

SIGNIFICANCE OF COLOUR POLYMORPHISM IN MOUNTAIN POPULATIONS OF ABUNDANT LEAF BEETLES (COLEOPTERA, CHRYSOMELIDAE)

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ABSTRACT.— Leaf beetles, especially common and abundant species, play significant role in the flow of biomass and energy in alpine ecosystems. They feed openly in the leafage of shrubs and herbs and their various metallic colourations or highly melanistic forms absorb solar radiation, promoting warming and decreasing penetration of UV. Therefore colour polymorphism is important for monitoring of status of exact populations. Polymorphism as ecologically selected variability serves for the most complete and effective use of environmental heterogeneity. That is why composition of morphs and its changes in space and time are especially sensitive. Eco-geographical regularities of colour polymorphism is shown for various mountain populations of *Chrysomela lapponica*, *Gonioctena arctica* and *Oreina sulcata* throughout their distribution area. These species together with related ones enable to make a sensitive network of biosensors for climate change monitoring in Holarctic region.

RÉSUMÉ.— Les Scarabées des feuilles deviennent spécialement communs, présentent de nombreuses espèces et sans doute peuvent jouer un rôle important sur le cycle de biomasse et le flux d'énergie des écosystèmes alpiens. Ces insectes mangent les feuilles des arbrisseaux ou des herbes et leurs colorations métalliques très variées ou leurs formes fortement mélaniques absorbent les radiations solaires; c'est comme cela qu'ils provoquent un réchauffement et arrivent à filtrer les rayons UV. En conséquence, le polymorphisme de couleurs se montre très important pour le monitoring de plusieurs populations concernées. Si nous considérons ce polymorphisme comme un type de variabilité sélectionnée écologiquement, il peut bien contribuer à une utilisation plus effective et complète de l'hétérogénéité environnementale. C'est pourquoi la composition des morphotypes et ses changements aussi bien dans l'espace que dans le temps deviennent très sensibles. Chez les populations montagnardes de *Chrysomela lapponica*, *Gonioctena arctica* et *Oreina sulcata* et au long de leur aire de répartition ont été observées certaines régularités ecogéographiques du poly-

morphisme couleur. Sans doute ces espèces et d'autres semblables pourraient aider à établir un réseau de bioindicateurs permettant un monitoring du changement climatique sur la région Holartique.

RESUMEN. - Los escarabajos de las hojas resultan especialmente comunes, presentan numerosas especies y sin duda juegan un papel destacado en el ciclo de biomasa o en el flujo de energía de los ecosistemas alpinos. Estos insectos se alimentan del follaje de arbustos o hierbas y sus variadas coloraciones metálicas o sus formas altamente melánicas absorben la radiación solar; por ese procedimiento provocan un calentamiento y filtran los rayos ultravioleta. Así, el polimorfismo de colores resulta importante para el seguimiento de unas poblaciones determinadas. Considerado dicho polimorfismo como variabilidad seleccionada ecológicamente, puede contribuir a una utilización más completa y efectiva de la heterogeneidad ambiental. Esa es la razón por la cual una composición de morfotipos y sus cambios en el espacio y en el tiempo resultan especialmente sensibles. Ciertas regularidades ecogeográficas del polimorfismo de colores pueden apreciarse en varias poblaciones montañas de *Chrysomela lapponica*, *Gonioctena arcaica* y *Oreina sulcata* a lo largo de su área de distribución. Tales especies y otras relacionadas permitirían el establecimiento de una red de biosensores para el seguimiento del cambio climático en la región Holártica.

Keywords: Mountain biodiversity, population ecology, colour polymorphism, leaf beetles.

1. Introduction

Leaf beetles are not so diverse as other groups of alpine insects, but among them there are representatives specifically associated with dominating plants in subalpine and alpine ecosystems. The species of *Chrysomela* and *Gonioctena* intensely feeding on prostrate willows, birch or mountain alder may completely defoliate the patches. The damage to perennial herbs is well seen wherever beetles of *Oreina* spp. are feeding on them and its extent became the subject for careful evaluation (PYSEK & BEZDEK, 1996). Thus these common and abundant species of leaf beetles play significant role in the flow of biomass and energy in alpine ecosystems.

Alpine insects openly feeding in the leafage of shrubs have two ways of adaptation: either using only the lower part of it close to the soil (temperature and humidity is higher and wind is light) or using the upper part, where they can use solar radiation for heating themselves (BOGACHEVA, 1990). It was found that various metallic colours (bronze, blue, green, violet, etc.) or highly melanistic forms are common in mountain populations of leaf-beetles. These colours absorb solar radiation more efficiently and promote warming, but simultaneously decrease penetration of ultraviolet (LOPATIN, 1996). And

this is one of the explanations why colour polymorphism may serve well for monitoring of exact populations under climate change. Furthermore, alpine species of leaf beetles have undergone major habitat shifts during the last glaciation and currently live in geomorphologically and climatically very diverse environments (KNOLL & ROWELL-RAHIER, 1998). Therefore now they have clear potential to act as sensitive biosensors of climate change.

2. Materials and methods

In the course of our research of diversity and ecology of alpine leaf beetles in the mountains of the Urals, Altai, Kuznetsky Alatau, West Sayan, Tuva and Swiss Alps in 1993-2001 we studied species composition and took representative samples from the populations of most abundant species. Such samples were taken on different altitudes if it were possible.

Studying of colour pattern polymorphism, distinguishing of separate morphs and constructing of polymorphic spectrums we made according to the principles of population phenetics (YABLOKOV, 1987; MIKHAILOV, 1999). The determination of colour morphs in *Oreina sulcata* Gebler we made using similar experience in other leaf-beetles with metallic colouration (SUZUKI & OZAKI, 1980).

Data processing was made by means of standard PC software Excel and Statistica.

3. Eco-geographical regularities of colour polymorphism in selected species

Chrysomela lapponica L.

Boreal-montane species widely distributed in Palaearctic from Western Europe to Kamchatka and Japan, northward to Novaya Zemlya islands and in alpine zone in Fennoscandia, the Urals, South Siberia and Tien-Shan (MATIS, 1986; LOPATIN, 1996).

We observed beetles and their larvae very numerous and intensely feeding on prostrate willow *Salix* spp. in the Urals and Kuznetsky Alatau mts., rarely on prostrate birch *Betula nana* (South Altai). In French Alps (Col Agnel) this species was recorded on mountain alder *Alnus viridis*, which was completely defoliated (LEPLAT, 1999). On willows they skeletonise the leaves (up to 100% of the leaf surface) remaining only nerves. Heavily feeding this leaf

beetle may damage 100% of leaves on some plants. Such plants with dry leaves are well seen in mt. tundra areas and among stones. Leaf-beetles, their larvae and pupae are living openly having defensive allomones from predators, which on willows are host-derived (PASTEELS *et al.*, 1988). Mass emergence of beetles from pupae takes place in the last decade of June - early July (after hibernation) and in first decade of August (new generation).

By means of colour pattern polymorphism we studied structure of several populations in alpine zone of Kuznetsky Alatau (KA), SE Tuva, South Altai (Tarbagatai range) and North Ural. We obtained data on characteristic composition of morphs in these populations (Figure 1) using spectrum of morphs of elytral colour pattern (Figure 2).

All investigated populations clearly divided in two groups (Figure 1). In Kuznetsky Alatau and South Altai typical form (20) is dominating, while in East Tuva and the Urals – other, more melanized morphs. Frequencies of light (1-6) and completely dark-metallic (50) morphs also varies greatly (Figure 1). These characters are convenient for long term monitoring and also comparisons with chosen lowland populations.

Ch. lapponica is trans-Eurasian species and is available for research in lowlands, e. g. the Netherlands (BEENEN, 1985) and mountain populations in

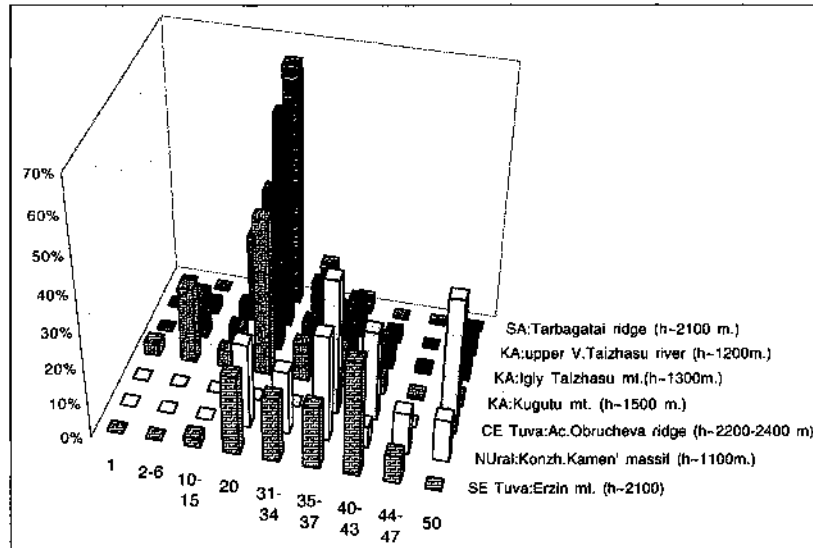


Figure 1. Frequencies of morphs in various populations of *Chrysomela lapponica* (Note: KA - Kuznetsky Alatau mts., SA - South Altai).

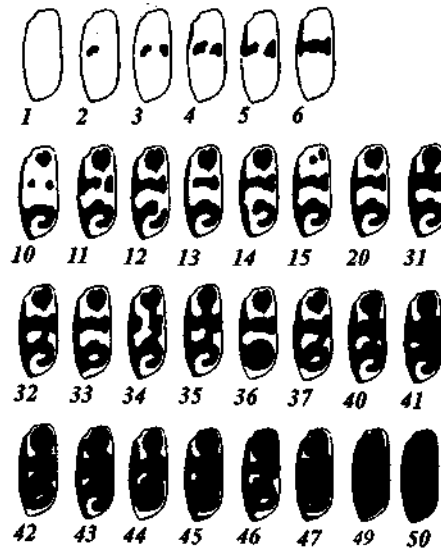


Figure 2. Polymorphic spectrum of colour pattern of *Chrysomela lapponica*.

many points as well. And more, several closely related species: *Chrysomela interrupta* Brown, *Ch. alnicola* Brown, *Ch. walshi* Brown, *Ch. knabi* Brown, *Ch. falsa* Brown, *Ch. aeneicollis* (Schaeffer) are distributed in North America from lowlands to mountains and their variability is within the same spectrum (BROWN, 1956). All this related group might be used for coordinated monitoring network in Holarctic region as a whole.

Gonioctena arctica (Mannh.) (=affinis (Gyll.)

As previous species inhabits northern forest zone of Eurasia but also North America and have isolated populations in the mountains of Siberia and the Urals distant southward. Its exact populations are highly polymorphic (Figure 3) and have specific composition of morphs in every investigated point. Usually typical form dominates, also in the lowlands of Finland (SILFVERBERG, 1994), but the relic population of the South Ural differs from many others like isolated populations of Sakhalin Island.

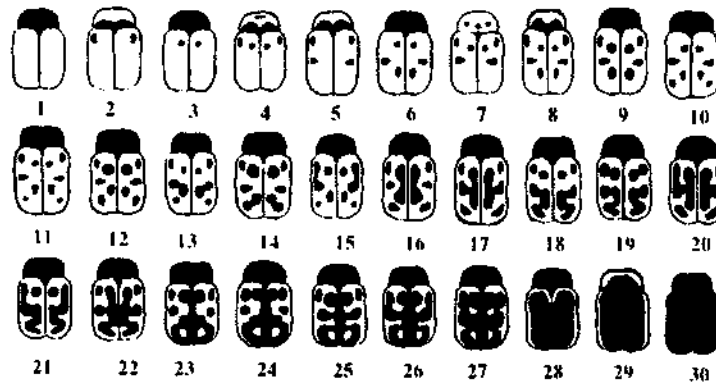


Figure 3. Polymorphic spectrum of colour pattern of *Gonioctena arctica* (= *G. affinis*) (from KRESLAVSKY, 1975 with corrections and additions).

Gonioctena arctica is abundant in all studied populations and feeding openly on *Salix* species in mountain forest-tundra and tundra.

Oreina sulcata Gebl.

This species is very common and abundant in the mountains of South Siberia. It inhabits Altai, the Sayans, mts. of Tuva, Cisbaikalia and Transbaikalia. Isolated lowland populations are known from the Yenisei valley northward to Arctic Circle and recently found in Tyumen region in Western Siberia far away from the main distribution area (MIKHAILOV, 2000). *Oreina sulcata* prefers tall herb montane or subalpine meadows with its host plants *Saussurea latifolia* (Asteraceae) and *Heracleum dissectum* (Apiaceae) (Altai, Kuznetsky Alatau mts., West Sayan). The most high mountain populations were found in mountain tundra of SE Tuva near snowbeds (host plant there unknown).

There are two forms distinguished mainly by the elytral sculpture (smooth or sulcate). They were initially described by GEBLER (1823) as two different species. In Russian works they have been treated as two subspecies - *Oreina basilea basilea* Gebl. and *O. basilea sulcata* Gebl. But recently it was shown that according to the principle of the first revisor this species must be called *O. sulcata* Gebl. (*O. basilea* is a synonym) and subspecies division was rejected due to continuous variation of elytral sculpture (BONTEMS, 2001). But there is

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still a problem how to treat smooth and sulcate forms, from which the former is dominating in the western part of distribution area (throughout Altai and Kuznetsky Alatau mts.) and the latter - in the eastern part (the Sayans, mountains of Tuva and Cisbaicalia) according both to our observations and BONTEMIS (2001).

This species has very wide range of colour morphs: purple red, reddish-brown, goldish-red, bronze, goldish-green, green, emerald, bluish-green, blue, bluish-violaceous, violaceous, blackish-violaceous, black and striped. The populations in various parts of distribution area have specific difference in composition of morphs.

Previously it was noticed, that generally in the western part of its distribution area beetles of *O. sulcata* of red and brown colour are more rare than in eastern part, in West Altai blue beetles are abundant on high altitudes. In the eastern part in some regions red beetles are dominating (KRESLAVSKY, 1975). But in fact main difference in composition of morphs first of all is between two forms, or more likely races. Dark-bronze, red-brown and bronze-green and emerald morphs are peculiar to *sulcata* race (polymorphic spectrum is wider), while purple red morph - to *basilea* race. Other morphs are common (Figures 4 and 5).

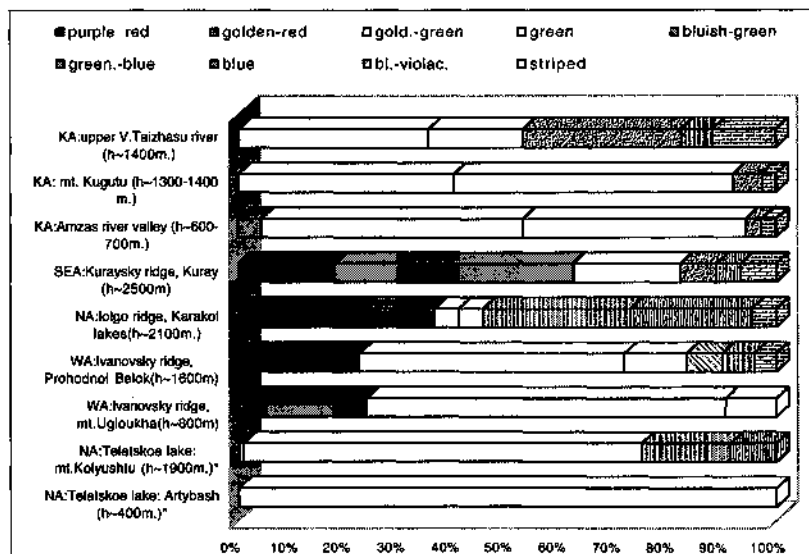


Figure 4. Frequencies of colour morphs in various populations of *Oreina sulcata* (*basilea* race). (Note: KA - Kuznetsky Alatau mts., WA - West Altai, NA - North Altai, SEA - South-East Altai; original data, except * - data from DOLGIN, 1978).

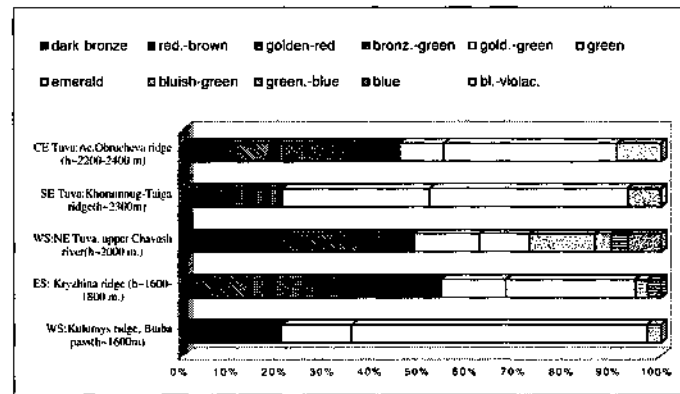


Figure 5. Frequencies of colour morphs in various populations of *Oreina sulcata* (*sulcata* race) (Note: WS - West Sayan, ES - East Sayan).

Also from the lowlands and foothills to subalpine meadows and mountain tundra this species has trends in composition of morphs of body colouration along altitudinal transects. Generally at the foothills green (together with goldish-green) morphs are dominating, while the higher above sea level the lower is their percentage. This correlation firstly was reported by DOLGIN (1978) but only based on three sites on various altitudes in North and Central Altai (two of them near Teletskoye lake is shown on Figure 4). We can prove this conclusion based on more sites (Figure 4) (for green and goldish-green morphs together) for *basilea* race in general and for populations of *sulcata* race from the Sayans. In other high ranges of East Tuva green and goldish-green morphs still dominates on the highest altitudes (Figure 5). In both forms the majority of other morphs appear on higher altitudes, usually 2000 m. a. s. l. and more (Figures 4 and 5).

The center of species diversity of the genus *Oreina* is situated in the mountains of South and Middle Europe – 22 species in 7 subgenera (KIPPENBERG & DÖBERL, 1994). Two Siberian species – *O. (s. str.) sulcata* Gebl. and *O. (Chrysochloa) redikortzevi* Jacobson – are both relics and represent only two subgenera.

In Europe population polymorphism is well studied in two species: *Oreina (Chrysochloa) cacaliae* (Schrank) and *O. (Chrysochloa) speciosissima* (Scop.), both distributed from NE Spain throughout the Alps to Karpatians, occur sympatrically feeding on the same host plant patches. Within populations individuals of both species show only minor colour variations. One of the explanations is that the colours are warning signals to possible predators. So mimicry and adaptation of individuals to the local dominating colour form

strongly restrict polymorphic spectrum in exact localities (KNOLL & ROWELL-RAHIER, 1998).

But also in general European species, including *Oreina cacaliae* (Schrank) and *O. speciosissima* (Scop.) has narrower polymorphic spectrum (KRESLAVSKY, 1975) in comparison with *O. sulcata*. This might be explained under niche - width variation hypothesis after VAN VALEN (1965). In Europe multispecies associations (guilds) are common on subalpine plants which include from 2 to 5 species of *Oreina* in one site (DOBLER, 1993; pers. obs.). Also usually several species are distributed along altitudinal gradients, changing one another from piedmonts to alpine zone. On the contrary, *O. sulcata* alone inhabits large mountain territories of South Siberia (only in some places of the Sayans in sympatry with *O. redikortzevi*) also along the whole altitudinal gradients, therefore its ecomiche is much wider. This is one of the explanations why *O. sulcata* – one of two species known from the mountains of South Siberia – has so wide polymorphic spectrum.

But despite different width of polymorphic spectrums European species also demonstrate similar regularities. For example, the colour of *O. cacaliae* showed a strong correlation with altitude: at higher altitudes beetles were dark blue, while lower - mostly green. (KNOLL & ROWELL-RAHIER, 1998). And this shows parallel trends with *O. sulcata* in Siberia.

4. Conclusion

Recognizing plants as the prime indicator organisms for the biological monitoring of climate change in alpine habitats, we consider other groups of organisms responding more rapidly and more predictably. The herbivorous insects specifically associated with common and widely distributed boreal plants provide better opportunities to develop longer term sampling networks. They have clear potential to act as more sensitive biosensors of climate change than their host plants (HODKINSON & BIRD, 1998). Among them leaf beetles (Coleoptera, Chrysomelidae), which have high abundances and present one of dominating groups in subalpine and alpine belts.

The distribution of host-specific herbivorous insects along latitudinal and altitudinal gradients may provide useful analogs for predicted future changes (HODKINSON & BIRD, 1998). But in fact the expected results would be very poor if biodiversity in this case is investigated on the species level only. However, biodiversity manifest itself on the population level as well and the most common example here is polymorphism (VASILYEV, 1996; MIKHAILOV, 1999). Polymorphism is ecologically selected variability, which

main function is the most complete and effective assimilation of environmental heterogeneity (SERGIYEVSKY, 1987).

Whether species track environmental changes is best evidenced by population structure. Composition and frequencies of morphs proved to be stable and specific in exact populations over a long-term observation period in various insects (NOVOZHENOV, 1989). At the same time a set of sensitive methods makes it possible to watch population structure changes, which track changes in their habitats. Firstly it was shown in anthropogenic biocoenoses (YEMETS, 1997; MIKHAILOV, 1998), but man made clearings under succession may be a model to some extent of predicted changes above timberline.

Several species of leaf beetles listed above would be among the key objects due to their high abundances, comparatively convenient collecting and complex of research methods already elaborated for monitoring of their population dynamics.

References

- BEENEN, R. (1985). *Chrysomela lapponica* L. in Nederland en het onderzoek naar de verspreiding van bladkevers [in Dutch]. *Natura*, 82: 175-177.
- BOGACHEVA, I. A. (1990). *Relationships of phytophagous insects and plants in ecosystems of the Subarctic* [in Russian]. UB AS USSR., 136 p., Sverdlovsk.
- BONTEMS, C. (2001). Les *Oreina* de Sibirie (Coleoptera, Chrysomelidae, Chrysomelinae). *Bull. Soc. ent. Fr.*, 106 (1): 65-77.
- BROWN, W. J. (1956). The New World Species of *Chrysomela* L. (Coleoptera, Chrysomelidae). *Can. Entomol.*, 88, Suppl. 3: 3-54.
- DOBLER, S. (1993). *Reproductive biology of the leaf beetle genus Oreina (Coleoptera, Chrysomelidae) and chemical ecology of the immature stages*. Ph. D. Inaugural dissertation, 104 p., Basel.
- DOLGIN, M. M. (1978). On the biology of *Chrysochloa basilea* Gebl. (Coleoptera, Chrysomelidae) in Altai [in Russian]. In: *Nasekomye Vostochnoi Sibiri*, pp. 154-161. Irkutsk University Press, Irkutsk.
- GEBLER, F. (1823). *Chrysomelae sibiriae rariores*. *Mem. Soc. Imper. Naturalist. Moscou*, 6: 117-126.
- HODKINSON, I. D. & BIRD, J. (1998). Host-specific Insect Herbivores as Sensors of Climate Change in arctic and Alpine Environments. *Arctic and Alpine Research*, 30 (1): 78-83.
- KIPPENBERG, H. & DÖBERL, M. (1994). Fam. Chrysomelidae. In GOECKE & EVERS. *Die Käfer Mitteleuropas*. 3. Supplementband, pp. 17-142, Krefeld.
- KNOLL, S. & ROWELL-RAHIER, M. (1998). Distribution of genetic variance

- and isolation by distance in two leaf beetle species: *Oreina cacaliae* and *Oreina speciosissima*. *Heredity*, 81: 412-421.
- KRESLAVSKY, A. G. (1975). Hereditary polymorphism, hereditary monomorphism and their role in the evolution of colour pattern in leaf beetles (Coleoptera, Chrysomelidae) [in Russian]. *Zhurn. Obshch. Biol.*, 36 (6): 878-885.
- LEPLAT, J. (1999). Quelques observations sur *Melasoma lapponica* Linné (Coleoptera, Chrysomelidae). *Rutilans*, 2(3): 82-83.
- LOPATIN, I. K. (1996). High altitude fauna of the Chrysomelidae of Central Asia: biology and biogeography. In P. H. A. JOLIVET & M. L. COX (eds.) *Chrysomelidae Biology, volume 3: General Studies*: 3-12. SPB Academic Publishing, Amsterdam.
- MATIS, E. G. (1986). *Insects of Asian Beringia: (Principles and experience of ecological-geosystem study)* [in Russian]. Nauka Publ., 312 p., Moscow.
- MIKHAILOV, Y. E. (1998). Population sexual dimorphism and dynamics of population structure in *Cryptocephalus quinquepunctatus* Scop. (Coleoptera, Chrysomelidae). In BRUNNHOFER V. & SOLDAN T. (eds.) *Book of abstracts, VIth European Congress of Entomology*: 443-444, Ceske Bud?jovice.
- MIKHAILOV, Y. E. (1999). *Hierarchical analysis of morphological and ecological-geographical aspects of biodiversity (Chrysomelidae, Coleoptera as an example)* [in Russian]. Abstract of Ph. D. Thesis. IPAE UB RAS, 20 pp., Yekaterinburg.
- MIKHAILOV, Y. E. (2000). New distributional records of Chrysomelidae from the Urals and Western Siberia [on some "less interesting" faunistic regions] (Insecta, Coleoptera). *Faun. Abh. Mus. Tierkde. Dresden*, 22 (3): 23-38.
- NOVOZHENOV, Y. I. (1989). Chronographic variability of populations [in Russian]. *Zhurn. Obshch. Biol.*, 50 (2): 171-183.
- PASTEELS, J. M., BRAEKMAN, J.-C. & DALOZE, D. (1988). Chemical defence in the Chrysomelidae. In P. JOLIVET, E. PETITPIERRE & T. H. HSIAO (eds.) *Biology of Chrysomelidae*, pp. 233-252. Kluwer Academic Publishers, Dordrecht.
- PYSEK, P. & BEZDEK, A. (1996). *Oreina speciosissima* - what is the extent of damage to the host plant? In P. H. A. JOLIVET & M. L. COX (eds.) *Chrysomelidae Biology, volume 2: Ecological Studies*, pp. 365-372. SPB Academic Publishing, Amsterdam.
- SERGIYEVSKY, S. O. (1987). Polymorphism as universal adaptive strategy of populations [in Russian]. *Trudy ZIN*, 160: 41-58.
- SILFVERBERG, H. (1994). Colour variation in Finnish Chrysomelidae (Coleoptera). 2. The genus *Gonioctena*. In D. G. FURTH (ed.) *Proceedings of the Third international symposium on the Chrysomelidae, Beijing, 1992*, pp. 31-37. Backhuys Publishers, Leiden.

- SUZUKI, K. & OZAKI, Sh. (1980). Supplementary Report on the Geographical Distribution of Two Color Forms of *Chrysolina aurichalcea* (Mannh.) (Coleoptera, Chrysomelidae) in the Chugoku District, SW Honshu, Japan, with an attempt at a New Categorization of Color Forms. *Journ. College of Liberal Arts, Toyama Univ., Japan*, 13 (1): 47-59.
- VAN VALEN, L. (1965). Morphological variation and width of ecological niche. *Am. Nat.*, 99: 377-390.
- VASILYEV, A. G. (1996). *Phenetic analysis of biodiversity on population level* [in Russian]. Abstract of Doctoral Thesis. IPAE UB RAS, 47 pp, Yekaterinburg.
- YABLOKOV, A. V. (1987). *Population biology* [in Russian]. Vysshaya Shkola, 302 p., Moscow.
- YEMETS, V. M. (1997). *Dynamics of population structure in insects and mechanisms of population resistance to anthropogenic influence* [in Russian]. Abstract of Doctoral Thesis. IPÉE RAS, 43 p, Moscow.