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A review of the millipede fauna of the south of the Middle-Russian Upland, Russia (Diplopoda)

Обзор фауны двупарноногих многоножек юга Среднерусской возвышенности России (Diplopoda)

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KEY WORDS: Diplopoda, fauna, distribution, Middle-Russian Upland, Russia.
КЛЮЧЕВЫЕ СЛОВА: Diplopoda, фауна, распространение, Среднерусская возвышенность, Россия.

ABSTRACT: The millipede fauna of the south of the Middle-Russian Upland, southern European Russia is reviewed and shown to comprise 16–17 species, three of which are new to the regional list. Information about their distribution between biotopes is presented. A brief zoogeographical analysis is attempted. Descriptions of three new varieties of *Rossiulus kessleri* (Lohmander, 1927) are provided.

РЕЗЮМЕ: Дан обзор фауны многоножек-диплопод юга Среднерусской возвышенности (юг европейской России), включающей 16–17 видов, в том числе трех, новых для региона. Представлены сведения об их распространении и распределении по биотопам. Сделан краткий зоогеографический анализ. Приведено описание трех новых форм вида *Rossiulus kessleri* (Lohmander, 1927).

Introduction

Millipedes (Diplopoda) are among the major components of soil/litter arthropod fauna in virtually any temperate biome or region, including Russia. Although the diplopod fauna is rather well studied over the Russian (= East European) Plain in general and in the south of the forest-steppe belt in particular [Lokshina, 1969; Golovatch, 1984, 1995; Boháč et al., 1984], both these regions are truly so vast and varied that faunistically they still contain numerous lacunae. It is only the forest-steppe, or forested steppe, of the Plain both within the Ukraine and Russia that is known to harbour the few regional millipede neoendemics and subendmics [Golovatch, 1984, 1995; Chornyi & Golovatch, 1993].

The previously published information about the fauna and ecology of millipedes in the Middle-Russian Upland appears to largely concern oak woodlands and meadow steppes at the Central Chernozem Nature Reserve, environs of Kursk, and the "Forest-on-Vorskla" Nature Reserve, environs of Borisovka, Belgorod Area, Russia. Only some 12 diplopod species have hitherto been recorded there [Boháč et al., 1984; Golovatch, 1995] while the southern parts of the Upland, especially the so-called "limestone south", have remained almost untouched by collecting. Considering that many millipedes are calciphiles, a faunistic survey of the Upland's south could readily be expected as a promising endeavor. Indeed, it is here that numerous relict plant and animal forms tend to get concentrated not only because of the entire forest-steppe belt being a major ecotone in itself but also due to occasional limestone denudations providing additional foci of increased and/or biased biological diversity.

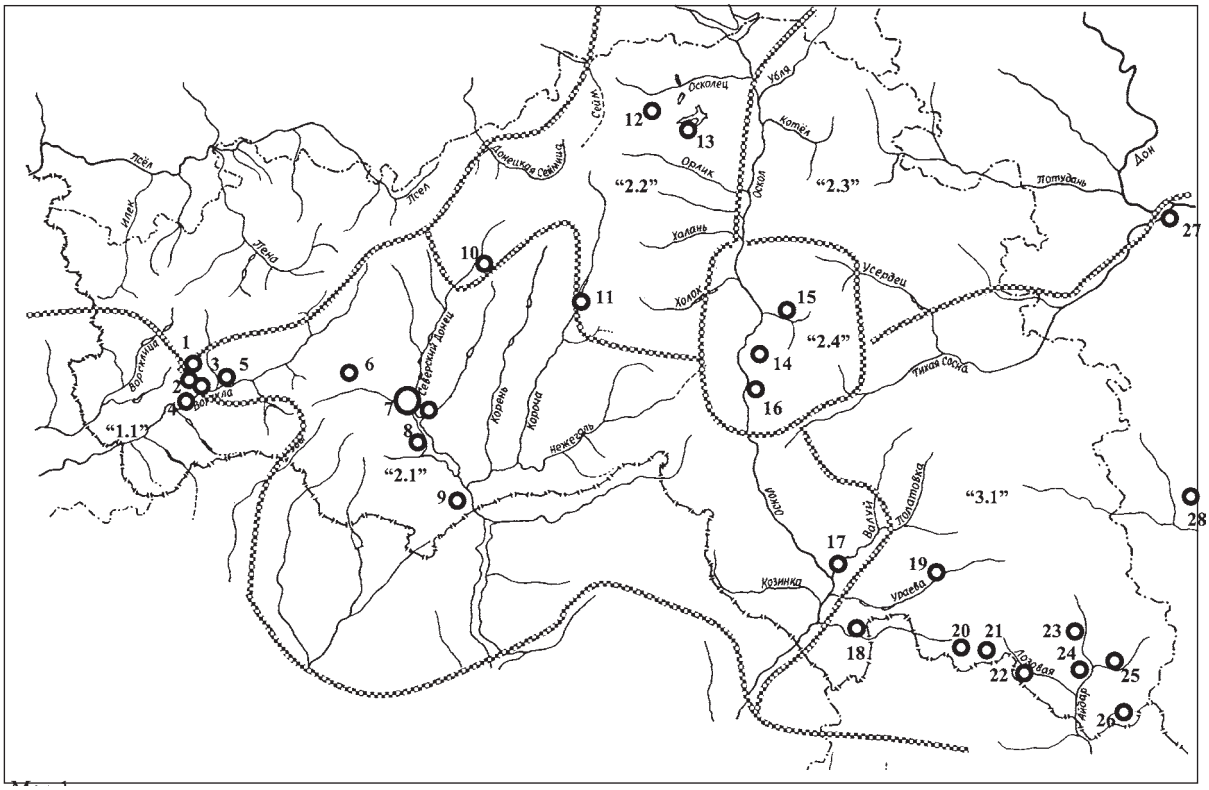
The present paper puts on record the collections made during a faunistic survey between 1997 and 2002 in 28 localities and 36 habitats scattered over the Belgorod and Voronezh areas of southern Russia. As expected, the millipede fauna appears richer there than previously considered, with virtually all new regional records confined to the southern areas largely bordering on the Ukraine. Furthermore, one of the regional subendemic species shows such an unexpectedly high degree of variation that it allows for discrimination of microgeographical forms.

Material and localities

Millipedes were largely collected by hand-sorting, only occasionally using pitfall trapping as well. The total number of specimens identified amounted to over 280. Altogether, 15 species have been determined using the keys in Lokshina [1969] and Golovatch [1995]. In addition, three local forms of a widespread subendemic have been revealed, all described below. Material is housed in the collection of the Belgorod State University.

The collecting localities, from west to east, are as follows, all shown on Map 1:

1. Akulinovka — oak forest near the village of Akulinovka, Borisovka Distr., Belgorod Area;
2. Nikitovka — forest plantation near the village of Nikitovka, Borisovka Distr., Belgorod Area;
3. Khotmizhsk — oak forests around the village of Khotmizhsk, Borisovka Distr., Belgorod Area;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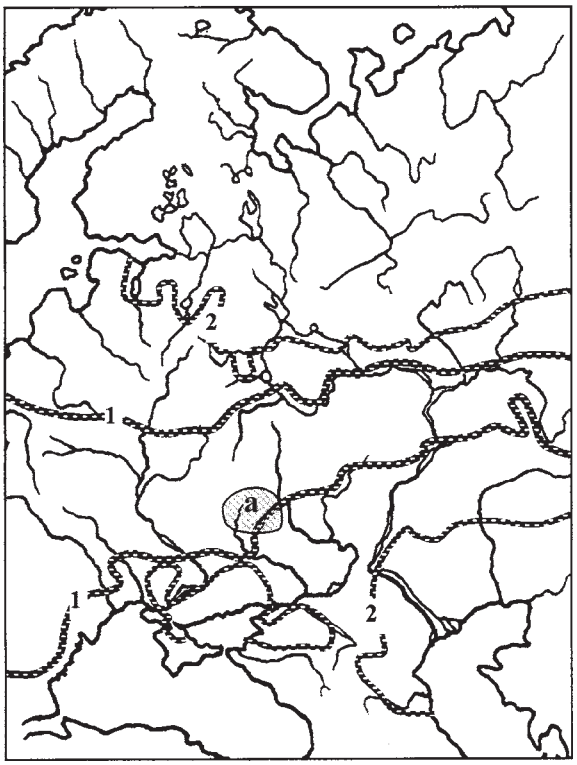
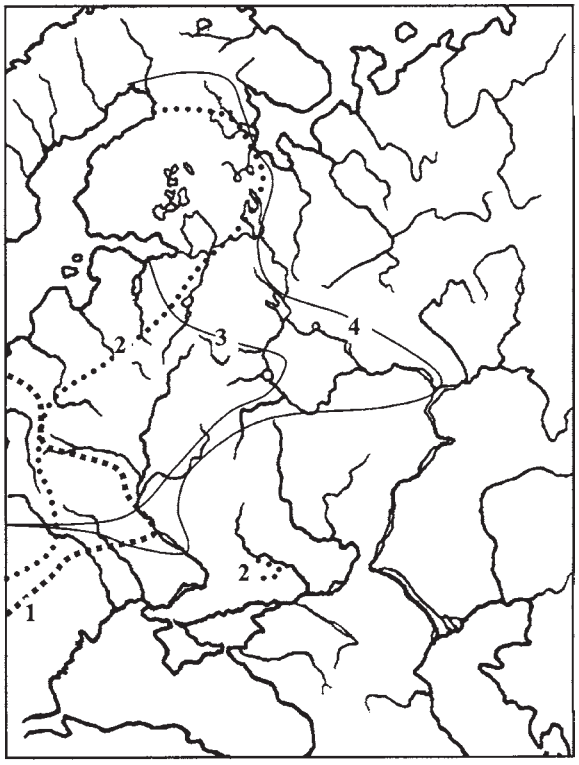


Map 2. Range limits of deciduous (= broadleaved) forest subzone (1) and of mixed coniferous-broadleaved forest zone in the Middle Holocene (2). (a) — the south of the Middle Russian Upland.

Карта 2. Границы подзоны широколиственных лесов (1) и зоны елово-широколиственных лесов в среднем голоцене (2). (а) — юг Среднерусской возвышенности.



Map 3. Relict boreal or nemoral distribution patterns: 1 — *Glomeris hexasticha*; 2 — *Polyxenus lagurus;* 3 — *Xestoiulus laeticollis mierzeyewskii;* 4 — *Leptoiulus proximus.*

Карта 3. Реликтовые бореальные и неморальные типы ареалов: 1 — *Glomeris hexasticha*; 2 — *Polyxenus lagurus;* 3 — *Xestoiulus laeticollis mierzeyewskii;* 4 — *Leptoiulus proximus.*

27. "Divnogorie" — calciphytic steppe and slopes with limestone denudations at the "Divnogorie" Historical and Archaeological Museum and Nature Reserve at the boarder between Ostrogozhsk and Liski districts, Voronezh Area;

28. Olkhovatka — limestone hills in a big coomb, 3 km northeast of the village of Olkhovatka, Voronezh Area.

Faunistic records

Order POLYXENIDA

Family Polyxenidae

1. *Polyxenus lagurus* (Linnaeus, 1758)

"Stenki Izgorya" 30.IV.2002; Rovenki 22.V.2001, 17.VI.2001, 19.VIII.2001; Nagolnoe 23.V.2001; "Divnogorie" 15.VI.2001; Olkhovatka 16.VI.2001: limestone.

NOTES: In the Russian Plain, this pan-European species has hitherto been known from Karelia to Baltia in the north-west, down to Ciscarpathia in the south, and in the Kirovograd and Donetsk areas of the Ukraine in the east [Chornyi & Golovatch, 1993] (Map 3). The above material from the Voronezh Area seems to represent the easternmost records of this species, most likely thelytokous populations only. Though the species mainly dwells in colonies in forests, in our region it has only been encountered in accumulations of more or less dry detritus under xeromorphic calciphilous low shrubs, sometimes at an abundance level of 50 ind. per dm^2.

Order GLOMERIDA

Family Glomeridae

2. *Glomeris hexasticha* Brandt, 1833

Material: 1 ♀, Khotmizhsk, 29.VII.1997; 2 ♂♂, 5 ♀♀, Belgorod: oak forest, 20.VI.1988, 15.VII.1994; "Les-na-Vorskle" [Golovatch, 1995].

NOTES: This nearly pan-European species is quite common in the forest (= Polesye) and forest-steppe belts of the Ukraine [Chornyi & Golovatch, 1993], while the above records in the Belgorod Area, Russia seem to be the easternmost (Map 3).

Order POLYDESMIDA

Family Polydesmidae

3. *Brachydesmus superus* Latzel, 1884

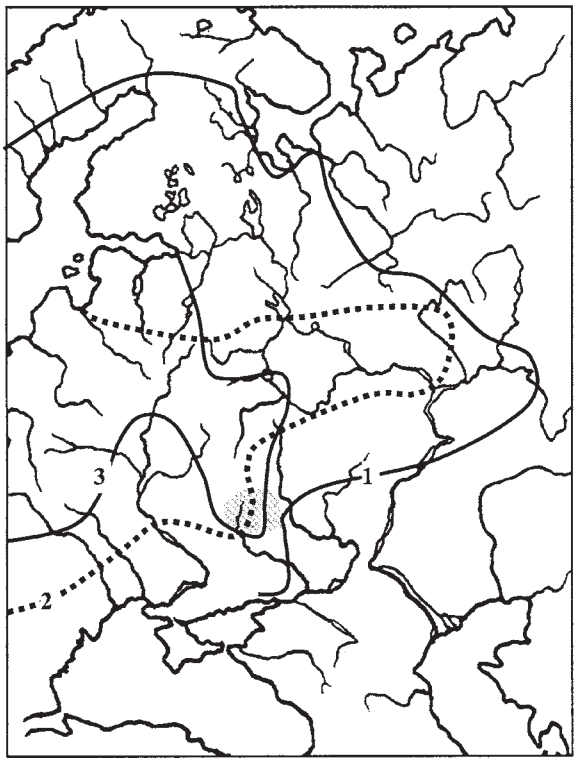
"Les-na-Vorskle" [Golovatch, 1995].

NOTE: This largely synanthropic species is common all over Europe, including the western and central parts of the Russian Plain within the Ukraine and Russia.

4. *Polydesmus inconstans* Latzel, 1884

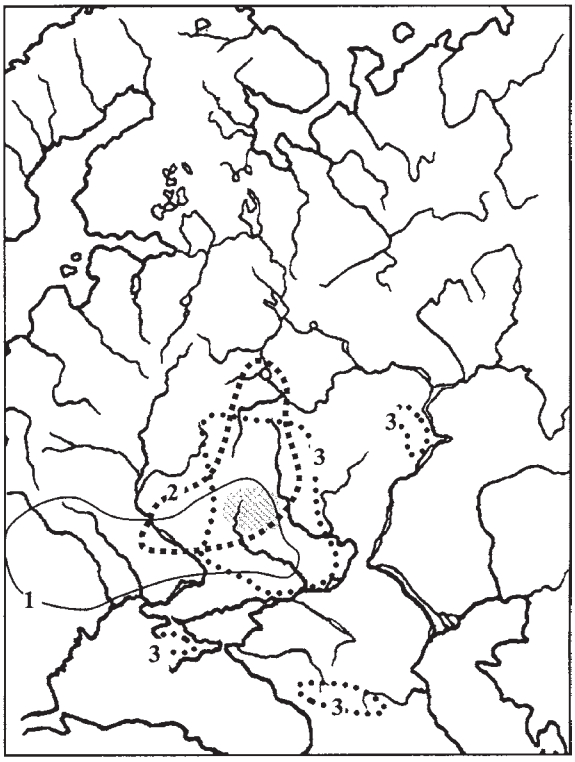
Material: 1♂, 1♀, Korocha: floodplain forest, 6.VII.1992; 2 ♂♂, 3 ♀♀, Belgorod: agrocoenose, IX.1977; 1 ♂, 1 ♀, Kulbaki: agrocoenose, 16.IX.89; 1 juv., Belgorod: oak forest, 20.VI.1988.

NOTES: This widespread European species is also a common anthropochore over the Russian Plain (Map 6). The above records near Belgorod are likewise the easternmost.



Map 4. Boreo-nemoral distribution pattern: 1 — *Megaphyllum sjaelandicum;* 2 — *Strongylosoma stigmatosum;* 3 — *Proteroiulus fuscus.*

Карта 4. Борео-неморальный тип ареала: 1 — *Megaphyllum sjaelandicum;* 2 — *Strongylosoma stigmatosum;* 3 — *Proteroiulus fuscus.*



Map 5. Endemic or subendemic distributions: 1 — *Megaphyllum kievense;* 2 — *Schizoturanius dmitriewi;* 3 — *Megaphyllum rossicum rossicum.*

Карта 5. Эндемичные и субэндемичные ареалы: 1 — *Megaphyllum kievense;* 2 — *Schizoturanius dmitriewi;* 3 — *Megaphyllum rossicum rossicum.*

5. ?*Polydesmus* sp.

Material: 1 juv., Nagolnoye: limestone, 23.V.2001.

6. *Schizoturanius dmitriewi* (Timotheew, 1897)

Material: 1♂, 1 ♀, Akulinovka, 15.V.1997; 1 ♀, "Les-na-Vorskle", 17.V.1997, 1 ♀, Belgorod, 20.VI.1988: oak forests; "Yamskaya Steppe" [Boháč et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTE: Endemic to the forest-steppe belt of the Russian Plain within the Ukraine and Russia [Golovatch, 1984, 1995] (Map 5).

Family Paradoxosomatidae

7. *Strongylosoma stigmatosum* (Eichwald, 1830)

Material: 1 ♂, 1 ♀, "Yamskaya Steppe": shrubs, 20.V.2001; 3 ♀♀, Belgorod: oak forest, VI.1982; "Yamskaya Steppe" [Boháč et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTES: This widespread East European species ranges from the south taiga in the north to the forest-steppe of the Ukraine and Russia in the south (Map 4). The above seem among the southeasternmost records in Russia, while in the Ukraine it occurs in the southeast down to the environs of Kharkov. Volga River seems to be the easternmost range limit of *S. stigmatosum*.

Order JULIDA

Family Blaniulidae

8. *Nopoiulus kochii* (Gervais, 1847)

Material: 1 ♀, 4 juv., Khotmizhsk: oak forest, 25.VI.1997, 29.VII.1997; 2 ♀♀, 1 juv., "Krasivo": pine forest, 15.V.1997; 3 ♀♀, Nikitovka: forest plantations, 17.IV.1997; 1 ♀, Belgorod: oak forest, 20.VI.1988; 1 ♀, Veidelevka: limestone, 22.V.2002; 1 ♀, Verkhnyaya Serebryanka: limestone, 21.V.2002; "Yamskaya Steppe" [Boháč et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTES: This widespread Euro-Caucasian species is solely anthropochoric all over Europe and beyond. It is also highly euryoecic (Map 6).

9. *Proteroiulus fuscus* (Am Stein, 1857)

Material: 1 ♀, Nikitovka: forest plantations, 17.IV.1997.

NOTES: This nearly pan-European, forest-dwelling, largely subcorticolous species shows parthenogenesis, with males being always fewer in the populations. The distribution covers much of the Russian Plain, including the forest-tundra of Yamal Peninsula in the north to the forest-steppe of the Ukraine and Russia in the south [Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 4).

10. *Archiboreoiulus pallidus* (Bride-Birks, 1920)

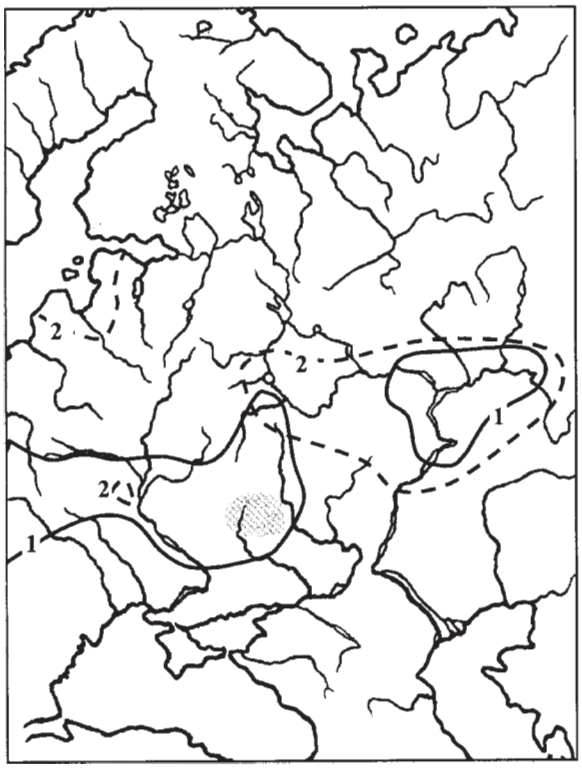
"Yamskaya Steppe" [Boháč et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTE: This pan-European species seems largely anthropochoric, this also being apparently correlated with parthenogenesis. In Russia, all populations seem to be thelytokous, i.e. male-free.

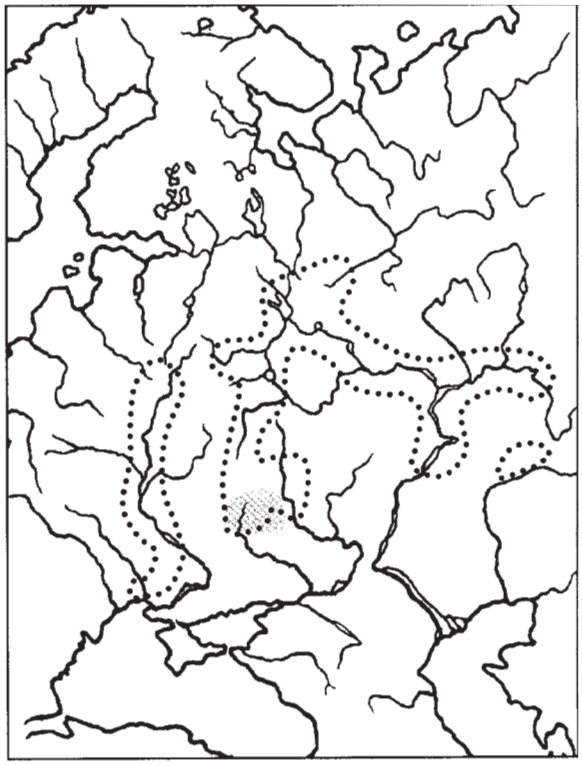
Family Julidae

11. *Xestoiulus laeticollis mierzeyewskii* (Jawlowski, 1925)

Material: 2 juv., "Krasivo": pine forest, 17.VI.1997; 1 ♂, Belgorod: oak forest, 27.VI.2000; 1 ♂, 2 ♀♀, 2 juv., Rovenki, 22.V.2001; Nagolnoye, 23.V.2001: limestone.



Map 6. Relict distributions in the uplands of the Russian Plain: 1 — *Brachyiulus jawlowskii;* 2 — *Polydesmus inconstans.*
Карта 6. Реликтовые ареалы возвышенностей Русской равнины: 1 — *Brachyiulus jawlowskii;* 2 — *Polydesmus inconstans.*



Map 7. Valley-nemoral distribution pattern: *Rossiulus kessleri.*
Карта 7. Долинно-неморальный тип ареала: *Rossiulus kessleri.*

NOTES: As the southeasternmost and easternmost range limits of this widespread East European, relatively hygrophilous subspecies have heretofore been considered as lying near Chernigov, Ukraine and Moscow, Russia, the above records in the Belgorod Area again extend considerably the known distribution to the east (Map 3).

12. *Leptoiulus proximus* (Němec, 1896)

Material: 1♀, Akulinovka, 15.V.1997; 1♂, 1♀, Belgorod: oak forest, 20.VII.1995, 5.VI.1996; "Les-na-Vorskle" [Golovatch, 1995].

NOTES: This widespread North, Central and East European forest-dwelling species also inhabits the northwestern, western and central regions of the Russian Plain, down to the forest-steppe belt of the Ukraine and Russia [Lokshina, 1969; Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 3).

13. *Brachyiulus jawlowskii* Lohmander, 1928

Material: 1 ♂, Belgorod: limestone, 1.V.1987; 1 ♀, Belgorod: steppe-meadow, 21.IX.1989; 1 ♀, 3 juv., "Yamskaya Steppe", 20.V.2001, 29.IV.2002; 1 ♀, "Lysye Gory", 17.V.2001; 2 ♂♂, 1 ♀, 1 juv., Veidelevka: limestone, 22.V.2002; 1 ♂, Nagolnoye: limestone, 20.V.2002; 2 ♀♀, 3 juv., Verkhnyaya Serebryanka: limestone, 21.V.2002; "Yamskaya Steppe" [Boháč et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTE: The species is another subendemic of the forest-steppe belt of the Russian Plain [e.g. Chornyi & Golovatch, 1993], reaching in the east the steppe-clad Volga-Don interfluve, Volgograd Area, Russia (Map 6).

14. *Megaphyllum sjaelandicum* (Meinert, 1868)

Material: 1 ♀, Krasivo: pine forest, 16.V.1997; "Les-na-Vorskle" [Golovatch, 1995].

NOTES: This North, Central and East European forest-dwelling species also occurs over most of the Russian Plain, reaching the taiga belt in the north and the forest-steppe zone of the Ukraine and Russia in the south [Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 4).

15. *Megaphyllum kievense* (Lohmander, 1928)

Material: 3 ♂♂, 4 ♀♀, 5 juv., Gherasimovka: limestone, VI-VII.2001; 1 ♀, Stanovoye: limestone, 21.V.2002; 3 juv., Loznoe: calciphytic meadow, 20.V.2002; 2 ♂♂, 1 ♀, 3 juv., Nagolnoye: limestone, 23.V.2001, 20.V.2002; "Yamskaya Steppe" [Boháč et al., 1984].

NOTE: The species is still another subendemic of the forest-steppe and north steppe belts of the Russian Plain both within the Ukraine and Russia [Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 5).

16. *Megaphyllum rossicum rossicum* (Timotheew, 1897)

Material: 1 ♀, Arkhangelskoye: oak forest, 1.V.1986; 1 ♂, 2 ♀♀, Akulinovka: oak forest, 15.V.1997; 2♂♂, 2♀♀, Belgorod: oak forest, 20.VI.1988, steppe-meadow, 24.VI.1992; 3 ♂♂, 6 ♀♀, "Yamskaya Steppe", 20 & 21.V.2001, 29.IV.2002; 2 ♂♂, 3 ♀♀, "Lysye Gory", "Stenki Izgorya", 17.V.2001, 30.IV.2002; 1 ♂, 1 ♀, Nechaevka: steppe-meadow, 29.IX.2000; 5 ♂♂, Gherasimovka: limestone, 10.VI.2000, VI.2001; 2 ♀♀, 3 juv., "Gniloye": meadow-steppe, 21.V.2002; 1 ♂, 2 ♀♀, 8 juv., Olkhovatka, "Divnogorie": limestone, 15.VI.2001, 16.VI.2001; "Yamskaya Steppe" [Вонби et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995].

NOTE: This subspecies is likewise subendemic to the forest-steppe and steppe of the Russian Plain [Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 5). The Dnieper obviously represents the western range limit.

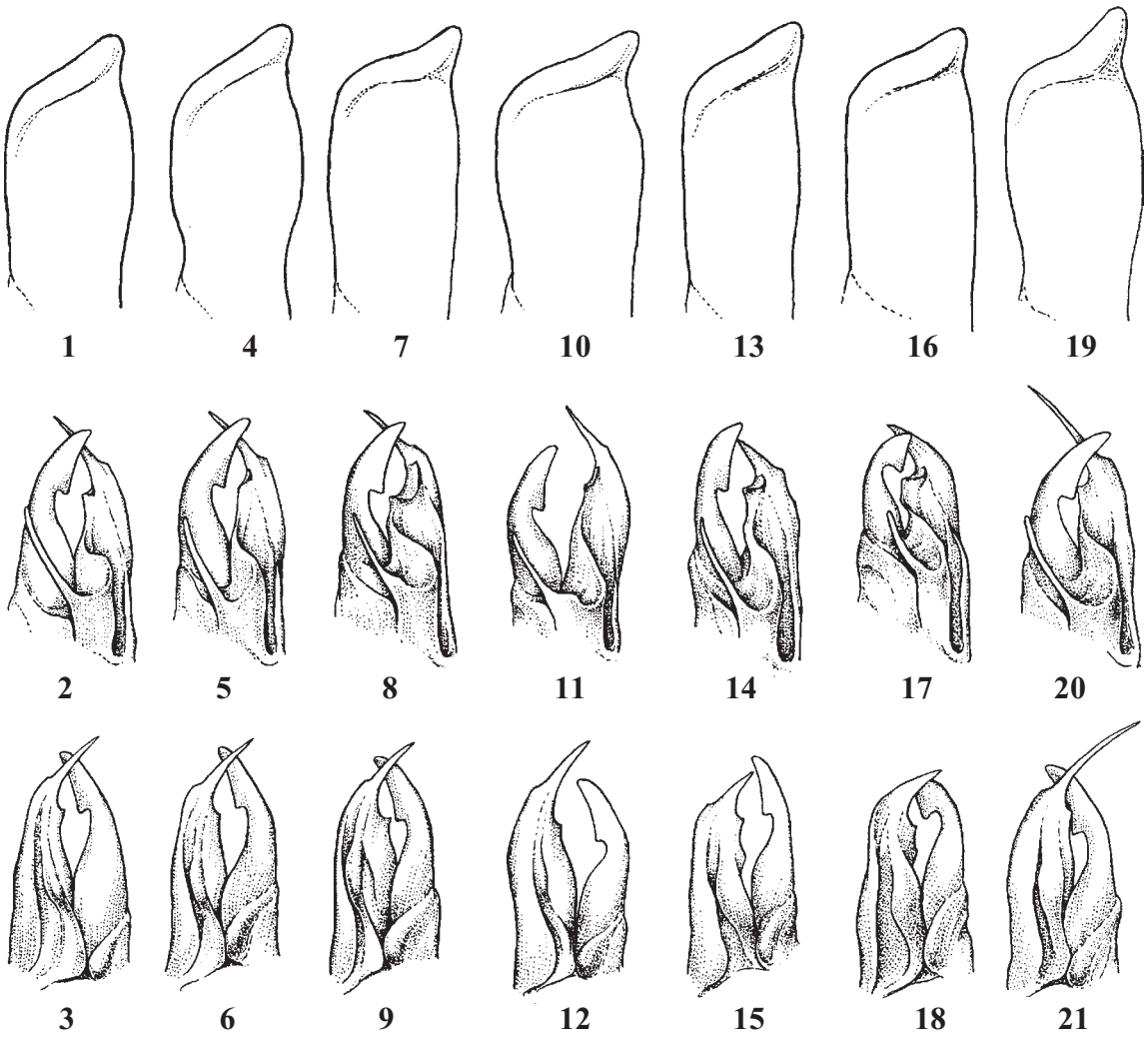


Fig. 1–21. Gonopods of different variations of *Rossiulus kessleri* (Lohmander) (1, 4, 7 10, 13, 16, 19 — promerite (front view), others — mesomerite and opisthomerite (2, 5, 8, 11, 14, 20 — front view, 3, 6, 9, 12, 15, 18, 21 — caudal view): 1–9 — typical form from "Lysye Gory" (1–3), Korocha (4–6) and "Krasivo" (7–9); 10–12 — f. *aidarica* from Pristen; 13–18 — f. *stepposa* from Rovenki (13–15) and Olkhovatka (16–18); 19–21 — f. *cretacea* from Gherasimovka.

Рис. 1–21. Гоноподии различных вариаций *Rossiulus kessleri* (Lohmander) (1, 4, 7 10, 13, 16, 19 — промерит (вид спереди), остальные — мезомерит и опистомерит (2, 5, 8, 11, 14, 20 — вид спереди, 3, 6, 9, 12, 15, 18, 21 — вид сзади): 1–9 — типичная форма из "Лысых Гор" (1–3), Корочи (4–6) и "Красиво" (7–9); 10–12 — f. *aidarica* из Пристени; 13–18 — f. *stepposa* из Ровенек (13–15) и Ольховатки (16–18); 19–21 — f. *cretacea* из Герасимовки.

17. *Rossiulus kessleri* (Lohmander, 1927)

Material presented according to the different types of gonopods:

Iindividuals with gonopods as in Figs 1–3: 2 ♀♀, 8 juv., "Yamskaya Steppe": meadow steppe, 20.V.2001, 29.IV.2002; 1 ♂, 2 ♀♀, "Lysye Gory": limestone, 17.V.2001;

Individuals with gonopods as in Figs 4–6: 1 ♂, 1 juv., Belgorod: oak forest, 20.VII.1995, steppe-meadow, 20.VI.1997; 3 ♂♂, 3 ♀♀, 4 juv., Korocha: calciphytic meadow, 10.VI.1994; 1 ♂, Nechaevka: steppe-meadow, 11.VI.2000; "Yamskaya Steppe" [Во-нби et al., 1984]; "Les-na-Vorskle" [Golovatch, 1995];

Individuals with gonopods as in Figs 7–9: 1 ♂, 9 ♀♀, 1 juv., Krasivo, 15.V.1997, 17.VI.1997, 25.VII.1997; 1 ♀, Khotmizhsk: oak forest, 29.VII.1997.

NOTES: This is yet another subendemic of the Russian Plain, highly calciphilous and characteristic of various ecotones within the forest, forest-steppe and north steppe belts [Lokshina, 1969; Golovatch, 1984, 1995; Chornyi & Golovatch, 1993] (Map 6). In the west, *R. kessleri* reaches the central parts of Belarus.

All above samples appear to represent the typical form of *R. kessleri* as described and depicted by Lohmander [1927], Attems [1927, sub *R. strandi* from Valuiki] and Lokshina [1969]. At "Lysye Gory", the abundance of this large species on bare limestone amounted to 30 ind. per m^2. In April, the uppermost, porous limestone horizon is represented by a spongy mass because of numerous cells 1–1.5 cm in diameter, in which one millipede or an exuvium can be found.

In addition to the typical form, further several (three) varieties have been encountered, yet apparently neither deserving a taxonomic rank. Their descriptions are provided below.

Rossiulus kessleri var. *aidarica,* **forma nova**

Material: 2♂♂, 2♀♀, Pristen: calciphytic meadow, 20.VIII.2001.

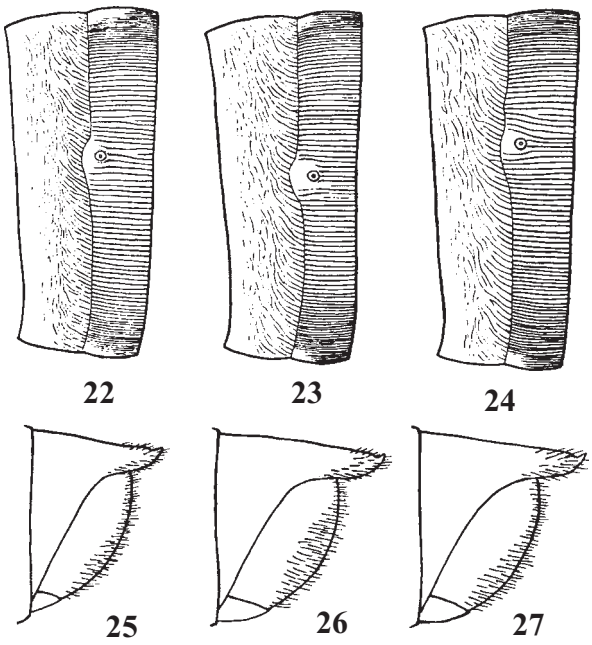


Fig. 22–27. Midbody segment (22–24) and telson and anal valves (25–27) of *Rossiulus kessleri* males: 22, 25 — typical form; 23, 26 — f. *cretacea;* 24, 27 — f. *stepposa.*

Рис. 22–27. Среднетуловищный сегмент (22–24) и тельсон и анальные лопасти (25–27) самцов *Rossiulus kessleri*: 22, 25 — f. *typica*; 23, 26 — f. *cretacea;* 24, 27 — f. *stepposa.*

NOTES: Externally this form is similar to var. *stepposa*, but the gonopod structure seems intermediate between the typical form and var. *stepposa* (Figs 10–12).

Rossiulus kessleri var. *stepposa*, **forma nova**

Material: 1 ♂, 3 ♀♀, 1 juv., Rovenki, 22.V.2001, 17.VI.2001, 19.VIII.2001; gonopods as in Figs 13–15; 1 ♂, Olkhovatka: limestone, 16.VI.2001; gonopods as in Figs 16–18.

NOTES: This form is even more disjunct, though only two males have become available for study. It has a short and wide apical outgrowth of the opisthomerite (Figs 14, 15, 17, 18). By the general structure of the opisthomerite this form approaches *R. vilnensis* (Jawlowski, 1925), the only congener that is known to occur in western Belarus, Baltia, and Central Europe [Golovatch, 1984]. The body colour is uniform dark oil gray to brown-black. The number of segments is 50–51. The body length is 35–38 mm.

Due to the apparently more difficult conditions of life at the eastern periphery of *R. kessleri* distribution, variation there seems higher than elsewhere. In this connection it remains to confirm the status of *R. vilnensis*, as no obvious range disjunction between *R. kessleri* and *R. vilnensis* seems to exist in central Belarus.

Rossiulus kessleri var. *cretacea*, **forma nova**

Figs 19–21.

Material: 1 ♂, Gnezdilovka: calciphytic meadow, 3.VI.1992; 1 ♂, Makeshkino: limestone 18.VII.1997; 10 ♂♂, 10 ♀♀, Gherasimovka: limestone, 10.VI.2000, VI.2001, VII.2001.

NOTES: As an analysis of 10 males shows, this variety appears pretty stable in its distinguishing characters, i.e. a longer apical outgrowth of the opisthomerite (Figs 20, 21).


Сейм
Псёл
Ворскла
Коренъ
Нежеголь
Ворскла
Тёмка
Ольшанка
Ольшанка
Ворскла
Ворскла
Ворскла

The colour is similar to that of the form *stepposa*. The number of leg-bearing segments is 47–50. The body length of adults is 40–44 mm.

Some differences between the two latter new forms have also been found in the structure of midbody segments (Figs 23–24), this being the same both in var. *aidarica* and the typical form (Fig. 22). In lateral view, the ozopore is removed from a midbody segment's dorsal edge by a distance equal to the segment's length dorsally in var. *cretacea* versus 0.8 length in var. *stepposa*. The stricture between pro- and metazona is again somewhat sinuous dorsally of the pore orifice in var. *stepposa*. The differences in the structure of the telson appear insignificant, variation being purely individual (Figs 25–27).

The distribution of all the forms of *R. kessleri* in the south of the Middle-Russian Upland (Map 8) shows increased body miniaturisation and tegument sclerotisation in the southeast where the air moisture is decreased while the temperature is increased. The form *cretacea* has only been discovered sporadically in places of growth of the relict plant *Androsace koso-poljanskii* Ovcz. (Primulaceae).

Ecogeographical background

An analysis of millipede distribution over the south of the Middle-Russian Upland, where the collecting localities have been grouped according to outlines [Prisnyi, 2000], shows that, in the southwest of this region, most of the species are associated with woodlands, largely being found only there. In the central part of the region, some forest species move into agrophytocoenoses, in the northern part into meadow steppe while in the southeast a few species occur on bare limestone. Besides, several species have only been discovered on limestone in the eastern and southeastern parts of the region. Based on the available records, the following ecogeographical division of the southern Middle-Russian Upland can be proposed (Map 1).

Provinces, districts and landscapes of the forest-steppe belt:

1. The East Ukrainian district of the Cisdnieper Lowland Province: Communities of forbs mesophytic meadows and oak woodlands moving onto interfluves.

1.1. Flood-meadow landscape: Slopes of different exposition supporting mesophytic forbs, more rarely steppoid, meadows; in the upper reaches of coombs small insular oak forests; in river valleys humid or wet, sometimes swampy meadows, bogs, including sphagnum ones, floodplain forests, alder groves, willow shrubs and pine woodlands.

2. The Donets-Don district of the Middle-Russian Upland Province: Communities of steppoid meadows and typical meadow steppe, comparatively extensive interfluve oak woodlands.

2.1. Upland oak forest landscape: The northern slopes supporting mesophytic or steppoid meadows; the southern ones steppoid meadows and meadow steppe with considerable participation of calciphytes and feather-grass, thyme steppe, steppe shrubs; elevated river banks with dry upland oak woodlands, including "Les-na-Vorskle", a part the "Belogorie" Nature Reserve, or residual pine forests; in the upper reaches of ravines with small insular oak stands with admixture of aspen as well as blackthorn at edges; along river valleys with floodplain oak or pine forests with considerable admixture of birch, willow shrubs, alder, also with mesophytic, humid and swampy meadows as well as bogs.

2.2. "Lowered alpine" landscape: The northern slopes covered with mesophytic or steppoid meadows, southern ones with meadow or forbs-feather-grass steppe with abundant calciphilous species, lowered alpine plants, thyme steppe, steppe shrubs; in the upper reaches of ravines with small oak spinneys ("Yamskaya Steppe" and "Lysye Gory"); in river floodplains and larger coombes with a constant or temporary rivulet with mesophytic, humid or sporadically swampy meadows, willow shrubs, rarely alder groves.

2.3. Calciphytic meadow landscape: Slopes of coombs supporting mesophytic or steppoid meadows with admixture of calciphytes and feather-grass, rarely small oak spinneys in steppe ravines, steppe shrub thickets; in river valleys with pine forests, alder groves, willow shrubs, mesophytic, humid or sporadic swampy meadows.

2.4. Oskol landscape: Combining all three above landscapes, with all types of relict communities, including the "Stenki Izgorya" part of the "Belogorie" Nature Reserve.

Provinces, districts and landscapes of the steppe zone:

3. The Donets-Don district of the Lower Don Province: Meadow and forbs-feather-grass steppe.

3.1. Calciphytic steppe landscape: Slopes clad with steppoid meadows, meadow or forbs-feather-grass steppe with abundant local calciphytes, hyssop, thyme, wormwood steppe, steppe shrub overgrowth; in places of high-level water-table with small oak spinnneys with aspen and lime, blackthorn thickets; in river valleys with mesophytic or humid meadows, willow shrubs, rarely with pine spinneys.

Zoogeographical analysis

The following millipede species groupings can be delimited based on their distribution in the region.

Upland oak forest landscape:

Glomeris hexasticha, Brachydesmus superus, Leptoiulus proximus — in oak forests;

Polydesmus. inconstans, Proteroiulus fuscus — in leafed and pine forests, forest plantations, rarely moving into agrophytocoenoses.

Upland oak forest and lowered alpine landscapes:

Schizoturanius dmitriewi, Strongylosoma stigmatosum, Archiboreoiulus pallidus — in leafed woodlands, shrub thickets, meadow steppe.

Flood-meadow and upland oak forest landscapes:

Megaphyllum sjaelandicum — in leafed and pine forests.

Upland oak forest, lowered alpine and calciphytic steppe landscapes:

Brachyiulus jawlowskii, Megaphyllum kievense — in meadow steppe in the north of the region, calciphytic meadows and limestone denudations.

Oskol and calciphytic steppe landscapes:

Polyxenus lagurus — on limestone denudations only.

From west to southeast, the following change in habitats can be observed:

Nopoiulus kochii, Xestoiulus laeticollis mierzeyewskii — flood-meadow landscape, upland oak forest landscape and calciphytic steppe landscape contours, with forest occurrences in the west but in calciphytic meadows and on bare limestone in the east.

Megaphyllum rossicum rossicum — all landscapes of the region, in the western and central parts in woodlands and agrophytocoenoses, in the northern part in shrub thickets and meadow steppe, in the southeastern part on bare limestone.

Rossiulus kessleri — also all landscapes of the region, in leafed and pine forests, meadow steppe and on limestone denudations, but in the various parts of the region displaying several variations occurring in different conditions.

Another interesting result is, that some widespread, largely European-type millipede species [Boháč et al., 1984], seem to show a more or less disjunct to insular distribution in the south of the Middle-Russian Upland. Such species appear to occur either in primary oak forests (*Glomeris hexasticha*) or on limestone denudations (*Polyxenus lagurus, Nopoiulus kochii, Leptoiulus proximus, Xestoiulus laeticollis mierzeyewskii*). This suggests a relict pattern probably Subboreal/Holocene or even Pleistocene in age, when the southern border of the mixed coniferous-broadleaved forest belt in the Russian Plain is known to have repeatedly shifted to the south of the modern steppe belt and sometimes formed several forested "bridges" with the Caucasus (Map 2). Strongly disparate as they might seem as an environment suitable for millipede life, woodlands and limestone denudations still show such important similarities as lower and more even temperatures, both daily and seasonal, increased humidity, presence of hard, "woody" detritus, etc. Combined with the group's basic calciphily, this explains both the relatively rich millipede fauna as well as the often high population numbers observed in the south of the Middle-Russian Upland. That the juloid morphotype dominates the fauna is also hardly surprising, as this region definitely represents one of the southeasternmost peripheries in the distribution of European Diplopoda [Golovatch, 1984; Kime & Golovatch, 2000; Kime, 2001].

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