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Some Patterns in the Distribution and Origin of the Millipede Fauna of the Russian Plain (Diplopoda)

by

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Abstract: The Russian Plain, a vast area occupying most of Europe and displaying a classical latitudinal nature zonation combined with an increasing longitudinal continentality, appears to support a not particularly rich millipede fauna: 70 species/subspecies from 32 genera, 11 families and 6 orders. An analysis of the landscape-zonal distribution of millipedes over the Plain supports the idea of treating practically all the Euro-Mediterranean Diplopoda as a nemoral group ecologically and historically associated primarily with broadleaved forests, since both northerly and southerly of the belts of (mixed) deciduous forests and forest-steppe, diplopods occur increasingly sporadically and tend to be mostly confined to intrazonal, particularly anthropogenous, habitats. Based on both chorological and ecological evidence, all the 8 local neo(sub)endemic forms appear to be more or less restricted to and/or favouring forest-steppe landscapes which may therefore be postulated to have served as a refuge biome since at least the last, Mikulino, Interglacial.

In the Russian Plain, the age of the modern diplopod fauna is mainly Holocene, while Pleistocene relicts are few. The routes of and pathways for the restoration of the region's fauna obviously repeated those of nemoral arboreal vegetation. In the Holocene, several larger nemoral refuges in W-Europe, in the Alps, the Carpathians and the Balkans seem to have provided a flow of migrants which dispersed mainly from the west and southwest toward the east and northeast. The role of a few smaller refuges in the southern part and south of the Russian Plain appears to be quite modest. An Asian influence is today hardly traceable. Along with such a (north)easterly spreading, that mostly European fauna has grown increasingly impoverished, totally declining in the Ural Mts.

1. Introduction:

The Russian Plain, a vast area covering most of the European part of the USSR, has long been known as displaying a classical latitudinal nature zonation combined with an increasing longitudinal continentality, presenting thereby a highly interesting and important arena for biogeographical studies. The belts/ zones of tundra, taiga, mixed coniferous-deciduous forests, broadleaved forests, steppe, semidesert, and desert form a full and practically ideal succession from north to south (e.g. MILKOV 1977).

European millipedes have already been extensively used for such investigations both on a larger scale (e.g. KIME 1990) and in the region concerned (LOKSINA 1966, GOLOVATCH 1984). As a result, being in the majority meso- to thermophilous phytosaprophages, practically all the Euro-Mediterranean Diplopoda are believed to represent a group both trophologically and historically strongly associated with a nemoral type of vegetation, primarily with broadleaved forests. Paleontology of arboreal formations being rather well-documented, especially as regards their Quaternary histories, reconstruction seems possible of faunogenesis of typical animal forest-dwellers. The lack of paleontological data on Russian millipedes seems therefore to be surmountable by indirect paleobotanical evidence.

The aim of the present paper is an up-to-date outline of the main regularities in the landscape-zonal distribution and origin of the diplopod fauna of the Russian Plain. Since my last contribution (GOLOVATCH 1984), new material has been accumulated that allows us to considerably correct and give detail to the generally reliable picture obtained earlier.

2. Landscape-zonal Distribution:

There is no need to give a historical review of faunistic diplopodology concerning the region's area, certainly the best studied among the major parts of the USSR. It is sufficient to give a total up-to-date figure of the fauna: 70 species or subspecies from 32 genera, 11 families, and 6 orders (cp. LOKSINA & GOLOVATCH 1979).

Before presenting a chorologic analysis, no fewer than 16 forms must evidently be excluded from consideration, being in this region purely synanthropic, i.e. restricted to anthropogenous habitats only: *Blaniulus guttulatus* (F.), *Boreoiulus tenuis* (BIGLER), *Choneiulus palmatus* (NEMEC), *Nopoiulus kochii* (GERVAIS), *Brachyiulus pusillus* (LEACH), *Julus scanicus* LOHMANDER, *Ophiulus fallax* (MEINERT), *Kryphioidiulus occultus* (C.L. KOCH), *Cylindroiulus britannicus* (VERHOEFF), *C. caeruleocinctus* (WOOD), *C. latestriatus* (CURTIS), *C. parisiorum* (BRÖLEMANN et VERHOEFF), *C. truncorum* (SILVESTRI), *Brachydesmus superus* LATZEL, *Oxidus gracilis* (C.L. KOCH), and *Strongylosoma jaqueti* VERHOEFF. The latter appears to be confined to human settlements, namely to city parks in and an agricultural research station near Kharkov, city parks in Poltava, as well as the town of Artyomovsk (= Bakhmut) in the Donetsk Area. *O. gracilis* is Oriental in its origin but must have colonized the Plain from the west just like the other anthropochores. Some of the remaining 54 taxa do occur synanthropically too, but in the Plain they also inhabit at least certain natural biotopes. Moreover, the degree of synanthropization appears to be a highly important feature of the distribution of the regional millipede fauna.

Millipedes first begin to show up in forest-tundra, i.e. *Proteroiulus fuscus* (AMSTEIN) near Stchutchye, S-Yamal Peninsula, perhaps one of the northernmost records of a diplopod. More to the south, in taiga, the above species is joined by *Polyzonium germanicum* BRANDT, *Megaphyllum sjaelandicum* (MEINERT), *Rossiulus kessleri* (LOHMANDER) within the subzone of northern taiga, then by *Polyxenus lagurus* (L.) (the parthenogenetic form only), *Diplomaragna golovatchi* SHEAR, *Polyzonium cyathiferum* MIKHALJOVA (?), *Polydesmus complanatus* (L.), *Leptoiulus p. proximus* (NEMEC), *Ommatoiulus sabulosus* (L.), *Brachyiulus jawlowskii* LOHMANDER in middle taiga, and by *Strongylosoma stigmatosum* (EICHWALD), *Polydesmus denticulatus* C.L. KOCH, *Nemasoma varicorne* C.L. KOCH (mainly the parthenogenetic form, whereas the sexual form seldom coexists only in the East Baltic), *Microiulus laeticollis mierzeyewskii* JAWLOWSKI in southern taiga. They are mostly uncharacteristic of taiga proper, being encountered more southerly as well. Their presence in taiga is due to either dwelling in intrazonal habitats (see CHERNOV 1975) or euryoecious character, or both. The total maximum abundance of Diplopoda in the taiga belt averages 20 ex. m⁻², normally being much less (CHERNOV 1975).

The above species have vast ranges as a rule. Thus, *M. sjaelandicum*, *R. kessleri*, *O. sabulosus*, *B. jawlowskii* are the only millipede species of European stock that manage to reach the Ural Mts. in the east. Moreover, the two clearly Siberian *D. golovatchi* and *P. cyathiferum* (?) occur from the Middle Volga flow to Krasnoyarsk (nearly 3000 km from west to east), and from Cisuralia to Kamchatka (over 6000 km!), respectively. Unfortunately, the identity of *Polyzonium* from the Ural area still requires confirmation. Both forms are probably among the most widespread "wildlife" diplopods and, judged from data on their abundance and habitat preference, they can best be attributed to taiga elements which were capable of penetrating the Plain and S-Ural (mixed) broadleaved forest and even forest-steppe belts due to euryoecious character.

The remaining Diplopoda of the E-European fauna may definitely be treated as being nicely characteristic of the zone of broadleaved forests, including forest-steppe as a subbelt. Although the

Table 1: Distribution of *Diplopoda* rather characteristic of the belt of broadleaved and mixed forests north of forest-steppe.

Taxa	DP	TG		BLF			FS	
		nm	s	w	c	e	n	s
<i>Polyxenus lagurus</i> (L.)	H	+	+	+	+	-	+	i
<i>Polyzonium germanicum</i> BRANDT	E	i	+	+	+	+	+	-
<i>Polydesmus complanatus</i> (L.)	E	i	+	+	+	+	+	i
<i>P. denticulatus</i> C.L. KOCH	E	-	i	+	+	+	i	-
<i>P. inconstans</i> LATZEL	E	-	ia	+	+	+	ia	-
<i>Archiboreoiulus pallidus</i> (BRADE-BIRKS)	E	-	-	+	+	-	+	ia
<i>Proteroiulus fuscus</i> (AM STEIN)	E	+	+	+	+	+	+	-
<i>Nemasoma varicorne</i> C.L. KOCH	E	-	+	+	+	-	+	i
<i>Cylindroiulus arborum</i> VERHOEFF	E	-	-	+	-	-	ia	-
<i>Ommatoiulus sabulosus</i> (L.)	E	i	+	+	+	+	+	i
<i>Unciger foetidus</i> (C.L. KOCH)	E	-	-	+	-	-	+	-
<i>Trachysphaera costata</i> (WAGA)	CE	-	-	+	-	-	+	-
<i>Glomeris connexa</i> (C.L. KOCH)	CE	-	-	+	+	-	+	+
<i>Mastigona bosniensis</i> (VERHOEFF)	CE	-	-	+	-	-	+	-
<i>M. vihorlatica</i> (ATTEMS)	CE	-	-	+	-	-	+	+
<i>Mastigophorophyllon saxonicum</i> VERHOEFF	CE	-	-	+	-	-	-	-
<i>Enantoiulus nanus</i> (LATZEL)	CE	-	-	+	-	-	-	-
<i>Julus terrestris</i> L.	CE	-	-	+	-	-	+	-
<i>Leptoiulus minutus</i> (PORAT)	CE	-	-	+	-	-	-	-
<i>L. p. proximus</i> (NEMEC)	CE	i	+	+	+	+	+	i
<i>Megaphyllum sjaelandicum</i> (MEINERT)	CE	i	+	+	+	+	+	i
<i>M. projectum kochi</i> (VERHOEFF)	CE	-	-	+	+	-	+	+
<i>Rossiulus vilnensis</i> (JAWLOWSKI)	EE	-	-	+	-	-	-	-
<i>Strongylosoma stigmatosum</i> (EICHWALD)	EE	-	+	+	+	+	+	i
<i>Microiulus laeticollis mierzeyewskii</i> JAWLOWSKI	EE	-	+	+	+	-	+	-
<i>Polyzonium transsilvanicum</i> VERHOEFF	SE	-	-	+	-	-	+	-
<i>Cylindroiulus boleti</i> C.L. KOCH	SE	-	-	+	-	-	-	-
<i>Megaphyllum p. projectum</i> VERHOEFF	SE	-	-	+	-	-	+	-
<i>M. rosenauense</i> (VERHOEFF)	SE	-	-	+	-	-	+	-
<i>M. transsilvanicum</i> (VERHOEFF)	SE	-	-	+	-	-	+	+
<i>Craspedosoma rawlinsii</i> LEACH	SA	-	-	+	-	-	-	-
<i>Microiulus l. laeticollis</i> (PORAT)	SA	-	-	+	-	-	-	-
<i>Trachysphaera gibbula</i> (LATZEL)	AC	-	-	+	-	-	-	-
<i>T. acutula</i> (LATZEL)	Cp	-	-	+	-	-	-	-
<i>Karpatophyllon polinskii</i> JAWLOWSKI	Cp	-	-	+	-	-	-	-
<i>Polydesmus m. montanus</i> DADAY	Cp	-	-	+	-	-	-	-
<i>P. m. walachicus</i> VERHOEFF	Cp	-	-	+	-	-	-	-
<i>Cylindroiulus horvathi</i> (VERHOEFF)	Cp	-	-	+	-	-	+	-
<i>C. burzenlandicus</i> VERHOEFF	Cp	-	-	+	+	-	+	-
<i>Megaphyllum silvaticum</i> (VERHOEFF)	Cp	-	-	+	-	-	-	-

Symbols used: DP distribution pattern; TG taiga; BLF belt of broadleaved and mixed forests; FS subbelt of forest steppe; c, e, n, nm, s, w central, eastern, northern, northern and middle, southern, western part respectively. — Distribution pattern: AC Alpine-Carpathian; CE Central European; Cp Carpathian; E European; EE Eastern European; SA Subatlantic; SE South(eastern) European. — + present; — absent; i mainly intrazonal habitats; ia intrazonal, mainly anthropogenous habitats.

borders between the (sub)belts are more or less conventional and, depending on the approach, drawn differently by different authors, the general patterns of diplopod chorology are very clear. Table 1 displays the chorology of the Diplopoda rather typical of the belt of broadleaved forests north of forest-steppe, with *Microiulus laeticollis mierzeyewskii* considered as perhaps one of the best examples. Table 2 lists the fauna that is rather characteristic of Russian forest-steppe, with *Glomeris hexasticha* BRANDT, *Megaphyllum kievense* (LOHMANDER), *Polydesmus montanus ukrainicus* LOHMANDER serving as probably the best illustrations (Map 1).

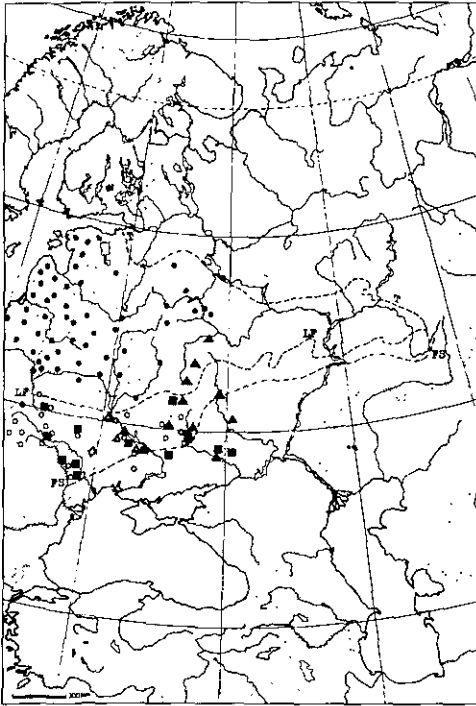
Table 2: Distribution of Diplopoda typical of the subbelt of forest-steppe of the Russian Plain.

Taxa	DP	TG	MC-B	B	FS		ST
					n	s	
<i>Glomeris hexasticha</i> BRANDT	CE	-	-	+	+	i	i
<i>Unciger transsilvanicus</i> VERHOEFF	EE	-	-	+	+	-	-
<i>Polydesmus schaessburgensis</i> VERHOEFF	Cp	-	-	-	-	i	-
<i>P. stuxbergi</i> ATTEMS	se	-	-	-	+	?	ia
<i>Brachyiulus jawlowskii</i> LOHMANDER	se	ia	+	+	+	i	ia
<i>Megaphyllum kievense</i> (LOHMANDER)	se	-	-	+	+	i	ia
<i>M. r. rossicum</i> (TIMOFEYEV)	se	-	-	+	+	+	ia
<i>Rossiulus kessleri</i> (LOHMANDER)	se	i	+	+	+	+	ia
<i>Polydesmus montanus ukrainicus</i> LOHMANDER	en	-	-	-	+	+	-
<i>Schizoturanius dmitriewi</i> (TIMOFEYEV)	en	-	-	+	+	i	ia
<i>Leptoiulus semenkevitchi</i> LOHMANDER	en	-	-	-	+	-	-

Symbols used: **DP** distribution pattern; **TG** taiga; **MCB** subbelt of mixed coniferous-broadleaved forests; **B** subbelt of broadleaved forests; **FS** subbelt of forest-steppe; **n, s** northern, southern border resp.; **ST** belt of typical steppe; **en** endemic; **se** subendemic; other symbols see Table 1.

The distribution patterns accepted in Tables 1 - 2 are quite conventional and provide at least a rough idea of the taxon's range. Patterns like **H, E, CE, EE**, are obviously too generalized and heterogeneous, whereas the elements like **SA, SE, AC, CP, se**, and **en** appear to be more restricted and their spatial history seems more easily explicable. One highly important conclusion immediately derivable from Table 1 is a clear west-east trend in the regional fauna's depauperation. All the 41 (sub)species that seem to be mainly characteristic of the belt of broadleaved forests north of forest-steppe occur in the Plain's western part (the Baltic, Byelorussia, the West- and Central Ukraine, Moldavia), but only 16 and 9 forms manage to reach to the central (ca. 35 - 40° N) and the eastern parts, respectively, totally declining in the Ural Mts. In other words, it is the Urals that clearly marks in the Diplopoda the easternmost limit of the influence of the entire Euro-Mediterranean realm at a species level.

Another clear feature of the patterns observed is that both southerly and northerly of the zone of nemoral arboreal vegetation, both the fauna and distribution of millipedes become increasingly sporadic and more strongly associated with intrazonal, particularly anthropogenous habitats. In the Plain, the total maximum abundance of millipedes in broadleaved forests and in meadow steppes averages 100 ex. m⁻², but drastically falls to 2 ex. m⁻² in the zone of typical steppe (GHILAROV & CHERNOV 1975). These are broadleaved forests offering a rather mild environment for numerous mesophiles that are definitely favoured by the Russian diplopods of Euro-Mediterranean origin, a group trophologically clearly belonging to a nemoral complex (Table 3).



Map 1: Modern distribution of some vegetation types and diplopods in the Russian Plain.

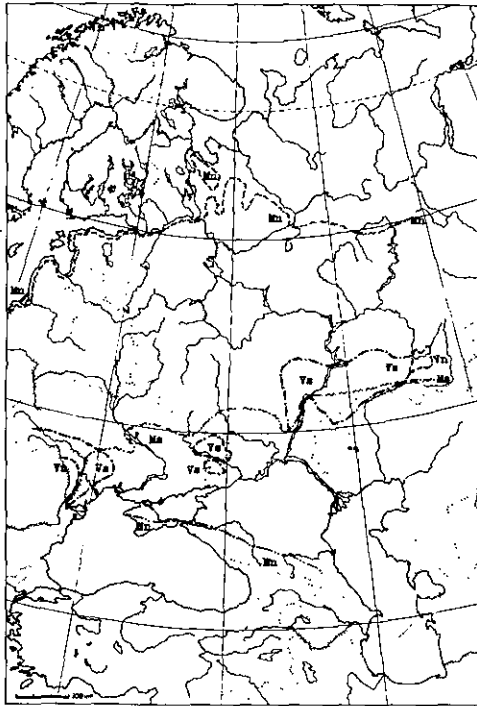
T southern border of the taiga belt; LF southern border of the belt of broadleaved and mixed forests north of forest-steppe; FS southern border of the subbelt of forest-steppe. — Filled circles *Microiulus laeticollis mierzeyewskii* JAWLOWSKI; Open circles *Glomeris hexasticha* BRANDT (shown only within the USSR); Filled squares *Megaphyllum kievense* (LOHMANDER); Open triangles *Polydesmus montanus ukrainicus* LOHMANDER; Filled triangles *Schizoturanius dmitriewi* (TIMOFEYEV); Open diamonds *Polydesmus schaessburgensis* VERHOEFF.

Tab. 3: Changes in diplopod species diversity from north to south of the Russian Plain.

Zonal category	Species
Northern taiga	4
Middle taiga	11
Southern taiga	15
Mixed coniferous-broadleaved forests	49
Northern forest-steppe	37
Southern forest-steppe	21
Typical steppe	5

3. Faunogenesis:

Fortunately, the Quaternary history of the nemoral vegetation in the region concerned is sufficiently documented to attempt a faunogenetical reconstruction. Since the entire modern dendro-



Map 2: Distribution of some vegetation types in the Late Pleistocene of the Russian Plain.

Mn, Ms northern and southern borders of the belt of nemoral forests, respectively, during a climatic optimum of the last, Mikulino, Interglacial, ca. 100.000 years ago; **Vn, Vs** larger islands of nemoral forests and of meadow steppes containing scattered *Betula* and *Pinus* forests with participation of several nemoral arboreal species, respectively, during the maximum phase of the last, Upper Valdai, Glaciation, ca. 20.000 years ago; **Nn** northern border of non-migratory nemoral forests (after GRICHUK 1989).

flora of the Russian Plain is known to be largely migratory, this being a direct reflection of both the Pleistocene glaciations and the Holocene restoration, the same presumption seems to be fully applicable to Diplopoda as an accompanying group.

Indeed, the pattern of distribution of millipedes practically coincides with that displayed by the belt of broadleaved forests. From west to east and, partly, from south to north, the Plain's nemoral arboreal flora is likewise increasingly impoverished, and the belt's latitudinal extension gradually shrinks to totally decline in the Southern Urals (e.g., MILKOV 1977). The above correlation is far too striking to be ignored and seems to provide a real basis for faunogenetical reconstructions (cp. Map 1).

According to the latest evidence (GRICHUK 1989), during the phase of a climatic optimum of the last, Mikulino, Interglacial (= Riss/Würm), ca. 100.000 years ago, a belt of nemoral vegetation, with dominance of the European hornbeam (*Carpinus betulus* L.), the durmast oak (*Quercus petraea* LIEBL.), and the large-leaved lime (*Tilia platyphyllos* SCOP.), reached in the north to the Gulf of Finland and extended far easterly into Siberia and Kazakhstan (Map 2, Mn). In the south, that belt bordered a wide steppe zone (Map 2, Ms). Boreal *Picea* and *Betula* stands with participation of *Carpinus*, *Quercus*, *Tilia*, etc., expanded northwards up to the coasts of the Barents Sea.

However, already during the maximum phase of the last, Upper Valdai, Glaciation (= Würm), ca. 20.000 years ago, most of the Russian Plain was entirely forestless. A wide belt of periglacial

steppe-like vegetation had developed instead. Apart from some valleys in the Carpathians, only two hilly areas managed to preserve larger islands of broadleaved forests, with a pronounced participation of conifers, one in the Kodry Hills in Moldavia, and the other in the Southern Urals (Map 2, Vn). Scattered insular *Betula* and *Pinus* stands with quite a modest share of the English oak (*Quercus robur* L.), the small-leaved lime (*Tilia cordata* MILL.), the European ash (*Fraxinus excelsior* L.), etc., are known to have survived within several larger isolated areas of meadow steppes in the south (Map 2, Vs). The northern border of autochthonous, non-migratory nemoral forests still retaining a good deal of Tertiary relicts fluctuated quite insignificantly and still delimits the N-Caucasus and the S-Crimea (Map 2, Nn). Naturally, it was from those rather few and mostly deficient refuges that the region's modern nemoral biota and its present-day nature zonation were restored during the Holocene (Map 1, T, LF, FS).

In the Holocene, the restoration of nemoral forests proceeded rapidly and somewhat heterochronously, its direction was mainly from (south)west to (north)east. Thus, the European beech (*Fagus sylvatica* L.) and the European hazel (*Corylus avellana* L.) penetrated the Plain's western areas via/from both Baltic and Carpathians, the European hornbeam via/from both the S-Baltic and a refuge at the delta of Southern Bug River. The English oak seems to have arrived from southwest and south, expanding a little slower than both lime and elm which spread rapidly from southwest, south, and southeast (NEISHTADT 1957, SEREBRYANNYI 1973, 1980).

Interestingly, the routes of, pathways for and trends in the restoration of nemoral vegetation during Pleistocene interglacials practically repeated each other and the ones reconstructed for the Holocene, although their extent differed considerably (MARKOV *et al.* 1965).

The fact that all the regional neoendemic diplopods are rather characteristic of forest-steppe allows to treat this complex separately and in further detail as it seems to be quite representative of the entire fauna. However, one should keep in mind that consideration of a forest-steppe set of species (Table 2) as opposed to the remaining broadleaved forest list (Table 1) is certainly artificial, with too many intergrades involved. It has been accepted here simply for convenience and actually a single nemoral complex dominates the Russian Plain millipede fauna.

The Central European *Glomeris hexasticha* BRANDT might have attained at least most of its present range in the region concerned (Map 1) only in the Holocene. As (a) possible Pleistocene refuge(s) and Holocene source(s) can apparently be considered the Carpathians and/or the Balkans. It seems noteworthy that the evidently easternmost, i.e. peripheral populations of *G. hexasticha* from the environs of Kharkov and Belgorod appear to be highly variable as regards both size and colour pattern, and TIMOFEYEV (1897) even mistook them for several other *Glomeris* species/varieties.

The same logic for reconstructing the faunogenesis can obviously be applied to *Unciger transsilvanicus* (VERHOEFF). The genus is known to comprise only 3 species: *U. foetidus* (C.L. KOCH) which is widespread almost throughout Europe and, in the Plain, confined to both the western part of the belt of broadleaved forests and the Carpathians; *U. transsilvanicus* which occurs in the Balkans, Rumania, SE-Poland and, via Moldavia and forest-steppe regions of the Ukraine, reaches to the Rostov-on-Don Area in the east; and *U. kubanus* LOHMANDER restricted to NW-Ciscaucasia. In general, *Unciger* must have first appeared on the region's arena much earlier than in the Holocene as witnessed by the presence of the Caucasian endemic *U. kubanus*. As regards *U. foetidus*, it could have (re)populated the Plain only in the Holocene from/via the Carpathians and the Baltic like numerous other, at least H, E, CE, EE, SA, Cp, etc., elements. A more southerly way of dispersal, from the Balkans and/or S-Carpathians, can possibly be postulated for *U. transsilvanicus* as well as for many E, CE, SE, Cp, and even se components.

Polydesmus schaessburgensis VERHOEFF, a species hitherto recorded only in Rumania, Hungary, and Yugoslavia, has just been discovered near Savran, Odessa area, being new to the USSR fauna (Map 1). The fact that the form seems to be absent from the adjacent Carpathians and

Moldavia is rather indicative of a dispersal pattern similar to the one suggested above for *Unciger transsilvanicus*.

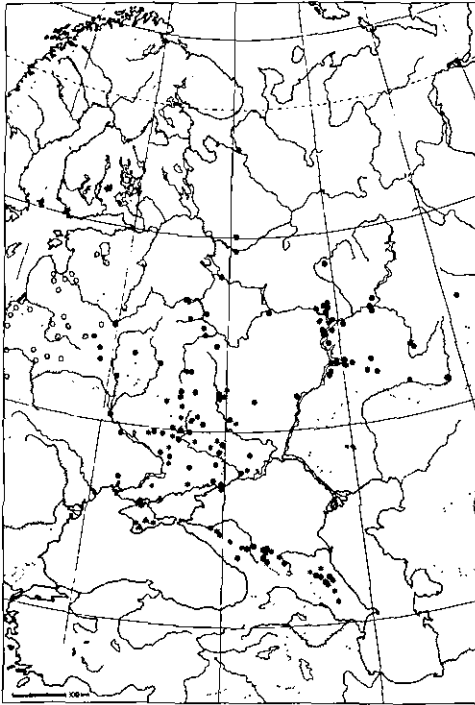
Megaphyllum rossicum (TIMOFEYEV) is a species traditionally divided into *M. r. rossicum*, widespread in the Caucasus Major, the Crimea, and the Russian Plain east of the Dnieper (Map 3), and *M. r. strandschanum* (VERHOEFF), endemic in S- and SE-Bulgaria and E-Greece. Morphologically, some of the montane populations of *M. r. rossicum* are a little disjunct, especially in the male having sole pads on the legs, a fact once regarded sufficient for allotting the S-Crimean representatives the rank of a separate species, *M. procerum* (ATTEMS), but now considered as being much overrated. The species' spatial history seems more likely to reflect at least three stages. The older one implies splitting into (sub)species which must have taken place somewhere in the E-Mediterranean, including the N-Pontic area, somewhat earlier (the Early Pleistocene?) than the origin and isolation of the Crimean and Caucasian montane *procerum* populations (Valdai Glaciation?). The modern wide range extending over the plain regions of the N-Crimea and Ciscaucasia far to the north until the Middle Volga flow and Orel certainly reflects Holocene migrations, with both N-Crimea and N-Caucasus as the most likely refuge and dispersal centres.

Rossiulus kessleri, another extremely widespread Russian subendemic (Map 3) also possessing high-montane populations in the Caucasus, but absent from the Crimea, has a range rather difficult to interpret if it were not for the striking resemblance to that of the previous case. Due to its pronounced euryoecious character, *R. kessleri* has reached Arkhangelsk in the north, Central Byelorussia and Kanev in the west, and the Ural Mts. in the east, although the highest abundance is observed within the forest-steppe and steppe belts where it sometimes reaches a level of ca. 300 ex. m⁻². A tendency to dwelling in/at secondary forest/bush clearings and edges is marked, too, the same as in the more hygro- and stenophilous *R. vilnensis* (JAWLOWSKI). Both forms are extremely closely related although the latter's range is not Balkan but rather Subatlantic, extending to NE-Germany in the west and Central Byelorussia in the east (Map 3). Special field observations in Byelorussia have failed to find a zone of intergradation; neither periodomorphosis nor significant infraspecific variations have been registered. The spatial history of *R. vilnensis* rather resembles that of, e.g., *Microiulus laeicollis mierzeyewskii* (cp. Map 1) and many others, implying a strictly easterly migration from a W-European refuge in the Holocene. Contrary to that, during the Valdai Glaciation *R. kessleri* must have survived at least in the N-Caucasus.

Polydesmus stuxbergi ATTEMS has previously been found only in the Crimea (both mountains and steppe) and near Kharkov (Map 3). It is the Crimea that seems to have served as the most likely Pleistocene refuge for that species whose closest relatives appear to be the Carpathian *P. burzenlandicus* VERHOEFF and *P. montanus* LATZEL. However, the only record of *P. stuxbergi* in the Plain is from a Kharkov agricultural research station (cp. *Strongylosoma jaqueti* VERHOEFF), so a "wildlife" occurrence of that species in the region concerned has still to be verified.

Judged from the pattern of relationships, the origins of *Polydesmus montanus ukrainicus* LOHMANDER, *Leptoiulus semenkevitchi* LOHMANDER, *Brachyiulus jawlowskii* LOHMANDER, and *Megaphyllum kievense* (LOHMANDER) seem to be likewise more easily explicable in terms of a pre-Valdai penetration of their respective ancestors from the west (? the Carpathians) and/or southwest (? the Balkans), subsequent isolations somewhere in (a) southern refuge(s) during the Valdai Glaciation, and Holocene repopulations of the Plain (Map 1).

The only Russian forest-steppe diplopod of a clear Asian origin appears to be *Schizoturanius dmitriewi* (TIMOFEYEV) (Map 1). Apart from the latter form restricted to the Russian Plain, the genus comprises at the moment 6 species from SW-Siberia and Central Asia, including *S. clavatipes* (STUXBERG) confined to forest-steppe areas of W-Siberia. The ancestor of *S. dmitriewi* is believed to have penetrated the Plain during an interglacial (? Mikulino) when broadleaved forests extended to the east far beyond the Urals. The discovery of a *Megaphyllum* aff. *sjaelandicum* (MEINERT) in the environs of Ust-Kamenogorsk, E-Kazakhstan, is another good example of



Map 3: Distribution of some diplopod species in the USSR.

Filled circles *Rossiulus kessleri* (LOHMANDER); Asterisks *Megaphyllum r. rossicum* (TIMOFEYEV); Open circles *Rossiulus vilnensis* (JAWLOWSKI); Filled triangles *Polydesmus stuxbergi* ATTEMS.

such faunal connections. Isolation and survival seem to have followed in situ at least during the last, i. e. Valdai, Glaciation whereas the present range has been attained as a result of Holocene recolonizations.

In short, during the Valdai Glaciation, the Diplopoda in Europe could have survived only in several, often very local, refuges, including those few lying in the southern part and/or south of the Russian Plain. During the Holocene, the millipedes have managed to restore/expand their areas to very different extents ranging from the present most widespread *Rossiulus kessleri* to the obviously relict *Leptoiulus semenkevitchi* or *Polydesmus montanus ukrainicus*.

The Dnieper evidently served as a prominent zoogeographical barrier in both easterly and westerly diplopod migrations. The main pathways for dispersal may be postulated to have followed river valleys, but not interflaves, this conclusion being consistent with both ne- and paleontological evidence obtained for such a strictly nemoral group as, e. g., the mollusc family Clausiliidae (SHIKOV 1982).

Using data on the fauna of the Caucasus Major, it appears possible to indirectly "revive" a few (sub)genera that once populated the Russian Plain but now are either entirely or partly missing there. *Unciger* as one of such elements has just been mentioned above. Similarly, *Megaphyllum* s. str. is represented in the NW-Caucasian fauna by a neoendemic species, *M. spathulatum* (LOHMANDER) whose ancestor may have penetrated the Caucasus from the north in the Plio- to Pleistocene. The same seems to hold true for the genus *Nemasoma*, the subgenus *Metamastigophorophyllon* of the genus *Mastigophorophyllon*, as well as the subgenera *Euxinoiulus*, *Orescoiulus*, and

Porrhoiulus of the genus *Julus* which, in the Caucasus, tend to form rather typical Elbrus fauna elements more or less restricted to high altitudes. Since *Porrhoiulus* spp. also occur in the Altai area, Siberia, it seems groundless to surmise an autochthonous subgeneric division of *Julus* in the Caucasus. Moreover, I rather think that an ancient, Plio-Pleistocene Ural faunogenetical centre may be assumed to have been involved in the history of the genus *Julus* as a whole, although at the present this hypothesis remains a mere speculation.

4. Conclusions:

Several chronological "layers" are quite evident in the present-day diplopod fauna of the Russian Plain. Since all the few regional (sub)endemic forms appear to be represented only by (sub)species at best, there seems to be no reason to surmise an age older than the Pleistocene. In other words, the 8 neoendemics may be postulated to form the earliest faunal "layer" still traceable. The bulk of the modern fauna seems to be fully migratory, Euro-Mediterranean in origin and Holocene in age. Finally, the anthropochores must have arrived the very last, again from the west, very recently, just a few centuries/decades ago, and solely due to the increasing impact of man.

During the Holocene, several larger refuges in western Europe, the Alps, the Carpathians and the Balkans seem to have provided the main, (north)easterly flow of migrants, increasingly impoverished and totally declining towards the Ural Mts. An Asian influence in the faunal composition is hardly traceable, being represented only by a single forest-steppe neoendemic and two modern Siberian taiga elements. The role of both Crimean and Caucasian refuges seems to be likewise quite modest, as witnessed by the reconstructed spatial history of a few neoendemic forms.

The main factor determining the landscape-zonal distribution pattern of the Euro-Mediterranean Diplopoda appears to be the degree of development of broadleaved forests. Both northerly and southerly of the belt of broadleaved forests, millipedes tend to occur in the Russian Plain increasingly sporadically and to be better associated with intrazonal, particularly with anthropogenous habitats. All the region's endemic and subendemic forms tend to be rather confined to forest-steppes which are believed to represent a refuge biome since at least the last, Mikulino, Interglacial.

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Additions to the proofs:

While the paper was in press, further accumulation of faunistic material has revealed the presence of *Polydesmus schaessburgensis* VERHOEFF also in Moldova (= Moldavia), namely from the environs of Briceani and Kotovsk (= Gancesti). Besides, the Russian list has been joined by *Cibiniulus phlepsii* (VERHOEFF) recently taken from under the bark of an oak tree near Sevsk, Briansk area (H. ENGHOFF det.). Finally, all the earlier records of *Megaphyllum unilineatum* (C.L. KOCH) in the Plain appear to actually concern *M. sjaelandicum* (MEINERT), judged from pertinent material.

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