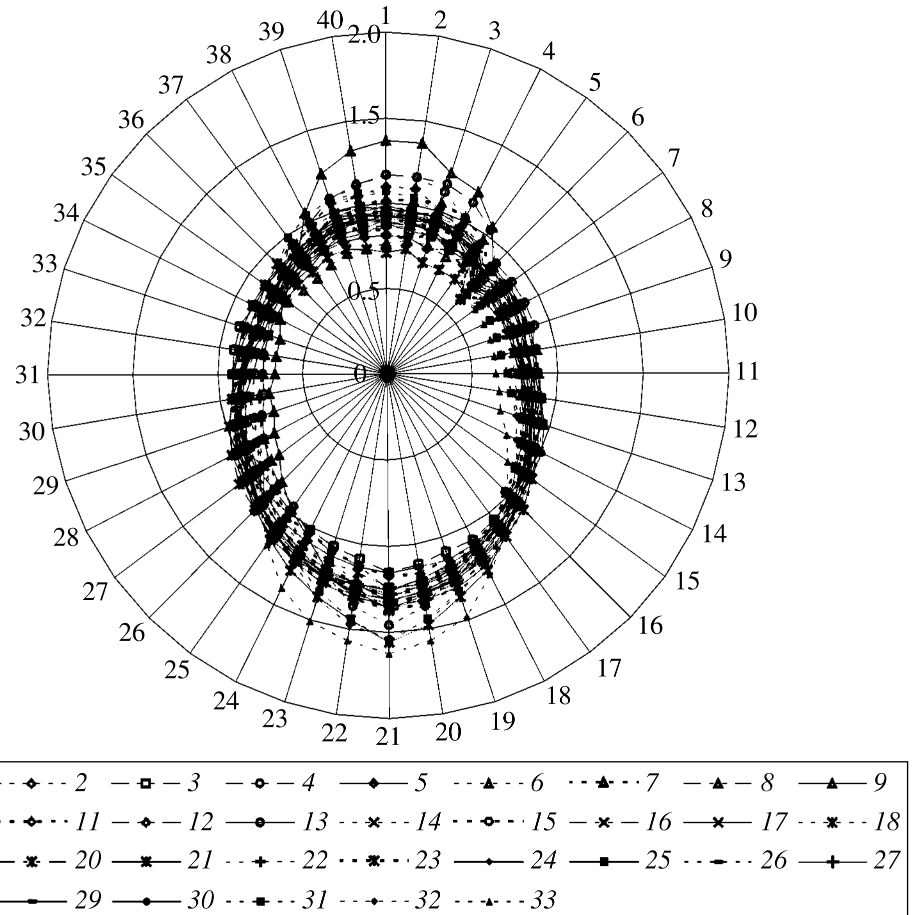

Fig. 1. The area of form diversity for ladybirds of the steppe zone of the Southern Urals and the south of Western Siberia: (*1*) *Thea vigintiduopunctata* L., (*2*) *Adonia variegata* Goese, (*3*) *Chilocorus renipustulatus* Scriba, (*4*) *Myrrha octodecimguttata* L., (*5*) *Subcoccinella vigintiquatuorpunctata* L., (*6*) *Epilanchna vigintioctomaculata* Motsch., (*7*) *Harmonia quadripunctata* Pont., (*8*) *Coccinella septempunctata* L., (*9*) *Anisosticta cobensis* Lew., (*10*) *Adonia amoena* Fald., (*11*) *Exochomus flavipes* Thunb., (*12*) *Vibidia duodecimguttata* Poda, (*13*) *Synharmonia conglobata* L., (*14*) *Calvia quatuordecimguttata* L., (*15*) *Bulaea lichatshovi* Hum., (*16*) *Calvia quinquedecimguttata* Eabr., (*17*) *Sospita vigintiguttata* L., (*18*) *Adalia bipunctata* L., (*19*) *Coccinella divaricata* Oliver, (*20*) *Anatis halonis* Lewis, (*21*) *Henosepilachna chrysomelina* Fabr., (*22*) *Semiadalia notata* Laich., (*23*) *Aiolocaria myrabilis* Motsh., (*24*) *Halyzia sedecimguttata* L., (*25*) *Neomysia gebleri* Crotch, (*26*) *Coccinella nivicola* Men., (*27*) *Neomisia oblongoguttata* L., (*28*) *Anatis ocellata* L., (*29*) *Coccinella trifasciata* L., (*30*) *Calvia decimguttata* L., (*31*) *Hippodamia tredecimpunctata* L., (*32*) *Hippodamia septemmaculata* Deg., (*33*) *Coccidula scutellata* Herbst.

the main pathways of feeding specialization in taxa of different ranks.

At the subfamily level, ladybirds differentiate into herbivorous and predatory species. Phyllophagous beetles comprise the subfamily Epilachninae (Savoiskaya, 1983). In the subfamilies Lithophilinae and Coccinellinae, the overwhelming majority of species are predators; however, there also are palinophages comprising the tribe Bulaeni and mycetophages associated into two tribes, the Psylloborini and Tytthaspini.

The subfamily Coccinellinae comprises the greatest number of trophic groups. Among the representatives of this subfamily, there are coccidophages (in the Scimnini, Coelopterini, Telsimini, Hyperaspini, Chilocorini, Noviini, Coccidulini, and Sukunahikonini tribes), aphidophages (the Coccinnelini and Platynaspini), and acariphages (the Stetthorini).

Among predatory ladybirds, aphidophages are the least specialized trophically and the richest in species composition. This is the group including the greatest number of species that can use pollen, nectar, fungi, psyllae, and thrips as additional food. It is related to palinophagous (the Bulaenini) and mycetophagous ladybirds (the Psilloborini and Tytthaspini), as follows from the fact that aphidophages can feed on pollen and fungi. It is considered that palinophagy and mycetophagy in ladybirds are secondary modes of feeding (Savoiskaya, 1983).

The distribution of trophic groups within the five habitus variants we distinguished is reflected in Fig. 4. It is seen that all the ladybird species studied are divided into two habitus types, Epilachninae and Coccinellinae. In addition to the fact that this division corresponds to the division into subfamilies, it reflects two

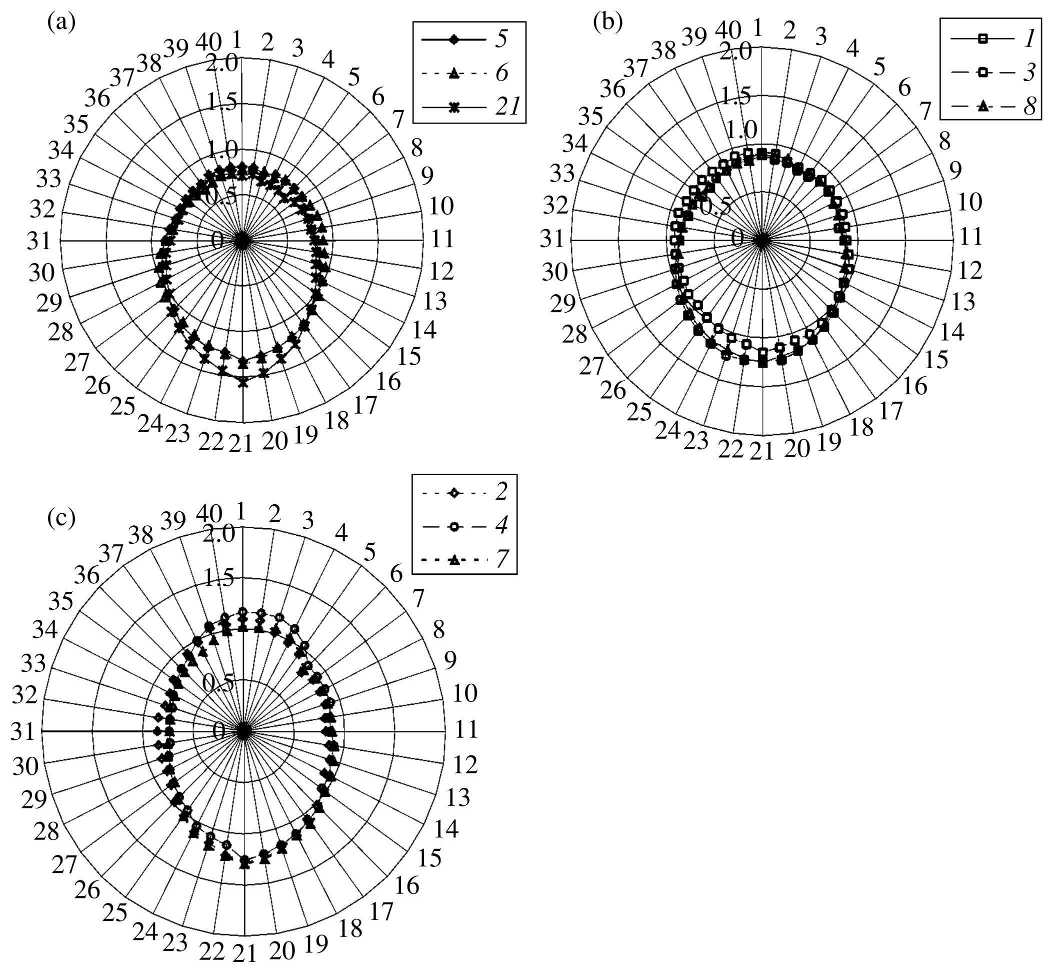

Fig. 2. Habitus types and forms: (a) the Epilachninae type, (b) the hemispherical form, and (c) the flat form. Designations are the same as in Fig. 1.

main directions of trophic specialization in the family. All phyllophagous species concentrate in the subfamily Epilachninae. In the proposed habitus system, all specialized phytophagous (more precisely, phyllophagous) ladybirds concentrate in the Epilachninae habitus type, and all predators, in the Coccinellinae type. The presence of mycetophages and palinophages in the universal variant is atypical of this habitus group. These trophic groups occurred in the habitus type comprising predatory ladybird species because mycetophagy and palinophagy in ladybirds are secondary phenomena (Savoiskaya, 1983). In this case, we apparently deal with the phenomenon that trophic specialization at the level of physiological adaptations has not yet affected the entire system of morphological adaptations and has not yet resulted in the formation of an original habitus.

At the second hierarchical level of the habitus system, with the flat and hemispherical forms distinguished in the Coccinellinae type, subsequent subdivision of trophic groups is observed. Thus, in the flat form, the groups of species specialized in aphidophagy are united. Trophic connections in the hemispherical form are more diverse. This form includes predatory ladybirds with different levels of trophic specialization and secondary herbivores.

At the final level of habitus hierarchy, the differentiation of ecological groups of ladybirds with respect to the degree of trophic specialization is observed. For instance, the narrow-bodied variant unites the species feeding exclusively on aphids from grasses: *Coccidula rufa*, *C. scutellata*, and *C. suturalis*. The hat-shaped variant includes mainly specialized coccidophages, such as *Chilocorus bipustilatus* and *Ch. renipustulatus.* The oval variant comprises aphidophages with different degrees of trophic specialization, and the universal variant includes a large number of trophically nonspecialized forms.

Thus, the use of a new method of describing the forms of insects in the polar coordinate system whose center coincides with the center of gravity of the insect body made it possible to reveal for the first time the diversity of forms in ladybirds without referring to morphological structures and to create the system of their habitus. This system for ladybirds of the steppe zone of

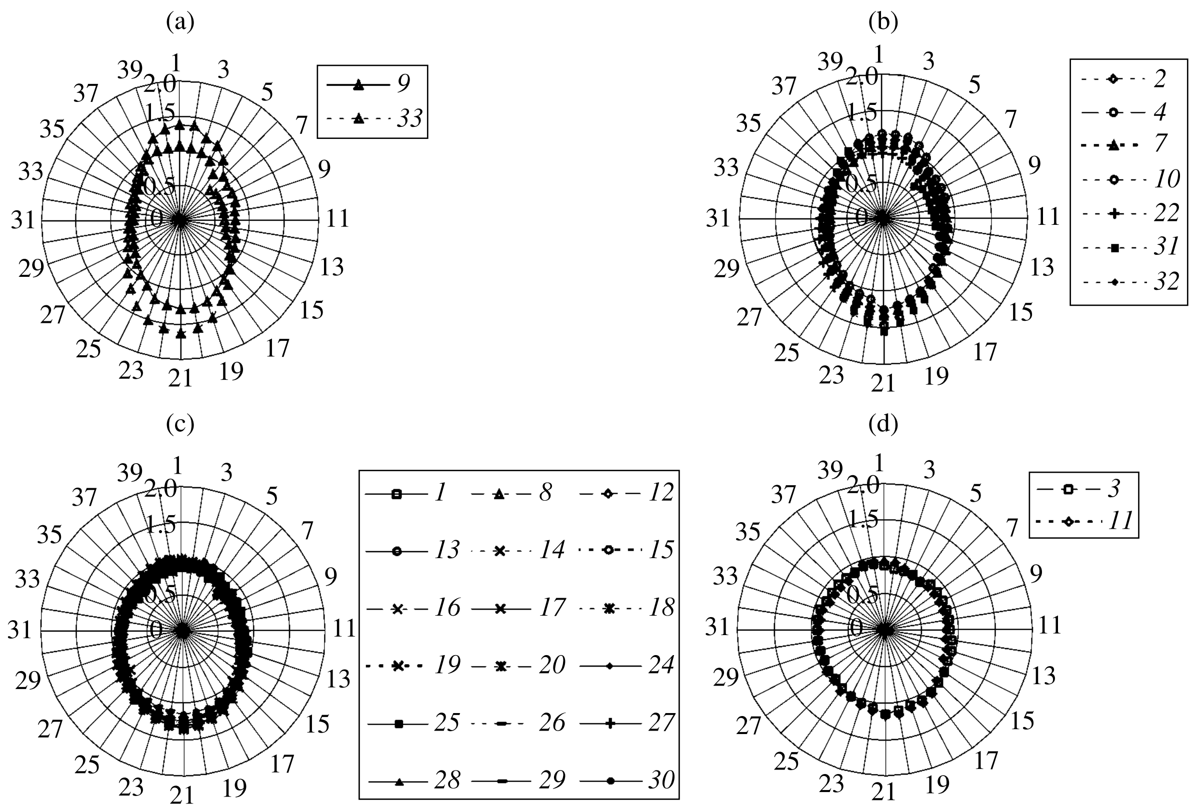

Fig. 3. Variants of ladybird habitus: (a) narrow-bodied, (b) oval, (c) universal, and (d) hat-shaped. Designations are the same as in Fig. 1.

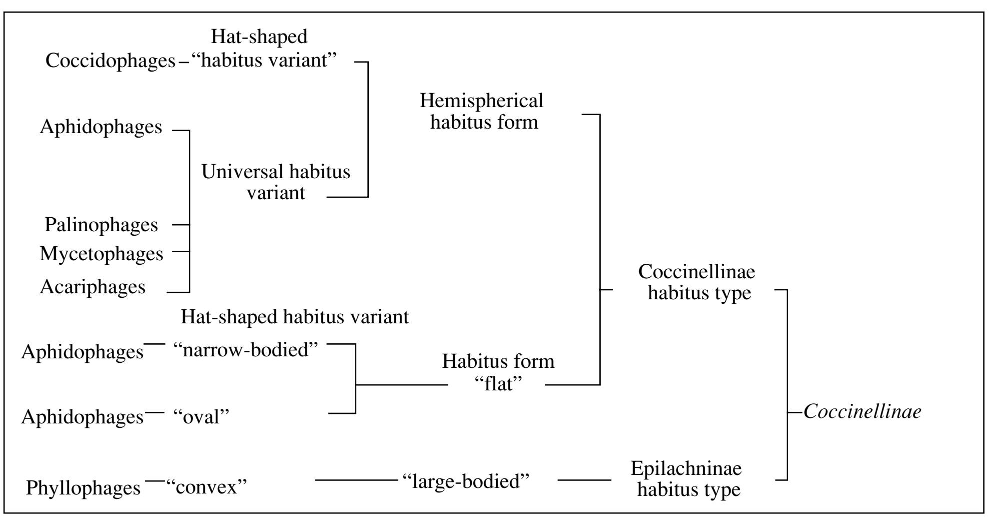

Fig. 4. Distribution of trophic groups of ladybirds according to habitus variants.

the Southern Urals and Western Siberia reflects the main directions of trophic specialization in the family. This is evidence for a close interaction of the two levels of the adaptive system: the complex of ecomorphological adaptations determining the habitus of a beetle and physiological–biochemical adaptations manifested in its trophic specialization. However, a broad trophic radiation observed in the family, which has resulted in the formation of distinct trophic groups (aphidophages, coccidophages, mycetophages, palinophages, and phyllophages) is not accompanied by the diversity of habitus variants.

Hence, proceeding from the principle that the hierarchy of the system of life forms must correspond to the general organization of the adaptive system, morphological adaptations determining the beetle habitus should be used for identifying higher categories of life forms in ladybirds, whereas physiological–biochemical adaptations determining trophic specialization describe life forms of lower ranks. In addition, the coincidence of habitus diversity in ladybirds with the taxonomic division of the family into subfamilies, together with the habitus specificity of the Coccinellidae, justifies the wide practice of developing the systems of life forms in entomology for insect families.

REFERENCES

Alexander, R., *Animal Mechanics*, London: Sidgwick and Jackson, 1968. Translated under the title *Biomekhanika*, Moscow: Mir, 1970.

Lyubarskii, G.Yu., Biostylistics and the Problem of Life Form Classification, *Zh. Obshch. Biol.*, 1992, vol. 53, no. 5, pp. 649–661.

Medvedev, L.N. and Samoderzhenkov, E.V., Life Forms of Leaf Beetles (Coleoptera, Chrysomelidae), in *Ekologiya zhiznennykh form pochvennykh i nazemnykh chlenistonogikh* (The Ecology of Life Forms of Soil and Terrestrial Arthropods), Moscow: Mosk. Gos. Pedag. Inst., 1986, pp. 91–104.

Mordkovich, V.G., *Zoologicheskaya diagnostika pochv lesostepnoi i stepnoi zon Sibiri* (Zoological Diagnosis of Soils in the Forest–Steppe and Steppe Zones of Siberia), Novosibirsk: Nauka, 1977.

Pavlinov, I.Ya., Analysis of Variation in the Shape of the Third Upper Molar in High-Mountain Voles of the Genus *Alticola* (Cricetidae) by the Methods of Geometrical Morphometry, *Zool. Zh.*, 1999, vol. 78, no. 1, pp. 78–83.

Savoiskaya, G.I., *Koktsinellidy (sistematika, primenenie v bor'be s vreditelyami sel'skogo khozyaistva)* (Ladybirds: Taxonomy and Use in Agricultural Pest Control), Alma-Ata: Nauka, 1983.

Sharova, I.Kh., *Zhiznennye formy zhuzhelits (Coleoptera, Carabidae)* [Life Forms of Ground Beetles (Coleoptera, Carabidae)], Moscow: Nauka, 1981.