ISSN 0013-8738, Entomological Review, 2011, Vol. 91, No. 9, pp. 1149–1166. © Pleiades Publishing, Inc., 2011.
Original Russian Text © A.O. Bieńkowski, M.Ya. Orlova-Bienkowskaja, 2011, published in Zoologicheskii Zhurnal, 2011, Vol. 90, No. 8, pp. 942–958.

The Subspecies of *Chrysolina limbata* (Coleoptera, Chrysomelidae)

A. O. Bieńkowski and M. Ya. Orlova-Bienkowskaja

Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia
e-mail: bienkowski@yandex.ru

Received March 16, 2010

Abstract—Examination of 1492 specimens of *Ch. limbata* (Fabricius, 1775) from the entire distribution range resulted in the discrimination of six subspecies: *limbata* (West Europe excluding the Apennine Peninsula, the Crimea, north and south of European Russia, the Great Caucasus, Northern Kazakhstan, and southern West Siberia), *discipennis* (Ménétriés, 1848) (southeast of European Russia, Western Kazakhstan), *hochhuthii* (Suffrian, 1851) (south of East Siberia, Eastern Kazakhstan, Mongolia, Northern China), *luigionii* (Depoli, 1936) (the Apennines, the Alps, Herzegovina, the Mediterranean coast of France); *russiella* ssp. n. (deciduous forests, forest-steppe and steppe of European Russia and Ukraine); *volodi* ssp. n. (alpine regions of the Lesser Caucasus and eastern Turkey). *Ch. limbata findelii* (Suffrian, 1851) is a new junior synonym of *Ch. limbata limbata*.

DOI: 10.1134/S0013873811090077

We continue the revision of the subgenus *Zeugotaenia* Motschulsky, 1860 of the genus *Chrysolina* Motschulsky, 1860, started in the previous communication (Bieńkowski and Orlova-Bienkowskaja, 2011). The type species of the subgenus, *Chrysolina limbata*, is characterized by distinct but insufficiently studied geographic variation (Warchałowski, 1993; Kippenberg and Döberl, 1994), which was reflected in the description of a number of intraspecific forms. A study of the literature has shown that different authors applied different taxonomic status to these forms.

The preceding communication was devoted to the diagnosis of the subgenus and analysis of the name-bearing types of the nominal taxa. This paper deals with the intraspecific structure of *Ch. limbata*.

MATERIALS

We have examined 1687 specimens of the subgenus *Zeugotaenia* of the genus *Chrysolina*: 748 males and 744 females of *Ch. limbata* (Table 1), 107 males and 88 females of *Ch. jenisseiensis*. The material was collected by the authors, kindly provided by the colleagues, and obtained from the following institutions: GGR, Galichia Gora Reserve, Lipetsk Province; ZIN, Zoological Institute, Russian Academy of Sciences, St. Petersburg; ZMD, Zoological Museum [Museum für Tierkunde], Dresden; ZMMU, Zoological Museum of Moscow State University, Moscow; ZMHU Zoological Museum of Helsinki University [Helsingin yliopiston eläinmuseo], Helsinki; IZUG, Institute of Zoology of Martin Luther University [Martin-Luther-Universität Halle-Wittenberg], Halle; MSU, Biological Faculty of Moscow State University, Moscow; NHMV, Natural History Museum [Naturhistorisches Museum Wien], Vienna; NHMUH, Natural History Museum of Humboldt University [Museum für Naturkunde der Humboldt-Universität], Berlin; MSPU, Moscow State Pedagogical University, Moscow; SMN, Senckenberg Museum of Nature [Naturmuseum Senckenberg], Frankfurt on Main; MU, Mordovian State University, Saransk; FTPM, Ferdinand Tirol Provincial Museum, Innsbruck; NMP, National Museum [Národní muzeum], Prague; SDEI, German Entomological Institute [Senckenberg Deutsches Entomologisches Institut], Müncheberg; PSU, Penza State University, Penza; ZMUC, Zoological Museum, University of Copenhagen [Zoologisk Museum, Københavns Universitet].

The holotypes of the new subspecies described in this paper will be deposited in ZIN, and the paratypes, in ZIN, ZMMU, MSU, SDEI, FTPM, ZMD, PSU, GGR, MSPU, MU, and the collections of L.N. Medvedev (KM) and the first author (KB).

METHODS

Species Identification

The best character distinguishing *Ch. limbata* from its sibling species *Ch. jenisseiensis* (Breit, 1920) is the

Table 1. *Ch. limbata*. The material examined

Subspecies	Number of specimens			Number of records		
	in series	solitary	total	series	solitary	total
russiella	78	20	98	8	17	25
limbata	445	144	589	37	92	129
volodi	33	2	35	4	2	6
luigionii	37	2	39	3	1	4
hochhuthii	359	29	388	22	20	42
discipennis	138	14	152	7	6	13
Mixed series						
limbata and *russiella*	23	0	23	4	0	4
russiella and *discipennis*	24	0	24	3	0	3
limbata and *discipennis*	7	0	7	1	0	1
Could not be identified	19	118	137	2	64	65
Total	1163	329	1492	91	202	292

Note: The specimens were regarded as "solitary" if the series included less than 4 specimens or if all the specimens were of the same sex.

structure of the aedeagus (Medvedev and Okhrimenko, 1991). Therefore we made preparations from all the males available in our material.

The specimens in series of *Ch. limbata* were found to vary in the length of their hind wings. The wings of macropterous specimens were wide, longer than the elytra in the unfolded state, those of brachypterous specimens were reduced, narrow, reaching only to the abdomen apex. No intermediate variants were found. The wings were reduced in all the specimens of *Ch. jenisseiensis*. This character was used to identify solitary female specimens.

Chrysolina jenisseiensis was recorded from East Siberia, Mongolia, the Caucasus, and European Russia (Medvedev and Okhrimenko, 1991). The record from European Russia was based on a single male labeled "Tambov 12.VII.23." We have examined this specimen and consider its label to be unauthentic. This label matches in design the labels of specimens collected in different regions and in different decades; therefore it must have been made during mass labeling of some old collections. Not a single male of *Ch. jenisseiensis* was discovered among the 648 examined specimens of the subgenus *Zeugotaenia* collected in Europe, including European Russia.

Thus, the following categories of specimens were assigned to *Ch. limbata*: males (identified by the aedeagus morphology) and females collected together with them; all the macropterous females; all the females collected in the regions where *Ch. jenisseiensis* does not occur.

The Distinguishing Characters of the Geographic Forms of Ch. limbata

We have studied all the characters which were previously used to describe the intraspecific forms of *Ch. limbata*. No geographic differences were revealed with respect to the body size, the degree of convexity (height to length ratio) of the elytra, the degree of development of the rows of punctures on the elytra, and the depth of the lateral impression of the pronotum. At the same time, we have found nine characters showing distinct geographic variation (Table 2): two metric characters, three qualitative characters with several ranged states, and four alternative qualitative ones.

(1) The metric characters: the width of the red margin at the elytron base related to the elytron length; the width of the red margin at the elytron base related to the width of the lateral margin. The measurements were carried out using a dissection microscope equipped with an eyepiece micrometer. The scheme of the measurements is shown in Fig. 1. The elytron length was measured from the anterior angle of the scutellum to the apex of the elytron; the width of the basal margin of the elytron was measured at the level of the 3rd row of punctures from the suture (not counting the incomplete row near the scutellum); the width of the lateral margin of the elytron together with the epipleuron was measured at the level of the hind coxa.

(2) The qualitative characters with ranged states: the tint of the metallic sheen of the elytra, the shape of the aedeagus apex, and the coarseness of the pronotal punctation. The state of each of these three characters in all the specimens was assessed by comparing them with a set of reference specimens showing the entire range of character variation.

The distribution of specimens in one series by the color was approximately normal. The tints were coded with numbers in the following way: 1 for bronze, 2 for green, 3 for blue, and 4 for purple. The tint of the metallic sheen within a series or a subspecies was characterized by the mean of these coded values.

The shape of the aedeagus apex varied considerably within the series (Fig. 2). We distinguished five states of this character, coded as follows: 1 for very short, 2 for short, 3 for medium, 4 for long, and 5 for very long.

We also distinguished five states of pronotal punctation: fine (about 20 μm), medium (30 μm), moderately coarse (40 μm), coarse (50 μm), and very coarse (60 μm).

(3) The qualitative characters with alternative variants: the fraction of specimens with black elytra (without metallic sheen); the fraction of macropterous specimens; the fraction of specimens with a basally convexly rounded (not emarginate) lateral margin of the pronotum; the fraction of specimens with the greatest width of the pronotum at its base (not in the middle).

In other to reduce the subjective bias, all the specimens were processed by the same person following the same techniques.

The Method of Complex Characters

The intraspecific structure of *Ch. limbata* proved to be so complex that it could not be studied without quantitative methods. Although our preliminary examination of the material did reveal some geographic differences, the variation of all the characters in this species was transgressive, i.e., the ranges of variation of each individual character overlapped between series of specimens from different regions.

In order to outline the morphological boundaries of the subspecies, we used the method of complex characters which had proved itself well in the study of various plant and animal groups (Filipchenko, 1978; Lubischew, 1982). Our work included two stages: (1) revealing the geographic forms by the pairwise comparison method and (2) testing the subspecific rank of these forms.

(1) The method of pairwise comparison of the series.

Each series of specimens was individually compared with other series with respect to the nine characters listed above. Each series can be represented by a point in the multidimensional space of characters, whose coordinates along the first, the second, etc. axis correspond to the mean values of the first, the second, etc. character for this series. Then, the difference between the two series (D) will be characterized by the squared distance between the two corresponding points in the character space:

$$D = \frac{(M_{a1} - M_{a2})^2}{\sigma_{a1}^2 + \sigma_{a2}^2} + \frac{(M_{b1} - M_{b2})^2}{\sigma_{b1}^2 + \sigma_{b2}^2} + \ldots + \frac{(M_{i1} - M_{i2})^2}{\sigma_{i1}^2 + \sigma_{i2}^2},$$

where M_{a1} and M_{a2} are the mean values of character a in the first and the second series, respectively; σ^2_{a1} and σ^2_{a2} are the variances of this character in the first and the second series; M_{b1}, M_{b2}, σ^2_{b1}, and σ^2_{b2} are the mean values and variances of character b, and so on. Each summand in this formula corresponds to the difference between the two series with respect to one particular character.

The variance (σ^2) for metric characters and qualitative characters with ranged states is equal to the sum of squares of deviations from the mean, divided by the number of specimens minus 1:

$$\sigma^2 = \frac{(V_1 - M)^2 + (V_2 - M)^2 + \ldots + (V_n - M)^2}{(n-1)},$$

where V_1 is the value of the character in the first specimen, V_2 is that in the second specimen, etc., M is the mean value of the character, and n is the number of specimens in the series.

For qualitative characters with alternative states, the variance is calculated differently:

$$\sigma^2 = pq / (p+q)^2,$$

where p is the number of specimens with one character state (for example, macropterous), q is the number of specimens with the alternative state (for example, brachypterous) in the given series.

The macropterous specimens were more frequent among females than among males in all the regions; therefore the fractions of macropterous specimens

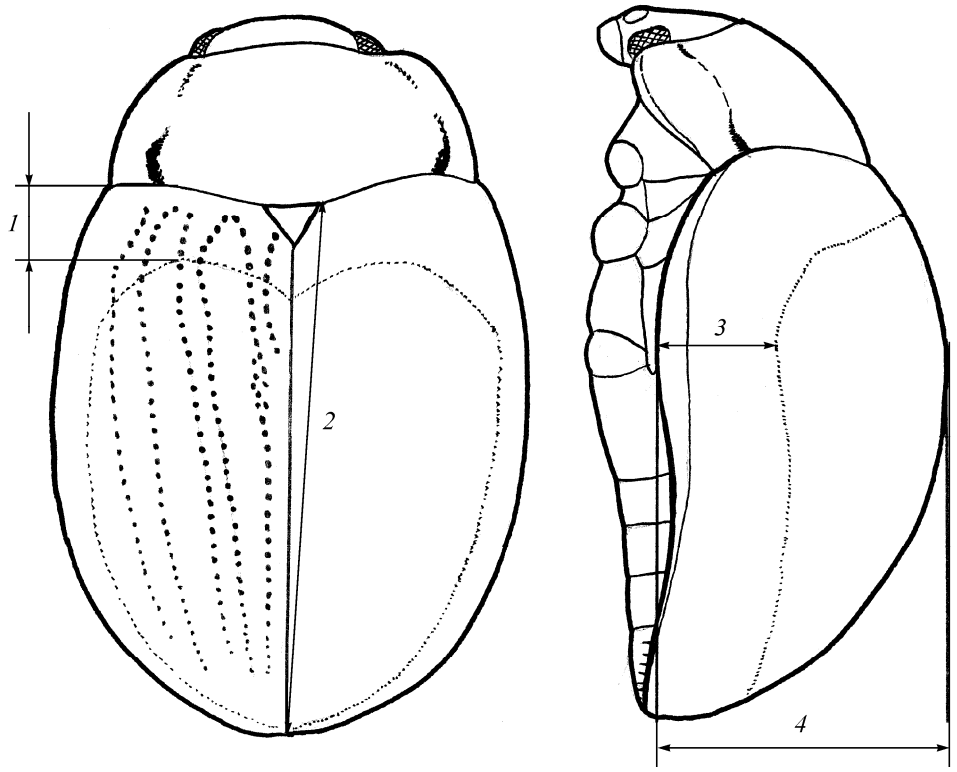

Fig. 1. The scheme of measurements: the width of the red margin at the elytron base (*1*), the elytron length (*2*), the width of the lateral margin of the elytron (*3*), and the height of the elytron (*4*).

were determined separately for each sex. The series collected in the Volga landwash zone (41 macropterous females) was excluded from these calculations because only the flying beetles were likely to get into the river and then to be brought ashore. No other series consisting exclusively of macropterous specimens was found.

Using the method of complex characters, the difference between two series with respect to all the nine characters can be estimated by a single parameter (*D*). This method works well even for small series. According to Filipchenko (1978), the more characters are used for comparison, the fewer specimens in each series will be required for significant results, since the random deviations tend to "neutralize" one another. The differences between series with respect to each character were normalized, i.e., the squared difference of means was divided by the sum of variances of the two series with respect to the given character. Owing to normalization, all the characters were given the same weight, so that differences in each character contributed equally to the final estimate of difference between the two series.

The difference parameter was calculated for each pair of series, with respect to the entire set of characters. Only homogeneous series comprising no less than four specimens of different sex were included in the analysis (83 series with a total of 1108 spms.). To differentiate between geographic and individual variation, we excluded solitary specimens from the analysis. The series showing a wide spread in the width of the basal margin (8 series with a total of 54 spms.) were also not included since such heterogeneous material could have been obtained from the subspecies intergradation zones.

The calculated differences were used to classify the series into geographic forms, using the graphical method. Each series was designated with a specific mark in the diagram (see below); then this mark was connected with two other marks representing the series that showed the smallest differences (*D*) from the first series.

(2) Testing the subspecific rank of the geographic forms obtained distinguished.

The rank of a subspecies corresponds to such a level of difference between the geographic forms at which no more than 25% of individuals from the range of the given subspecies can be identified as a different subspecies (Simpson, 2006). To find out if the geographic

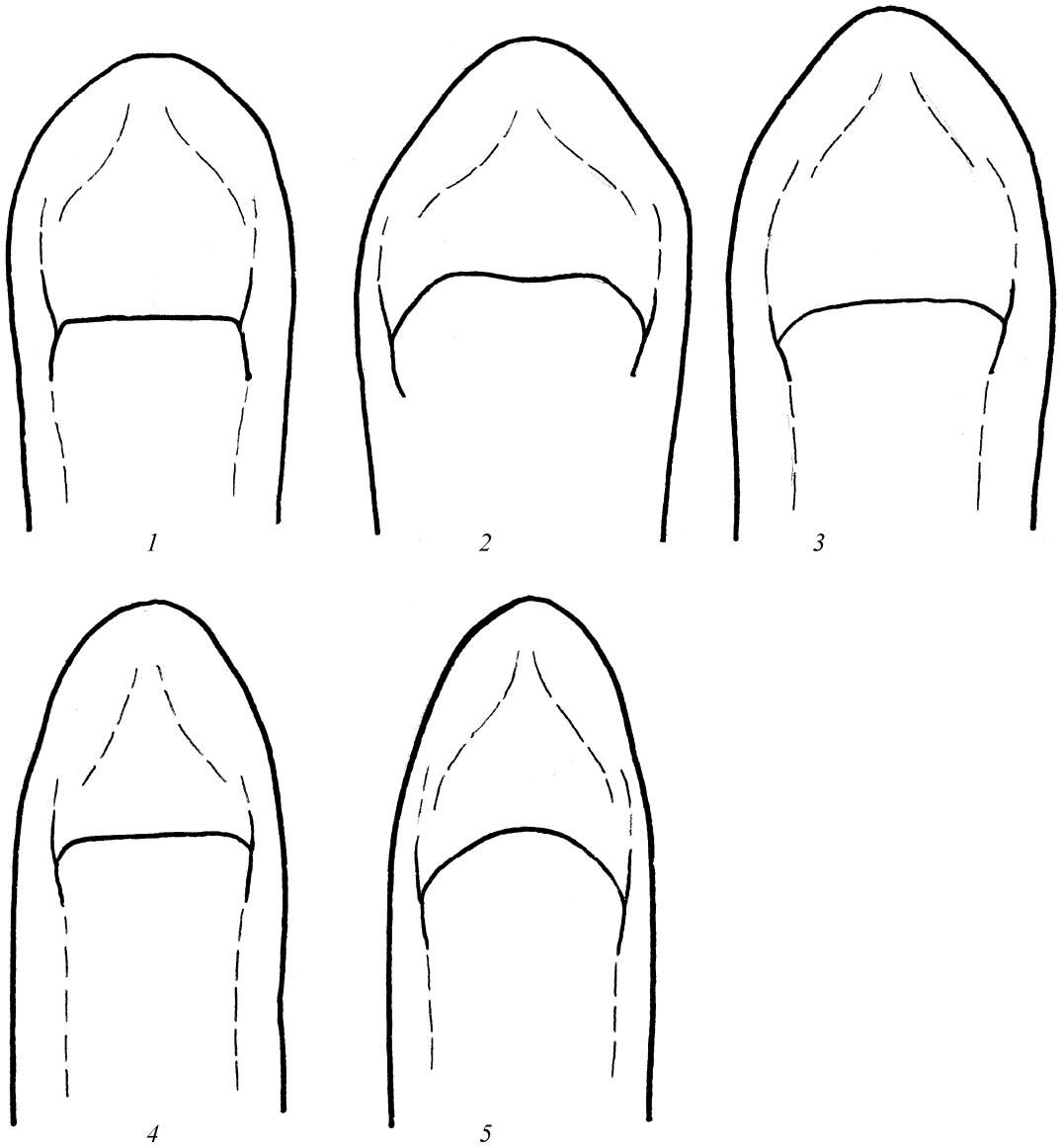

Fig. 2. Variability of the aedeagus apex: very short (*1*), short (*2*), medium (*3*), long (*4*), and very long (*5*).

forms distinguished by our analysis conformed to this criterion, we tested each specimen, i.e., determined which form it most closely resembled.

The testing was carried out in a way similar to comparison of series by the method of complex characters (Filipchenko, 1978). Each particular specimen was considered to be "morphologically close" to the geographic form from which it showed the smallest difference with respect to the entire set of characters.

The total difference between a particular specimen and a geographic form is a sum of differences in the individual characters:

$$d = \frac{(V_a - M_a)^2}{\sigma_a^2} + \frac{(V_b - M_b)^2}{\sigma_b^2} + \ldots + \frac{(V_i - M_i)^2}{\sigma_i^2},$$

where V_a, V_b, etc. are the values of characters *a*, *b*, etc. in the specimen, M_a, M_b, etc. are the mean values of characters *a*, *b*, etc. within the geographic form, and σ^2_a, σ^2_b, etc. are the variances of characters within the geographic form.

The males with metallic sheen were tested by all the nine characters. For obvious reasons, the character of aedeagus morphology was not used for females, and the character of tint was not used for specimensof both sexes without metallic sheen.

RESULTS

The Geographic Forms and Their Subspecific Status

Six geographic forms were distinguished by pairwise comparison of the series (Figs. 3–5). The series

Table 2. The diagnostic characters of subspecies of *Chrysolina limbata*

Diagnostic characters	Specimens condidered	*Ch. limbata russiella*	*Ch. limbata limbata*	*Ch. limbata volodi*	*Ch. limbata luigionii*	*Ch. limbata hochhuthii*	*Ch. limbata discipennis*
Metric characters							
Width of basal margin / length of elytron	All specimens	0.101±0.006 (0.028–0.167)	0.157±0.004 (0.070–0.309)	0.198±0.008 (0.147–0.240)	0.156±0.007 (0.106–0.191)	0.272±0.004 (0.164–0.384)	0.317±0.005 (0.177–0.398)
Width of basal margin / width of lateral margin	All specimens	0.670±0.038 (0.273–1.167)	0.818±0.015 (0.375–1.250)	0.875±0.035 (0.586–1.100)	0.741±0.024 (0.588–0.875)	1.048±0.012 (0.684–1.476)	1.043±0.016 (0.649–1.310)
Qualitative characters with ranged states							
Tint of metallic sheen of elytra	Colored spms.	1.00 ± 0.00	1.94 ± 0.08	2.89 ± 0.13	3.25 ± 0.80	3.00 ± 0.06	3.64 ± 0.09
bronze (1)		100	34	0	0	2	0
green (2)		0	40	11	0	7	1
blue (3)		0	25	89	75	80	33
purple (4)		0	1	0	25	11	66
Shape of aedeagus apex	Males	2.00 ± 0.34	2.60 ± 0.11	4.24 ± 0.27	3.85 ± 0.35	3.41 ± 0.12	2.16 ± 0.20
very short (1)		22	13	0	0	1	21
short (2)		56	31	0	5	17	42
medium (3)		22	42	10	20	26	37
long (4)		0	12	57	60	50	0
very long (5)		0	2	33	15	6	0
Punctation of pronotum	All specimens	2.08 ± 0.14	2.10 ± 0.08	1.64 ± 0.26	1.46 ± 0.20	2.35 ± 0.09	2.15 ± 0.14
fine (1)		13	25	52	60	14	22
medium (2)		67	47	33	35	46	47
moderately coarse (3)		19	23	15	5	31	25
coarse (4)		1	5	0	0	8	5
very coarse (5)		0	0	0	0	1	1
Characters with alternative states							
Elytra black (no metallic sheen)	All specimens	5 ± 5	18 ± 4	15 ± 13	89 ± 10	24 ± 5	14± 6
Macropterous	Females	61 ± 25	20 ± 5	0 ± 0	0 ± 0	16 ± 6	91 ± 7
Macropterous	Males	37 ± 24	9 ± 4	0 ± 0	0 ± 0	2 ± 2	62 ± 13
Sides of pronotum convexly rounded at base (not emarginate)	All specimens	75 ± 10	79 ± 4	94 ± 8	70 ± 15	59 ± 5	77 ± 7
Pronotum widest at base (not in the middle)	All specimens	67 ± 11	55 ± 5	39 ± 17	78 ± 14	72 ± 14	49 ± 14

Notes: The confidence level is 95%. For metric characters, the mean values and confidence intervals are given; the limits of variation are shown in parentheses. For qualitative characters with ranged states, each state is coded with a number (in parentheses); the mean va lues and confidence intervals are given, as well as the fractions of specimens (%) with different states of the character. For characters with alternative states, the fractions of specimens (%) and their confidence intervals are given.

belonging to each form were much closer to each other than to series from other forms; in other words, the difference parameter between series from the same geographic form was smaller than that between any series from this form and any series from another form (Fig. 5). The mean parameters of difference between series within each geographic form and between the forms are shown in Table 3.

Two series (15 spms. from "Tomsk Province" and 4 spms. from Tuva) could not be assigned to any of the geographic forms since they deviated strongly from all the forms by the entire set of characters. We do not consider it feasible to establish two additional geographic forms for these series, because the former series lacks a precise indication of locality, and the latter is too small.

As a result of testing all the specimens by the entire set of characters, most of them were found to be morphologically close to the geographic form from the range of which they were collected (Table 4). Therefore, all the six geographic forms should be regarded as subspecies.

The Subspecies Intergradation Zones

Mixed series were discovered in the material from Moscow Province, Moldova, and Kharkov Province of Ukraine, i.e., from the regions where the ranges of *Ch. limbata russiella* and *Ch. limbata limbata* are contiguous (Fig. 3). Such series included specimens clearly corresponding to any of the subspecies in their morphology, and also specimens with intermediate characters.

In Western Kazakhstan (Uralsk, Aktyubinsk, Dzhanybek), at the boundary between the subspecies *russiella* and *discipennis*, and in Volgograd Province, at the boundary between the subspecies *limbata* and *discipennis*, individuals morphologically corresponding to the two subspecies were found in the same localities, but no individuals with intermediate characters are available. It may therefore be assumed that the subspecies *discipennis* does not interbreed with *russiella* or *limbata* in the boundary territories, i.e., that it behaves like a distinct species. However, we do not regard *discipennis* a separate species since morphologically it is very close to the subspecies *hochhuthii* distributed in Mongolia and East Siberia, and the latter, in turn, is close to the subspecies *limbata*. In addition, the differences between *Ch. limbata discipennis* and other subspecies are smaller than the differences between closely related species of the genus *Chrysolina*.

Identification of Solitary Specimens

Identification of solitary specimens to subspecies is very difficult due to the wide range of individual variation. We assigned solitary specimens to a certain subspecies if two conditions were met simultaneously: (1) the specimen could be assigned to this subspecies by the method of complex characters (identification was carried out in the same way as testing specimens from series), and (2) the specimen was obtained from the range of this subspecies. The localities of such solitary specimens were also mapped (Figs. 3, 4).

A Review of the Subspecies

The differential diagnoses of the subspecies include only the most important and statistically significant differences.

Chrysolina limbata limbata (Fabricius, 1775)

Chrysomela limbata Fabricius, 1775 : 101.

Chrysomela limbifera Küster, 1846 : 91.

Chrysomela findelii Suffrian, 1851 : 70, syn. n.

Chrysolina limbata kavani Bechyné, 1950 : 170.

Material. *Chrysomela limbata* Fabricius: neotype ♂, England, ZMUC. *Chrysomela limbifera* Küster: neotype ♂, the Caucasus, FTPM. *Chrysomela findelii* Suffrian: lectotype ♀, Croatia, Fiume, ZMD. *Chrysolina limbata kavani* Bechyné: syntype ♂, Slovakia, Rarbok, NMP. Additional material examined: 302 ♀ and 283 ♂, France, Germany, Austria, Poland, Lithuania, Belarus, the Balkan states, Bulgaria, Moldova, Romania, Slovakia, Ukraine (including the Crimea), Azerbaijan, Georgia, Turkey, Kazakhstan, Russia: north of the temperate zone of European Russia, the North Caucasus, West Siberia.

Differential diagnosis (Table 2). The width of the basal margin of the elytron is about 0.16 of the elytron length, i.e., considerably greater than in *Ch. limbata russiella* (0.10) and considerably smaller than in *Ch. limbata volodi* (0.20), *Ch. limbata hochhuthii* (0.27), and *Ch. limbata discipennis* (0.32). The mean ratio of the width of the basal margin to that of the lateral margin is about 0.8, i.e., significantly greater than in *Ch. limbata russiella* (0.7) and significantly smaller than in *Ch. limbata hochhuthii* (1.0) and

Table 3. The mean values of difference determined by pairwise comparison of series within and between the subspecies

Subspecies	*russiella*	*limbata*	*volodi*	*luigionii*	*hochhuthii*	*discipennis*
russiella	2.9	12.7	31.6	21.8	46.6	62.3
limbata		6.7	10.1	9.6	19.3	30.4
volodi			1.2	7.7	23.1	18.9
luigionii				3.2	23.1	37.4
hochhuthii					4.5	9.0
discipennis						1.7

Table 4. The results of testing individual specimens

From the range of the subspecies	Number of spms.	Fraction (%) of specimens matching the subspecies in the complex of characters					
		russiella	*limbata*	*volodi*	*luigionii*	*hochhuthii*	*discipennis*
russiella	78	87.8	12.2	0.0	0.0	0.0	0.0
limbata	445	4.6	73.1	3.9	6.9	10.6	0.9
volodi	33	0.0	21.2	63.6	3.1	12.1	0.0
luigionii	37	0.0	10.8	5.4	83.8	0.0	0.0
hochhuthii	359	0.0	2.0	2.5	0.3	81.9	13.3
discipennis	138	0.0	0.0	0.0	0.0	6.1	93.9

Note: Only the specimens from samples including no less than 4 spms. were included in the calculation.

Ch. limbata discipennis (1.0). The aedeagus apex is medium or short in most cases, whereas in most specimens of *Ch. limbata volodi*, *Ch. limbata luigionii*, and *Ch. limbata hochhuthii* it is long or very long. The fraction of specimens having black elytra without metallic sheen is less than one-fourth, i.e., considerably smaller than in the subspecies *luigionii*. About 20% of females and 10% of males are macropterous. This character reliably differentiates the nominotypical subspecies, on the one hand, from *Ch. limbata volodi* and *Ch. limbata luigionii* which include no macropterous individuals, and on the other hand, from *Ch. limbata discipennis* and *Ch. limbata russiella* in which most individuals are macropterous.

Distribution (Figs. 3, 4). The subspecies is widely distributed in western, central, and southern Europe except for the Apennine Peninsula. Further to the east, its range is clearly subdivided into the southern and northern parts. The southern part includes the Crimea, Rostov Province, and the Russian territory of the Caucasus, whereas the northern part covers the north of the temperate zone of European Russia (the mixed forest zone and the southern boundary of taiga) and extends as far eastwards as the Ob river, in a narrow stripe along the north of Kazakhstan and the south of West Siberia.

In the northern and eastern parts of its range, *Ch. limbata limbata* mostly occurs in the valleys of big rivers: the Elbe, Vistula, the upper course of the Danube, Dnieper, Volga, Klyazma, Kama, Tobol, Ishim, Irtysh, and Ob. The landscape distribution is quite different in the southern part of the range: there, *Ch. limbata limbata* largely occurs in the mountains (the Pyrenees, Alps, Apennines, Balkans, Carpathians, Crimea, and Caucasus) and is almost never found in river valleys and lowlands.

The color forms. *Chrysolina limbata limbata* is a widespread and quite heterogeneous subspecies. As can be seen from Table 3, the mean difference between series within this subspecies is greater than within other subspecies. A question arises, whether this form can still be regarded a single subspecies. To answer this question, we compared the groups of all the specimens of this subspecies from five regions: northern Europe (including European Russia), southern Europe, the Crimea, the Caucasus, and Kazakhstan. Significant differences were observed only in the tint of the metallic sheen (Table 5): the bronze tint prevailed in northern Europe and in the Caucasus, the green and blue tints, in southern Europe, the green one, in the Crimea, and the blue and purple ones, in Kazakhstan. Thus, the beetles from northern Europe

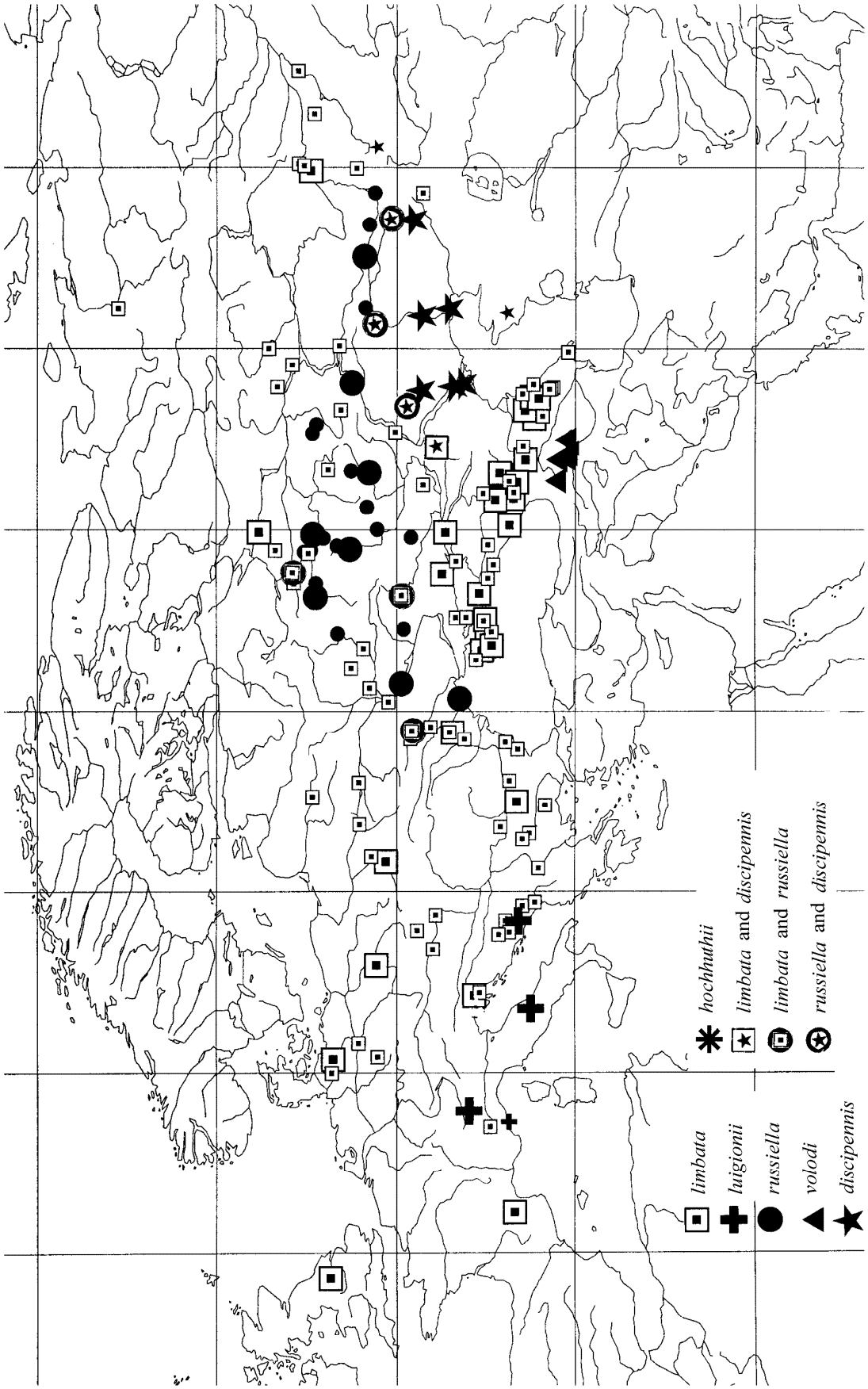

Fig. 3. Distribution of the subspecies of *Ch. limbata* in Europe. The localities of series are shown as large marks, those of solitary specimens, as small marks.

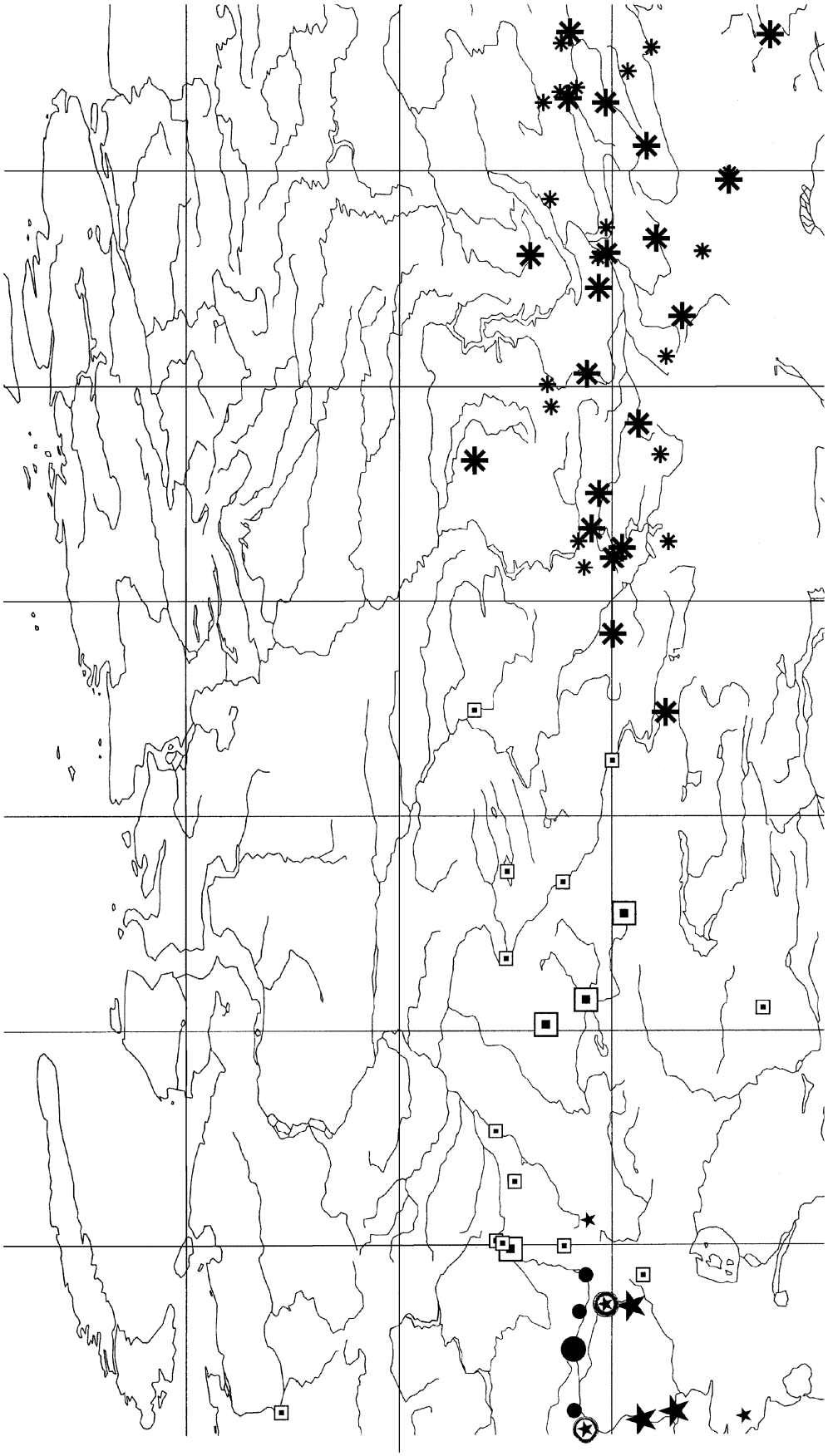

Fig. 4. Distribution of the subspecies of *Ch. limbata* in Asia. Designations as in Fig. 3.

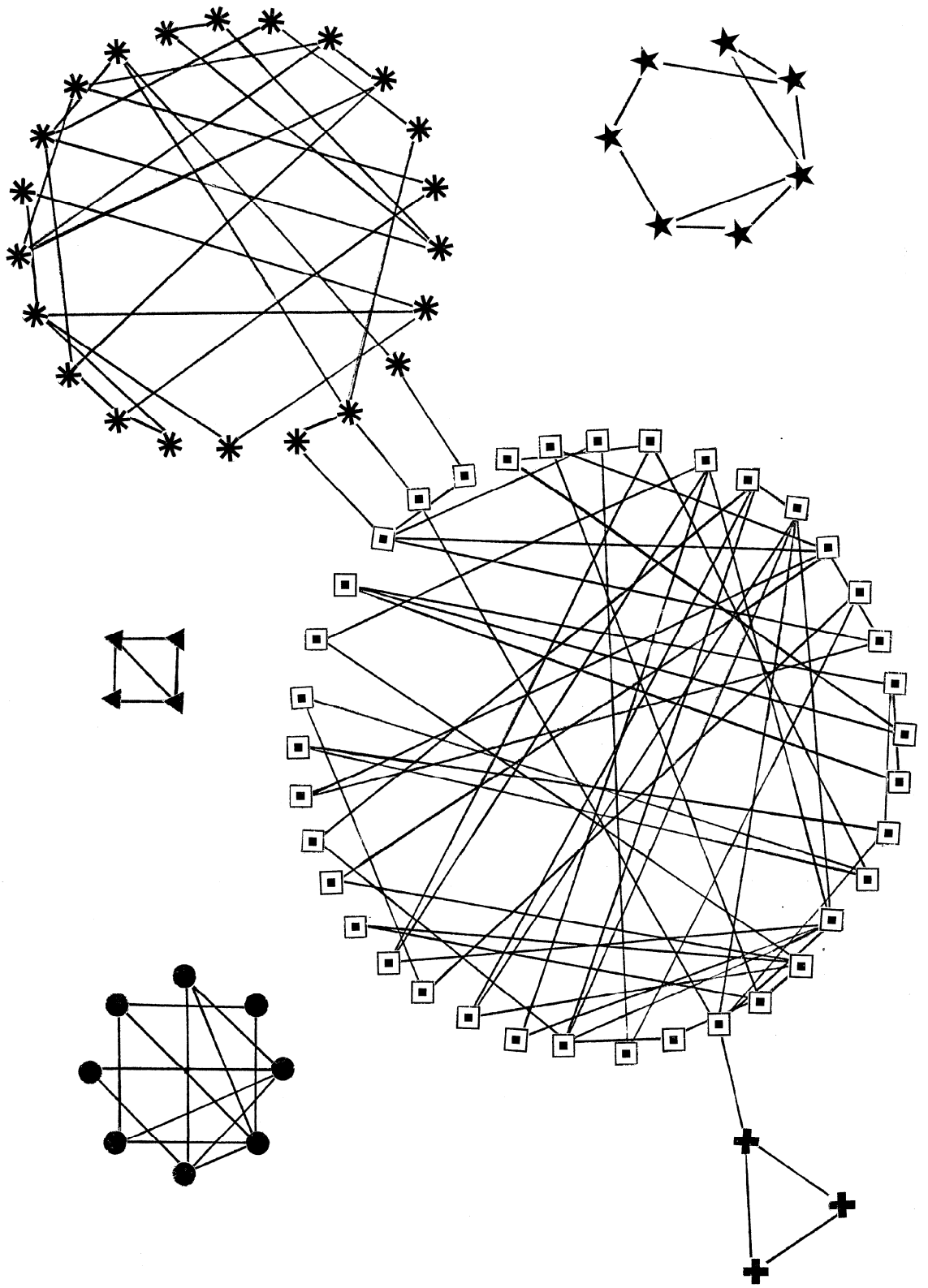

Fig. 5. Graphical analysis of the results of pairwise comparison of series. Each series is designated by the same mark as its locality on the map (Figs. 3, 4). Each mark is connected with two marks representing the series showing the smallest differences by the entire set of characters.

Table 5. The geographic variation of the metallic sheen of elytra in *Ch. limbata limbata*

Region	Fraction (%) of specimens with metallic sheen	Fractions (%) of specimens with different tints of metallic sheen			
		bronze	green	blue	purple
Northern Europe	89.7	**80.8**	7.7	9.6	1.9
The Great Caucasus	87.1	**59.3**	15.7	25.0	0.0
Southern Europe	90.9	26.7	**36**.7	**36.6**	0.0
The Crimea	82.6	3.3	**78.0**	18.7	0.0
Kazakhstan	62.9	8.7	8.7	**43.5**	**39.1**

Note: The prevalent tints of metallic sheen are shown in bold.

were clearly different from the Kazakhstan specimens in coloration: 88.5% of the specimens from Europe were bronze or green, whereas 82% of the specimens from Kazakhstan were blue or purple. However, in our opinion, this character is insufficient for a new subspecies to be established. Moreover, the populations from other regions occupied intermediate positions with respect to this character.

Notes. *Chrysolina limbifera* was described from "the Caucasus and southern Russia." According to the original description (Küster, 1846), it differs from *limbata* in the black-blue coloration with a green tint, more elongate body, narrower pronotum (twice as wide as long), finer pronotal punctation, and narrower red margin of the elytra. The neotype morphologically corresponds to other specimens from the Great Caucasus examined by us. We have found no significant differences between the specimens from the Great Caucasus and those from northern Europe in any character. Therefore we can confirm the synonymy of *Chrysolina limbifera* and *Chrysolina limbata limbata* (Warchałowski, 1993).

Chrysolina findelii was described from southern Austria and the Istrian Peninsula. According to the original description (Suffrian, 1851), *findelii* differs from *limbata* in greater body length, black coloration, different shape of the pronotum, finer pronotal punctation, less distinct lateral impression at the base of the pronotum, and a coarser punctation of the elytra. Our examination of the lectotype as well as 3 males and 2 females from the type locality (Istria) has shown that these specimens belong to the nominotypical subspecies as seen in the the complex of characters. Thus, *Ch. findelii* is a new junior synonym of *Ch. limbata limbata*.

Ch rysolina limbata kavani was described from Slovakia. According to the original description (Bechyné, 1950), it differs from the nominotypical subspecies in black-blue coloration, a dull pronotum, and a wider red margin on the base of the elytra. The type specimen does have a metallic sheen with a blue tint. According to our data, the blue tint of the elytra occurs in approximately 10% of specimens from northern Europe and in 37% of specimens from southern Europe. In other characters, including the width of the elytral margin, the syntype also fits within the limits of variation of *Ch. limbata limbata*. We can therefore confirm the synonymy of *kavani* and *Ch. limbata limbata* (Barabás, 1977).

Chrysolina limbata discipennis (Ménétriés, 1848)

Chrysomela discipennis Ménétriés, 1848 : 268.

Material. Lectotype: ♂ with labels: "Lehmann in itinere ad Bokhoram" [Lehmann, on his trip to Bukhara], "Menetr," "Coll. Mannerh.," "*Discipennis* Falderm.," ZMHU; paralectotypes with labels: "type," "Turcm.," "*Zeugotaenia discipennis* Turcm. D. Kirg. Fald.," 1 ♀, ZMMU; "*Chr. discipennis* Fald.—Lehmann," 1 ♀, ZIN. Additional material: 61 ♂, 91 ♀ from Western Kazakhstan and the southeast of European Russia (Astrakhan and Orenburg Provinces).

Differential diagnosis (Table 2). The red margin on the base of the elytra is much wider than in all the other subspecies, comprising on average 0.32 of the elytron length. The lateral margin of the elytra is as wide as the basal one; this character reliably differentiates this subspecies from *russiella*, *limbata*, *luigionii*, and *volodi*, in which the margin is wider laterally than basally. Two-thirds of the specimens having the metallic sheen are purple; in all the other subspecies purple specimens are considerably less frequent or entirely absent. The apex of the aedeagus of most males is short or very short; no specimens with a long or a very

long apex were found. The shape of the aedeagus reliably differentiates this subspecies from *hochhuthii*, *volodi*, and *luigionii* in which specimens with long or very long apices prevail. The pronotal punctation is usually medium or moderately coarse. The specimens with fine punctation comprise 22%, whereas in *volodi* and *luigionii* fine punctation is observed in more than half of the specimens. The fraction of black specimens without metallic sheen is 10–20%, i.e., much smaller than in *Ch. limbata luigionii*. Most specimens are macropterous; this character clearly distinguishes this subspecies from *Ch. limbata limbata* and *Ch. limbata hochhuthii* (which include few macropterous individuals), and also from *Ch. limbata volodi* and *Ch. limbata luigionii* (which are never macropterous).

Distribution (Fig. 3). This subspecies is distributed in the semi-desert and desert zones of the southeast of European Russia and Western Kazakhstan. In the desert zone, it was found only in valleys of big rivers: the Volga and Ural.

Chrysolina limbata hochhuthii (Suffrian, 1851)

Chrysomela hochhuthii Suffrian, 1851 : 72.

Material. Lectotype: ♂, Baikal, IZUG. Additional material: 151 ♀, 236 ♂ from East Siberia, Eastern Kazakhstan, Mongolia, and Northern China.

Differential diagnosis (Table 2). The width of the red margin on the base of the elytron is on average about 0.27 of the elytron length, which is more than in *russiella* (0.10), *limbata* (0.16), *luigionii* (0.16), and *volodi* (0.20) but less than in *discipennis* (0.32). The basal margin of the elytra is as wide as the lateral one; this character differentiates this subspecies from *Ch. limbata russiella*, *Ch. limbata limbata*, *Ch. limbata luigionii*, and *Ch. limbata volodi*, in which the basal margin is narrower than the lateral one. The metallic sheen is blue in most specimens, whereas *Ch. limbata discipennis* mostly includes purple specimens, *Ch. limbata limbata*, bronze and green ones, and *Ch. limbata russiella*, only bronze specimens. The fraction of males with a long or a very long apex of the aedeagus is 56%, i.e., considerably smaller than in *Ch. limbata volodi* (90%) and considerably greater than in *Ch. limbata limbata* (14%). Specimens of the subspecies *russiella* and *discipennis* never have long or very long apex of the aedeagus. The pronotal punctation is usually medium or moderately coarse; specimens with fine punctation comprise only 14%, as compared to over 50% in *Ch. limbata volodi* and *Ch. limbata luigionii*. Black specimens without metallic sheen comprise 24%, which is much fewer than in *Ch. limbata luigionii* (about 90%) but more than in *Ch. limbata russiella* (less than 10%). Unlike *Ch. limbata volodi* and *Ch. limbata luigionii*, the subspecies *Ch. limbata hochhuthii* includes some macropterous individuals. However, such individuals are rare: no more than 4% of males and no more than 20% of females, as compared to *russiella* and *discipennis* in which most individuals are macropterous.

Distribution (Fig. 4). This subspecies is distributed in the mountain regions of the south of East Siberia, Eastern Kazakhstan, Mongolia, and Northern China, including the valleys of the mountain rivers. In Mongolia the adults were collected on *Artemisia* sp. and *Thymus* sp. (Medvedev and Voronova, 1979), and the I instar larvae, on *Artemisia frigida* (Zaitsev, 1982).

Notes. The examined type specimen of *Ch. hochhuthii* is a macropterous male with a very wide basal margin of the elytra. Specimens with such a combination of characters are rare in East Siberia and Mongolia but much more frequent in the Caspian region. Therefore, according to the method of complex characters, the type specimen of *hochhuthii* more closely resembles the subspecies *discipennis* than the subspecies distributed in Mongolia and East Siberia. However, it is not required that the type specimen should possess the characters "typical" of its subspecies. It is more essential that individuals resembling the type specimen do occur in Mongolia and East Siberia; therefore, the combination of characters present in the type specimen is rare but still possible for the subspecies in question.

Chrysolina limbata luigionii (Depoli, 1936)

Chrysomela limbata luigionii Depoli, 1936 : 139.

Material. Topotypes: 7 ♀, 12 ♂, Italy, Abruzzo, Gran Sasso. Additional material: 2 ♀, 2 ♂, Monte-Rosa Pass on the boundary of Switzerland and Italy; 8 ♀, 6 ♂, Herzegovina, the Bjelasica Range; 2 ♂, France, Nice.

Differential diagnosis (Table 2). The width of the red margin on the base of the elytron is on average about 0.16 of the elytron length, i.e., more than in *russiella* (0.10) but less than in *volodi* (0.20), *hochhuthii* (0.27), and *discipennis* (0.32). The mean width ratio of the basal and lateral margins is about 0.7, which is less than in *limbata* (0.8), *volodi* (0.9), *hochhuthii* (1.0), and *discipennis* (1.0). A long or very long apex of the

aedeagus occurs in 75% of males, whereas no such specimens were found in *Ch. limbata russiella* and *Ch. limbata discipennis* and only 13% of such males occur in *Ch. limbata limbata*. Most specimens of the subspecies *luigionii* have fine punctation on the pronotum, whereas medium punctation is prevalent in *russiella*, *limbata*, *hochhuthii*, and *discipennis*. The great majority of specimens are black without metallic sheen, whereas in the other subspecies the fraction of black specimens does not exceed 30%. All specimens of *Ch. limbata luigionii* are brachypterous; by contrast, the series of *Ch. limbata limbata* and *Ch. limbata hochhuthii* always include a small fraction of macropterous specimens, while in the series of *Ch. limbata discipennis* and *Ch. limbata russiella* more than half the specimens are macropterous.

Distribution (Fig. 3). This subspecies has mostly a mountain distribution, occurring in the Apennines, the Alps, Herzegovina, and on the Mediterranean coast of France (Nice).

Notes. The correctness of the use of the name "*luigionii*" for this form was confirmed by examination of a series from the type locality on the Apennine Peninsula. In the south of France and on the Balkan Peninsula, its range partly overlaps with that of the nominotypical subspecies; however, the two subspecies remain morphologically distinct and no transitional forms have been found.

It is interesting that both mountain subspecies, *Ch. limbata luigionii* and *Ch. limbata volodi*, differ from all the other forms by the absence of macropterous individuals. This trend can be observed in other groups of leaf beetles as well. For example, the beetles of *Entomoscelis adonidis* (Pallas, 1771) usually possess normally developed wings but the populations inhabiting the mountains of Middle Asia are apterous (Lopatin, 1996).

Chrysolina limbata russiella Bieńkowski et Orlova-Bienkowskaja, ssp. n.

Material. Holotype ♂: Saratov Province, western environs of Khvalynsk, meadow steppe, under *Plantago lanceolata*, 10.VII.2009, A.O. Bieńkowski and M.Ya. Orlova-Bienkowskaja, ZIN. Paratypes: 41 ♀, Saratov Province, Khvalynsk, 12.VII.2009, A.O. Bieńkowski and M.Ya. Orlova-Bienkowskaja, ZIN, ZMMU, MSU, KB, KM; 1 ♂, Saratov Province, Balashov, ZIN; 2 ♀, 3 ♂, same locality, A. Silant'ev, 9–17.VI.1890, KM; 2 ♀, "Balashov District," A. Jacobson, VI.1902, ZIN; 1 ♀, Penza Province, Tamala District, Nikol'skoe, S. Shibaev, 21.VI.2008, PSU; 1 ♀, 2 ♂, Lipetsk Province, 30 km E of Elets, Morozova Gora, M.N. Tsurikov, 14.VII.2001, Kuznetsova, 6.VI.1978, A.O. Bieńkowski and M.Ya. Orlova-Bienkowskaja, 8.VIII.2007, GGR, KB; 1 ♀, same locality, Galichia Gora, E. Antonova, 13.VII.1964, ZMMU; 1 ♀, Lipetsk Province, Dankov, A. Semenov, 10.VII.1912, ZIN; 1 ♂, Voronezh Province, "Bobrov District, Kamennaya steppe," Silant'ev, 19.V.1898, ZIN; 1 ♀, Voronezh Province, "Kozlov District, Goritsy," Nadezhin, 1867, ZIN; 1 ♂, Ryazan Province, "Pronsk District," 1883, ZMMU; 2 ♀, 2 ♂, Ryazan Province, ZIN; 1 ♀, Moscow Province, Stupino District, Bol'shoe Khoroshovo, A. Greve, 11.VII.1894, ZMMU; 1 ♂, Moscow Province, Zaraisk District, Rybakov, ZMMU; 1 ♂, Kaluga, 20.VI.1927, MSU; 1 ♂, same locality, Chernyshev, ZIN; 1 ♀, 3 ♂, same locality, Chernyshev, 12.V.1913, 20.VI.1913, 5.VI.1911, ZIN; 1 ♀, 1 ♂, Bryansk Province, Bezhitsa, G. Kostylev, 5.VII.1915, 20.VII.1916, ZMMU; 1 ♂, Tula Province, Aleksin, 19.VI.1913, ZMMU; 1 ♀, Mordovia, Chamzinka District, Komsomol'skii, M.K. Ryzhov, VI.2008, MU; 1 ♀, Mordovia, Ichalkovskii District, Smolny National Park, A.B. Ruchin, 14.VII.2007, MU; 1 ♂, Orenburg, ZIN; 1 ♀, same locality, Ganzen, 1892, ZIN; 3 ♀, same locality, Skornyakov, ZMMU; 1 ♂, Orenburg Province, Orsk District, Goncharov, 7.VII.1984, MSPU; 1 ♀, Orenburg Province, Embulatovka River, Rudolf, 9.VII.1949, ZIN; 1 ♀, Orenburg Province, Kuvandyk District, Chalpan, V. Belyaeva, 2.VI.1952, ZIN; 1 ♀, Odessa, 24.VI.1960, ZIN; 1 ♀, 1 ♂, same locality, D. Znoiko, 27.VI.1920, ZIN; 1 ♂, same locality, Kiritshenko, 23.VI.1925, ZIN; 3 ♀, 3 ♂, Cherkassy Province, near Kanev, Dubrovin, IV.1966, MSU; 1 ♀, Poltava, Borovka, VI.1894, ZIN; 1 ♀, same locality, V.N. Rodzyanko, 10.VII.1893, ZIN; 1 ♂, Poltava Province, Dubny, O. Butovich, 31.V.1923, ZIN; 1 ♂, Lugansk Province, Belovodsk, K. Arnoldi, 3.VII.1953, ZMMU; 1 ♂, Chernigov Province, env. of Novgorod-Severskii, Domotkanovo, 1886, ZIN.

Differential diagnosis (Table 2, Figs. 6, *1*; 6, *2*). *Ch. limbata russiella* can be easily differentiated from all the other subspecies by a very narrow red margin on the base of the elytra (on average, about 0.1 of the elytron length). The margin is on average 0.7 times as wide as in *Ch. limbata limbata* and *Ch. limbata luigionii*, and 1/3–1/2 times as wide as in other subspecies. The basal margin of the elytra is much nar-

rower than the lateral one: the mean width ratio of the basal and lateral margins is about 0.7, which is significantly smaller than the same ratio in *Ch. limbata limbata* (0.8), *Ch. limbata volodi* (0.9), *Ch. limbata hochhuthii* (1.0), and *Ch. limbata discipennis* (1.0). An important character clearly distinguishing *Ch. limbata russiella* from all the other subspecies except *Ch. limbata discipennis* is the large fraction of macropterous specimens: more than half of the females and more than one-third of the males. For comparison, only one-fifth of the females and less than one-tenth of the males of *Ch. limbata limbata* and *Ch. limbata hochhuthii* possess normally developed wings, whereas *Ch. limbata volodi* and *Ch. limbata luigionii* are never macropterous. The metallic sheen is always bronze-tinted, whereas every fifth specimen of *Ch. limbata limbata* from northern Europe is differently colored; the bronze tint is rare in *limbata* specimens from other regions and in adults of other subspecies. Black specimens without metallic sheen very rarely occur in the subspecies *russiella*. In this character, *Ch. limbata russiella* is significantly different from *Ch. limbata hochhuthii* (where about one-fourth of specimens are black) and *Ch. limbata luigionii* (where most specimens are black). The apex of the aedeagus is short or very short in the great majority of males, whereas long and very long variants prevail in *Ch. limbata volodi*, *Ch. limbata luigionii*, and *Ch. limbata hochhuthii*, and the medium variant is most common in *Ch. limbata limbata*. Punctation of the pronotum is usually medium; fine punctation is observed only in 13% of specimens, whereas more than half of specimens of *Ch. limbata volodi* and *Ch. limbata luigionii* have fine punctation of the pronotum.

Distribution (Fig. 3). The subspecies is distributed in the southern half of the temperate zone of European Russia: Saratov, Penza, Lipetsk, Voronezh, Ryazan, Moscow, Kaluga, Bryansk, Tula, and Orenburg provinces, Mordovia, and also in Odessa, Cherkassy, Chernigov, Poltava, and Lugansk provinces of Ukraine. Its range lies in the steppe, forest-steppe, and broadleaf forest zones. Nearly all the specimens were collected in the valleys of big rivers: the Dnieper, Don, Khoper, Sura, Oka, Volga, and Ural. In the type locality, the adults of *Ch. limbata russiella* feed on the ribwort plantain *Plantago lanceolata* and the broadleaf plantain *P. major*, which was confirmed by observations of caged insects.

Chrysolina limbata volodi Bieńkowski et Orlova-Bienkowskaja, ssp. n.

Material. Holotype ♂, Armenia, the Karakatar Range, 2450–2550 m above sea level, V. Savitsky, M. Savitsky, 1.VIII.2000, ZIN. Paratypes: Armenia, 4 ♀, 10 ♂, collected together with the holotype, ZIN, ZMMU, MSU, KB, KM; 1 ♂, Aragats Mt., 2000 m above sea level, V. Murzin, 12.VI.1970, KB; 6 ♀, 1 ♂, Gukasyan, the Dzhavakhet Range, subalpine belt over 2000 m above sea level, M. Savitsky, 2–5.VII.1997, ZIN, MSU, KB; 1 ♀, 1 ♂, Lake Sevan, 20.VI.1961, KB; 3 ♂, S slope of the Pambak Range, near Takyarlu, M. Savitsky, 21.VI.1997, ZIN, ZMMU, MSU; 1 ♂, 60 km NE of Erevan, Tsakhkadzor, 1800–2050 m above sea level, H. Muche, 8.VIII.1970, ZMD; 1 ♂, "Transcaucasia, road from Dzhala to Zurzun," under a rock, Troitskii, 1923, ZMMU; Northeast Turkey: 1 ♂, 2 ♀, env. of Kars, "Merdenik, 2300–2600 m, Achtelig, Naumann," 6.IX, 24.VIII, 3.IX.1965," SDEI; 1 ♂, env. of Kars, "Aygir-gölü, 2200 m, Heinz," 24.VII.1983, FTPM; 1 ♂, "Uludağ, 2300–2500 m, H. Kippenberg," 25.VIII.1960, FTPM.

Differential diagnosis (Table 2, Fig. 6, *3*, *4*). The width of the red margin on the base of the elytra is about 0.20 of the elytron length, i.e., on average greater than in *Ch. limbata russiella* (0.10), *Ch. limbata limbata* (0.16), and *Ch. limbata luigionii* (0.16) but smaller than in *Ch. limbata hochhuthii* (0.27) and *Ch. limbata discipennis* (0.32). The mean width of the basal to lateral margins ratio is about 0.9, i.e., greater than in *Ch. limbata russiella* (0.7) and *Ch. limbata luigionii* (0.7) but smaller than in *Ch. limbata hochhuthii* (1.0), and *Ch. limbata discipennis* (1.0). The metallic sheen is blue in most specimens; no bronze or purple specimens were found. This character reliably distinguishes this subspecies from the European and Caucasian specimens of *Ch. limbata limbata* (most of which are bronze or green) as well as from *Ch. limbata russiella* (all specimens are bronze) and *Ch. limbata discipennis* (most specimens are purple). The apex of the aedeagus is long or very long in 9 out of 10 males. In the shape of the aedeagus the subspecies clearly differs from *Ch. limbata russiella* and *Ch. limbata discipennis*, in which no specimens with long or very long apices were found, and also from *Ch. limbata limbata*, in which specimens with long or very long apices comprise only 14%. Punctation of the pronotum is fine in most specimens, whereas medium punctation prevails in the subspecies *russiella*, *limbata*, *hochhuthii*,

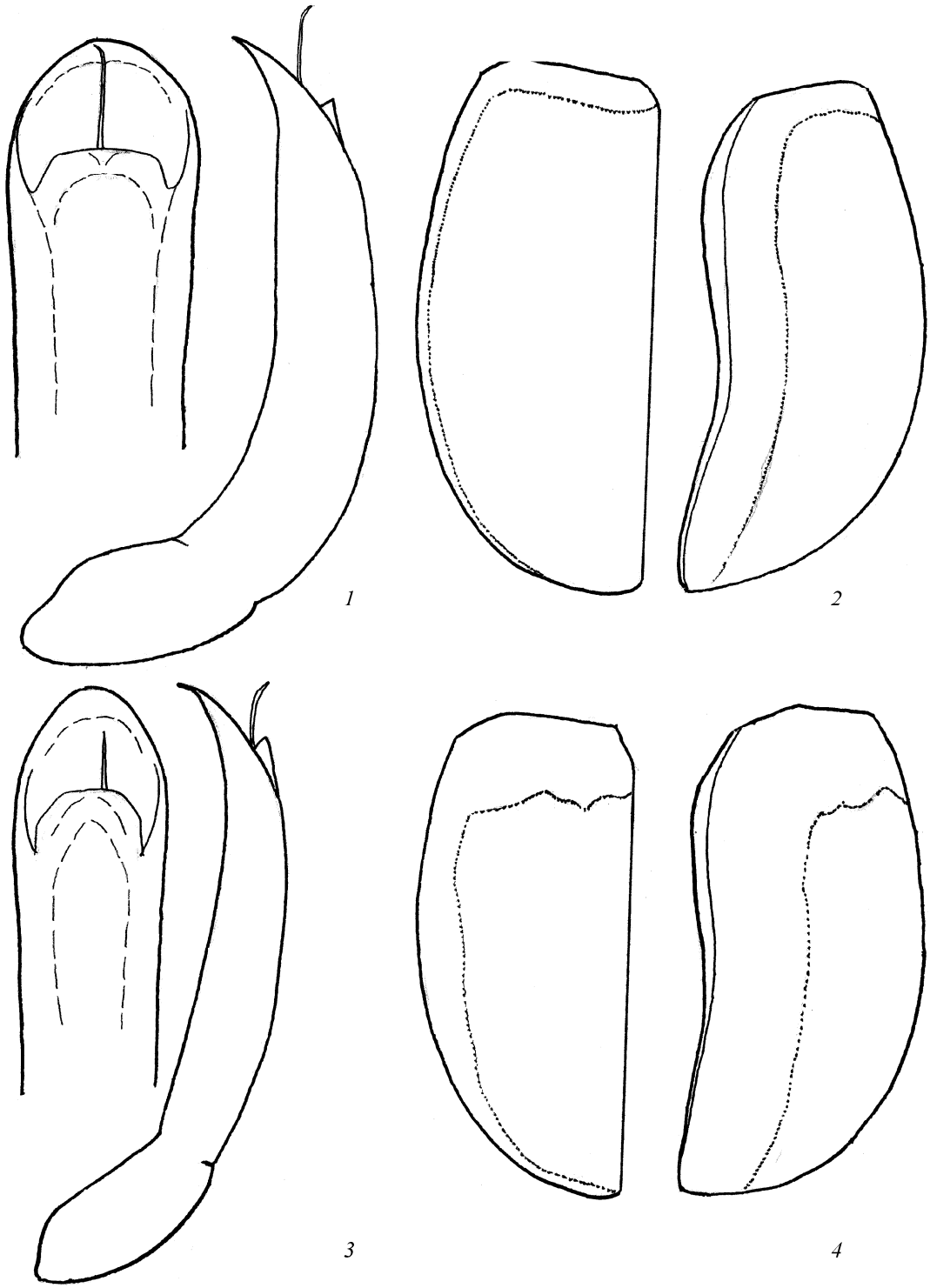

Fig. 6. Morphological details of *Chrysolina*: (*1*, *2*) *Ch. limbata russiella*, holotype, male [(*1*) aedeagus, dorsal and lateral view; (*2*) left elytron, dorsal and lateral view]; (*3*, *4*) *Ch. limbata volodi*, holotype, male [(*3*) aedeagus, dorsal and lateral view; (*4*) elytron in dorsal and lateral view].

and *discipennis*. The fraction of black specimens without metallic sheen is less than one-fourth; this character clearly distinguishes this subspecies from *Ch. limbata luigionii*. An important trait distinguishing *volodi* from most other subspecies is that all its specimens are brachypterous. By contrast, the series of *Ch. limbata limbata* and *Ch. limbata hochhuthii* always include a small fraction of macropterous speci-

mens; in *Ch. limbata discipennis* and *Ch. limbata russiella* most of the specimens are macropterous.

Distribution (Fig. 3). The subspecies is distributed in high mountain regions of the Lesser Caucasus and eastern Turkey, occurring in subalpine meadows at 1800–2600 m above sea level.

Notes. To confirm the subspecific status of this form, we additionally compared the specimens from the Lesser Caucasus and the Great Caucasus by the complex of three characters: the tint of the metallic sheen of the elytra, the width of the basal margin related to the elytron length, and the shape of the aedeagus apex. The mean values and variances of these characters were calculated separately for the Lesser and the Great Caucasus. Then each specimen was tested for its difference (see *Methods*) from these two geographic groups. It was found out that 89.5% of specimens from the Great Caucasus could be identified as *Ch. limbata limbata* by the complex of three characters, whereas 79% of specimens from the Lesser Caucasus could be identified as *Ch. limbata volodi*. Thus, the difference between the two forms was greater than 75%, which confirmed the subspecific rank of *volodi* by Amadon's "overlap rule" (Simpson, 2006). The Kura valley, where the species has not been found at all, forms a distinct geographic boundary between the subspecies *Ch. limbata limbata* and *Ch. limbata volodi*.

The subspecies was named after Vladimir (Volodya) Yu. Savitsky who collected some of the type specimens.

DISCUSSION

A subspecies is a group of populations occupying a large territory and morphologically more similar with one another than with populations from other regions. A subspecies can be distinguished both by a specific mean value of a metric character and by the relative abundance of individuals with different states of a qualitative character. For example, the fraction of macropterous females is about 90% in *Ch. limbata discipennis* and only about 20% in *Ch. limbata limbata*. Although a single specimen cannot be reliably assigned to one of these subspecies based on the degree of wing development, they can obviously be distinguished due to the statistically significant difference in the percentage of macropterous individuals.

The study of *Ch. limbata* subspecies clearly shows that geographic variation in leaf beetles can be quite complicated and cannot be adequately characterized by examination of single specimens. Reliable data on ranges of the subspecies and morphological differences between them can be obtained only by examination of numerous series of specimens from the entire species range and application of statistical methods.

ACKNOWLEDGMENTS

The authors are very grateful to J. Hajek (NMP), R.D. Zhantiev and V.Yu. Savitsky (MSU), H. Kippenberg (FTPM), R. Krause (ZMD), K.V. Makarov (MSPU), G.S. Medvedev, A.K. Chistyakova, and S.V. Andreeva (ZIN), N.B. Nikitsky and A.A. Rusakov (ZMMU), I.G. Pronina (PSU), H. Silfverberg (ZMHU), A.Yu. Solodovnikov (ZMUC), Z.A. Timraleev and A.B. Ruchin (MU), J. Frisch (NHMUH), L. Zerche (SDEI), M.N. Tsurikov (GGR), H. Schönmann (NHMV), K. Schneider (IZUG), R. zur Strassen and D. Kovac (SMN) for the provided opportunity of examination of the material from the corresponding museums and collections, to L.N. Medvedev, V.Yu. Savitsky, M.Yu. Savitsky, and many other colleagues for the material provided, to S.V. Pushkarev for help with compiling the map, to the staff of the Khvalynsk National Park and the Galichia Gora Reserve for the opportunity of carrying out research, and to A.A. Bieńkowski for the proposed method of sorting the results of pairwise comparison of series.

REFERENCES

1. Barabás, L., "Poznámky o niektorých slovenských liskavkách (Col., Chrysomelidae)," Entomol. Problémy (Biol. Pracé) **14**, 9–12 (1977).
2. Bechyné, J., "7e contribution à la connaissance du genre *Chrysolina* Motsch. (Col. Phytophaga, Chrysomelidae)," Entomol. Arbeit. Mus. G. Frey **1**, 47–185 (1950).
3. Bieńkowski, A.O. and Orlova-Bienkowskaja, M.Ya., "Composition of the Subgenus *Zeugotaenia*, Genus *Chrysolina* (Coleoptera, Chrysomelidae), and Examination of the Name-bearing Types," Zool. Zh. **90** (4) 428–437 (2011) [Entomol. Rev. **91** (4) 498–507 (2011)].
4. Filipchenko, Yu.A., *Variation and Methods of Its Study* (Nauka, Moscow, 1978) [in Russian].
5. Kippenberg, H. and Döberl, M., "Familie: Chrysomelidae," in *Die Käfer Mitteleuropas. Vol. 3. Suppl.* (Krefeld, 1994), pp. 17–144.
6. Küster, H.S., *Die Käfer Europas. Nach der Natur beschrieben von Dr. H.C. Küster. 4 Heft* (Nürnberg, 1846).
7. Lopatin, I.K., "High Altitude Fauna of the Chrysomelidae of Central Asia: Biology and Biogeography," in

Chrysomelidae Biology. Vol. 3. General Studies (SPB Academic Publ., Amsterdam, 1996), pp. 3–12.
8. Lubischew, A.A., Problems of Form, Systematics, and Evolution of Organisms. Collected Papers (Nauka, Moscow, 1982) [in Russian].
9. Medvedev, L.N. and Voronova, N.V., "On the Fauna of Leaf Beetles (Coleoptera, Chrysomelidae) of Mongolia. Communication 3," in *Insects of Mongolia, Issue 6* (Nauka, Leningrad, 1979), pp. 296–307 [in Russian].
10. Medvedev, L.N. and Okhrimenko, N.V., "To the Knowledge of Leaf Beetles of the Genus *Chrysolina* Motsch. (Coleoptera, Chrysomelidae) of the Caucasus," Entomol. Obozr. **70** (4), 866–874 (1991).
11. Mironovskii, A.N. and Kas'yanov, A.N., "Multidimensional Analysis of Morphological Variation of the Roach *Rutilus rutilus* (Cyprinidae) in the USSR," Zool. Zh. **66** (3), 393–401 (1987).
12. Simpson, G.G., *Principles of Animal Taxonomy* (Columbia Univ., 1990; KMK Press, Moscow, 2006) [in Russian].
13. Suffrian, E., "Zur Kenntniss der Europäischen Chrysomelen," Linn. Entomol. **5**, 1–280 (1851).
14. Warchałowski, A., "Chrysomelidae. Stonkowate. III," in *Fauna Polski. Vol. 15* (Dział Wydawnictw MiIZ PAN, Warszawa, 1993).
15. Zaitsev, Yu.M., "Larvae of Leaf Beetles (Coleoptera, Chrysomelidae) from Mongolia," in *Insects of Mongolia, Issue 8* (Nauka, Leningrad, 1982), pp. 97–134 [in Russian].