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Zoogeography of the millipedes (Diplopoda) of eastern Germany

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Abstract

In the framework of extensive studies of the millipede fauna of eastern Germany, 68 species are recorded from this area. The distribution of selected species is illustrated with maps and discussed in the light of their total distribution.

Eastern Germany is clearly divided into two major regions: the Central German Uplands in the south and the adjacent lowlands which extend to the Baltic Sea in the north. Several species are, in part strictly, restricted to the Central German Uplands and do not or hardly cross the 200 m contour towards the lowlands. Thus, the species number increases by 44 % from north to south. Other species are restricted to the lowlands.

In agreement with the Central European position of eastern Germany north of the Alps, the area can be expected to be a postglacial dispersal pathway for species from the western and eastern glacial refugia. A zoogeographical evaluation of the millipede species of eastern Germany confirms this. Approximately the same numbers of species have their main distribution of the western (18 %) and eastern (19 %) part of the area. Forty-one % of the species reach their eastern (8 species), western (9) or northern (11) distribution limit in eastern Germany.

The postglacial distribution history of selected species is discussed, under consideration of constancy, hybridisation, and evolution of subspecies.

Keywords: distribution, ice age, re-immigration, post-glacial dispersal

1. Introduction

It is thought (Kime & Golovatch 2000) that only a few millipede species survived during the last ice age in the area now occupied by eastern Germany, and that almost all of the species found there today must have migrated to the area within the last 10 000 years. Refugial areas to the south-west and south-east of the Alps are believed to have been the centres from which these species dispersed. As eastern Germany is situated about midway between these glacial refugia, about the same numbers of migrants from east and west might be expected. Besides these two groups, some southern European species might be expected to have migrated north postglacially from the Alps over the Central German Uplands.

Using many new records, we summarise here the millipede distribution patterns found in eastern Germany and discuss the likely faunogenesis of European Diplopoda north of the Alps.

2. Study area and sources of data

The distribution maps are based on 4490 records (species per location and time) of millipedes from 1045 localities (Fig. 1) and cover the eastern German federal states. From south to north, these are Thuringia (TH), Saxony (SN), Saxony-Anhalt (ST), Brandenburg including Berlin (BB) and Mecklenburg-Western Pomerania (MV). Thuringia is situated in the centre of the Central German Uplands, whose mountains continue through the southern parts of Saxony-Anhalt and Saxony as the Harz Mountains, the Ore Mountains and the mountains of the Oberlausitzer Bergland. Brandenburg and Mecklenburg-Western Pomerania are outside the Central German Uplands in the North German Lowland. The northern border of the Central German Uplands corresponds to the 200 m contour (Fig. 2) and is the most important biogeographical boundary in eastern Germany (Liedtke & Marcinek 1995).

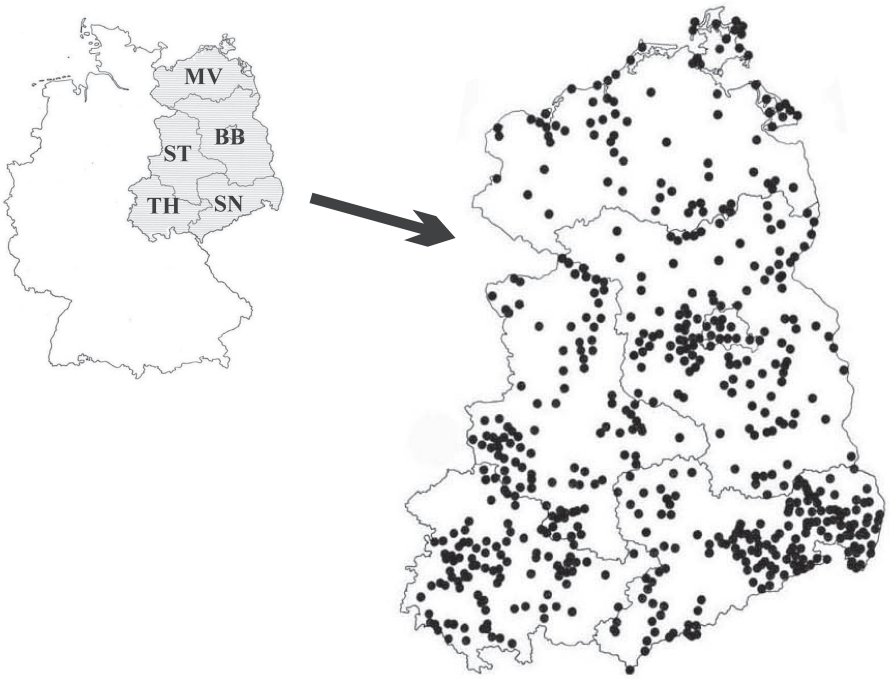


Fig. 1 Eastern Germany and study sites. Federal states in eastern Germany: TH = Thuringia, SN = Saxony, ST = Saxony-Anhalt, BB = Brandenburg/Berlin, MV = Mecklenburg-Western Pomerania.

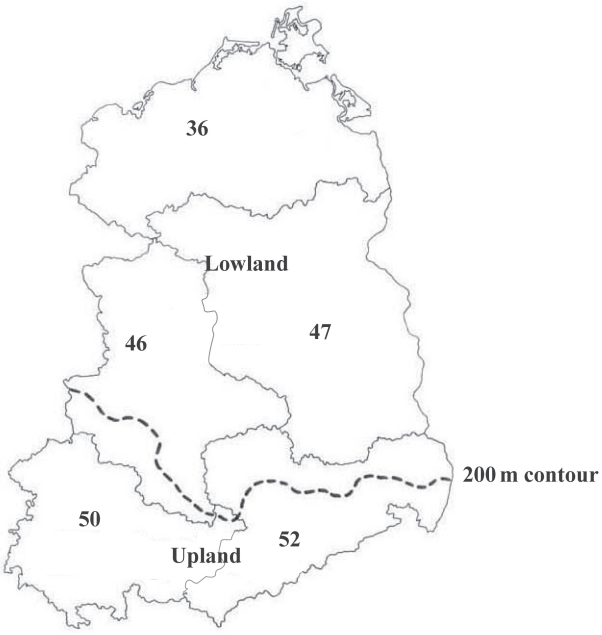


Fig. 2 Species numbers in the different federal states of eastern Germany. The 200 m contour divides the area between the lowland (north) and the Central German Uplands (south).

Faunistic data were obtained from the literature (summarised in Hauser & Voigtländer 2009) and from museum specimens. Most of the latter records are from the Senckenberg Museum of Natural History Görlitz, especially from the collections by W. Dunger, K. Voigtländer, H. Hauser, R. Ibisch, P. Schnitter and H. Richter. We were also able to use previously unpublished records of Otto Schubart from his collection in the Natural Science Museum of Berlin; the new records are mainly from the federal state of Brandenburg. Records from the private collections of H. Reip and N. Lindner were also included.

3. Results

In the eastern German area 68 millipede species were recorded (Tab. 1). Of the 68 species, 20 are very common over the whole area (Fr = 5), 16 are common but more concentrated in particular states (Fr = 4), 11 are less common (Fr = 3), 12 are rare and 9 are only very occasionally collected.

Numbers of millipede species typically increase in Europe from north to south (Kime 1990, 2000). This pattern can also be seen even on the area of eastern Germany. The number of species increases from 36 species in MV to 46 and 47 in ST and BB, and to 50 and 52 in TH and SN, the southern federal states (Fig. 2).

Tab. 1 Species distribution in eastern Germany. For locations of the federal states (TH, SN, ST, BB, MV) see Fig. 1. Fr = frequency class in eastern Germany: 5 = very common, more than 30 records over the whole area; 4 = common, more than 30 records in one part of the area only; 3 = regular, 10 to 30 records in one part of the area only; 2 = rare, 3 to 9 records; 1 = sparse, 1 to 2 records. Di = distribution in Europe: a = mainly in the Alps, e = in most parts of Europe, h = holarctic, m = Central Europe, n = widespread in northern Europe, o = mainly in eastern Europe, w = mainly in western Europe, ? = distribution uncertain. Bo = range limit occurs in eastern Germany: → = eastern border, ← = western border, ↑ = northern border.

	TH	SN	ST	BB	MV	Fr	Di	Bo
Polyxenus lagurus (Linnaeus, 1758)	x	x	x	x	x	5	h	
Glomeris pustulata Latreille, 1804	x	x				3	m	↑
G. marginata (Villers, 1789)	x	x	x	x	x	4	w	→
G. undulata C. L. Koch, 1844	x	x	x	x		4	m	↑
G. tetrasticha Brandt, 1833*	x	x	x	x		4	m	↑
G. hexasticha Brandt, 1833	x	x	x	x		4	o	↑
Geoglomeris subterranea Verhoeff, 1908		x				1	?	
Trachysphaera costata (Waga, 1857)	x	x				2	o	↑
Chordeuma sylvestre C. L. Koch, 1847	x	x				2	w	→
Melogona voigtii (Verhoeff, 1899)	x	x	x	x	x	4	m	
M. gallica (Latzel, 1884)	x					1	w	→
Mycogona germanica (Verhoeff, 1892)	x	x	x			4	m	↑
Orthochordeumella pallida (Rothenbühler, 1899)		x				1	?	
Mastigophorophyllon saxonicum Verhoeff, 1910		x			x	2	o	←
Haploporatia eremita (Verhoeff, 1909)	x	x				3	a	↑
Mastigona bosniensis (Verhoeff, 1897)	x	x	x			3	o	
Haasea flavescens (Latzel, 1884)	x	x				3	a	↑
H. germanica (Verhoeff, 1901)	x	x				3	m	↑
Brachychaeteuma bagnalli Verhoeff, 1911	x					1	w	→
B. bradeae (Brölemann & Brade-Birks, 1917)	x	x	x	x	x	2	e	
Craspedosoma rawlinsii Leach, 1815	x	x	x	x	x	5	m	
Ochogona caroli (Rothenbühler, 1900)	x	x				3	a	↑
Brachydesmus superus Latzel, 1884	x	x	x	x	x	5	e	
Polydesmus angustus Latzel, 1884	x	x	x	x		4	w	→
P. complanatus (Linnaeus, 1761)	x	x		x	x	4	o	←
P. denticulatus C. L. Koch, 1847	x	x	x	x	x	5	e	

*The distinguishing of the species *G. connexa* C. L. Koch, 1847 and *G. tetrasticha* Brandt, 1833 by Hoess & Scholl (2001) makes a evaluation of both areas necessary. The records mentioned here have been checked to concern only *G. tetrasticha*.

Tab. 1 cont.

	TH	SN	ST	BB	MV	Fr	Di	Bo
P. inconstans Latzel, 1884	x	x	x	x	x	5	w	
Propolydesmus germanicus (Verhoeff, 1896)			x			1	?	
P. testaceus (C. L. Koch, 1847)	x		x			3	w	→
Macrosternodesmus palicola Brölemann, 1908				x		1	w	
Ophiodesmus albonanus (Latzel, 1895)			x			1	w	
Strongylosoma stigmatosum (Eichwald, 1830)	x	x	x	x	x	4	o	←
Nemasoma varicorne C. L. Koch, 1847	x	x	x	x	x	5	e	
Choneiulus palmatus (Němec, 1895)	x	x	x	x	x	5	e	
Nopoiulus kochii (Gervais, 1847)	x	x	x	x	x	5	e	
Proteroiulus fuscus (Am Stein, 1857)	x	x	x	x	x	5	n	
Archiboreoiulus pallidus (Brade-Birks, 1920)	x					1	e	
Boreoiulus tenuis (Bigler, 1913)		x	x	x		2	n	
Blaniulus guttulatus (Fabricius, 1798)	x	x	x	x	x	5	e	
Allajulus nitidus (Verhoeff, 1891)	x	x	x	x	x	4	w	→
Kryphioiulus occultus (C. L. Koch, 1847)	x	x	x	x	x	5	o	
Cylindroiulus caeruleocinctus (Wood, 1864)	x	x	x	x	x	5	e	
C. punctatus (Leach, 1815)	x	x	x	x	x	5	w	
C. truncorum (Silvestri, 1896)	x			x	x	2	e	
C. arborum Verhoeff,1928			x	x		2	o	
C. parisiorum (Brölemann & Verhoeff, 1896)			x	x		2	w	
C. latestriatus (Curtis, 1845)		x	x	x	x	4	w	
C. britannicus (Verhoeff, 1891)	x			x	x	2	w	
Enantiulus nanus (Latzel, 1884)	x	x	x	x	x	5	m	
Pachypodoiulus eurypus (Attems, 1895)		x				1	a	↑
Julus scandinavius Latzel, 1884	x	x	x	x	x	5	w	
J. terrestris Linnaeus 1758				x	x	2	o	←
J. scanicus Lohmander, 1925			x	x	x	3	?	
Xestoiulus laeticollis (Porat, 1889)			x	x	x	4	w	
Leptoiulus trilobatus (Verhoeff, 1894)		x				3	o	←
L. proximus (Němec, 1896)	x	x	x	x	x	5	o	
L. belgicus (Latzel. 1884)	x		x			3	w	→
L. cibdellus (Chamberlin, 1921)		x	x	x		3	o	←
Ophyiulus pilosus (Newport, 1842)	x	x	x	x	x	5	?	

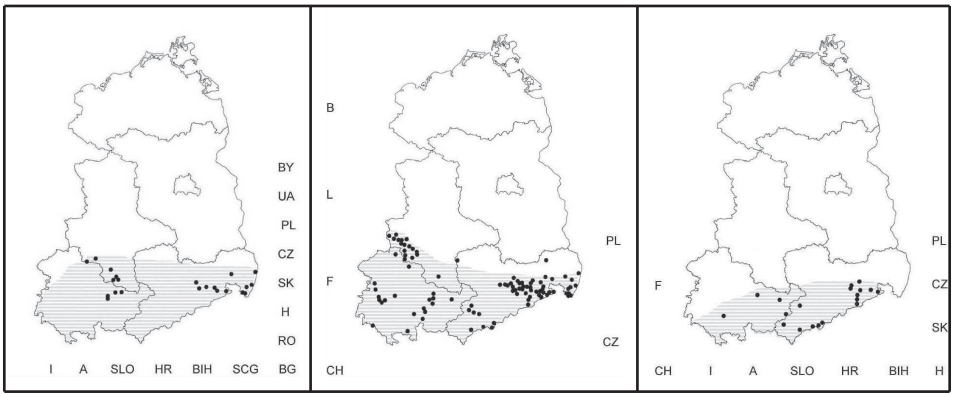
Tab. 1 cont.

	TH	SN	ST	BB	MV	Fr	Di	Bo
Unciger foetidus (C. L. Koch, 1838)	x	x	x	x	x	5	o	
Brachyiulus pusillus (Leach, 1815)	x	x	x	x	x	5	o	
Megaphyllum projectum Verhoeff, 1894	x	x	x	x		4	o	
M. sjaelandicum (Meinert, 1868)				x	x	2	o	
M. unilineatum (C. L. Koch, 1838)	x	x	x	x	x	4	o	←
Ommatoiulus vilnense (Jawłowski, 1925)		x		x		2	o	←
O. sabulosus (Linnaeus, 1758)	x	x	x	x	x	5	e	
Tachypodoiulus niger (Leach, 1815)	x	x	x	x		4	w	→
Polyzonium germanicum Brandt, 1831	x	x	x	x	x	4	o	

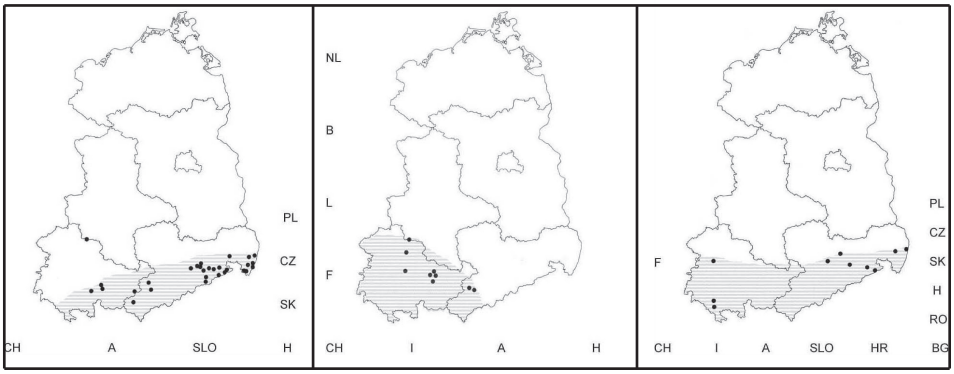
Species occurring mainly in the Central German Uplands. The ranges of a number of eastern German millipedes coincide approximately with the Central German Uplands area. These include the chordeumatidans *Mastigona bosniensis*, *Mycogona germanica*, *Haasea flavescens*, *Ochogona caroli* and *Chordeuma sylvestre* (Figs 3–7) as well as the glomeridans *Glomeris pustulata* and *Trachysphaera costata* (Figs 8, 9). The ranges of *Leptoiulus belgicus* and *Propolydesmus testaceus* are concentrated in the western uplands (Figs 23, 24) whereas *Leptoiulus trilobatus* only occurs in the eastern uplands (Fig. 27). Some other species also have a few records outside of the mountains: *Glomeris hexasticha*, *Glomeris undulata*, *Melogona voigtii*, *Allajulus nitidus* (Figs 10–13) and *Tachypodoiulus niger* (Fig. 25).

Species occurring mainly in the eastern German lowland. Three species are restricted to the northern lowlands. These are *Cylindroiulus latestriatus* (Fig. 14), *Xestoiulus laeticollis* (Fig. 15), and – to a less clear extent – *Leptoiulus cibdellus* (Fig. 28).

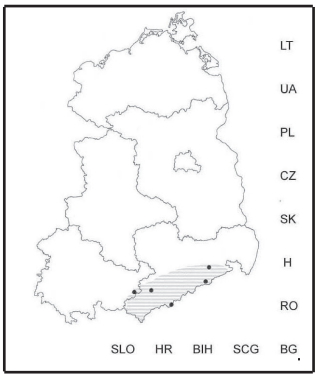
Species with other distribution. *Strongylosoma stigmatosum* (Fig. 16) occurs widely in the Central German Uplands and does not cross the 200 m contour towards the north. However, it has additional occurrences 150 km further north in the BB and MV lowlands along the eastern border of Germany.



3 *Mastigona bosniense* 4 *Mycogona germanica* 5 *Haasea flavescens*

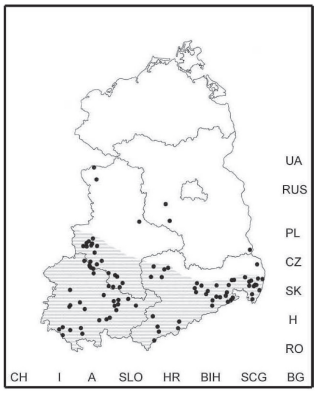


6 *Ochogona caroli* 7 *Chordeuma sylvestre* 8 *Glomeris pustulata*

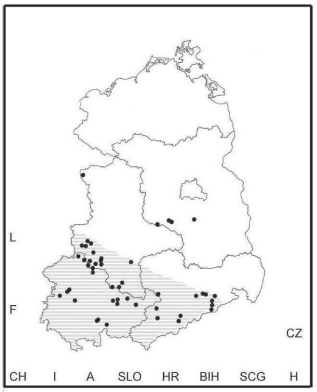


9 *Trachysphaera costata*

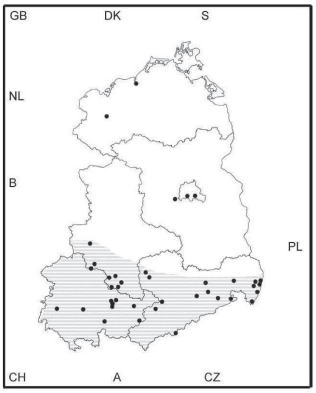
Figs 3–9 Species only distributed in the Central German Uplands.



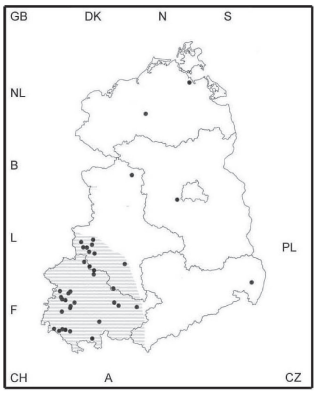
10 *Glomeris hexasticha*



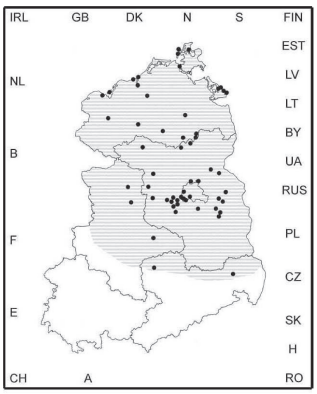
11 *Glomeris undulata*



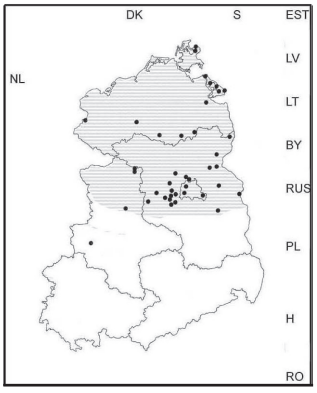
12 *Melogona voigtii*



13 *Allajulus nitidus*

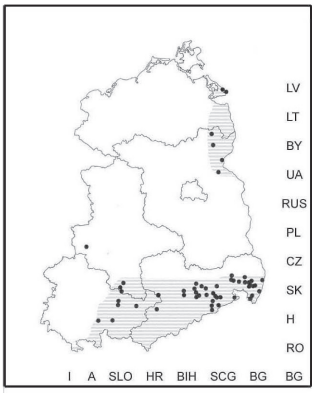


14 *Cylindroiulus latestriatus*



15 *Xestoiulus laeticollis*

Figs 10 to 15 10–13: Species mainly distributed in the Central German Uplands. 14–15: Species distributed in the lowland of eastern Germany.



16 *Strongylosoma stigmatosum*

Fig. 16 Distribution of *Strongylosoma stigmatosum*.

4. Discussion

The distribution of millipedes in eastern Germany at the background of European fauna. The central European position of eastern Germany is clearly reflected in the millipede species list (Tab. 1). Nearly the same numbers of species are West European (18 species), East European (19) and Central European or widespread European (19). Only four species inhabit the alpine/pre-alpine area with a main centre of distribution in the Alps.

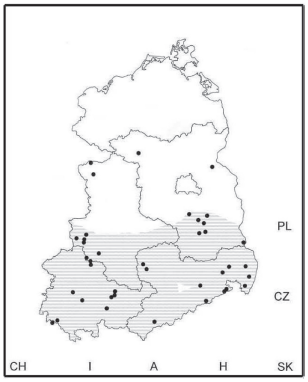
Twenty-eight of the eastern German millipede species (41 %) have a distribution limit in eastern Germany (Tab. 1). Nine species mainly distributed in West Europe have eastern limits, eight species mainly in South-Eastern and East Europe have western limits and 11 species of the Alps and Central or East Europe have northern limits in the area.

Julida is the geographically and ecologically dominant millipede order in all parts of Europe (Golovatch 1997, Kime 2000, Kime & Golovatch 2000). In eastern Germany 35 species (51 %) belong to the order Julida and about half of the 35 species are distributed over the whole area; nearly all biotopes are inhabited.

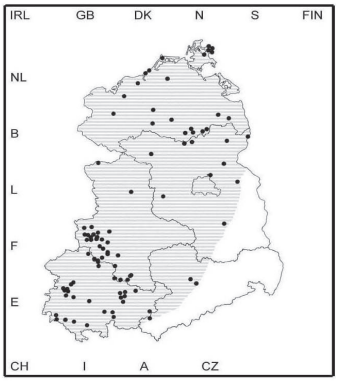
For Chordeumatida and Glomerida the border between the ‘zone containing one to about five species’ and the ‘zone containing several species’ of Kime (2000) corresponds almost exactly with the border of the Central German Uplands in eastern Germany. Only *G. marginata* (Fig. 18) and *C. rawlinsii* (Fig. 19) are widespread north of the uplands.

In contrast, Polydesmida do not show distinctive zonal trends in Europe (Kime 2000), and polydesmidan species are often widely distributed over the continent. The same is true in eastern Germany, where five of the seven eastern German species of the family Polydesmidae are distributed over the whole area including the lowlands (*Polydesmus denticulatus*, *P. inconstans*, *Brachydesmus superus*: Figs 20–22) or large parts of it (*P. angustus*, *P. complanatus*: Figs 30, 31). Unlike Chordeumatida and Glomerida, Polydesmidae are not limited by the Central German Uplands.

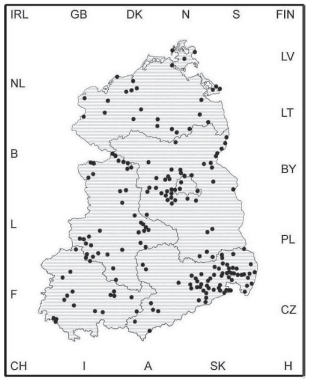
Only one species of the Chordeumatida and Glomerida are widespread in eastern Germany including the lowlands. These are *Craspedosoma rawlinsii* (Fig. 19) and *Glomeris marginata* (Fig. 18) which is therefore characterised by Haacker (1968) as expanding species of the genus. The other three Glomerida, *G. hexasticha* (Fig. 10), *G. undulata* (Fig. 11) and *G. tetrasticha* (Fig. 17), mainly occur in the Central German Uplands but are also known from a few localities in Saxony-Anhalt and Brandenburg. Among Chordeumatida, *M. voigtii* has been found outside of its main distribution area in the uplands (Fig. 12). However, these northern localities are all in cities (Potsdam, Berlin, Rostock, Schwerin), which suggests passive dispersal by humans (Schubart 1934). In contrast to *C. rawlinsii* populations of *M. voigtii* have not yet been found in natural biotopes in northern Germany as well as in Scandinavia (Andersson et al. 2005).



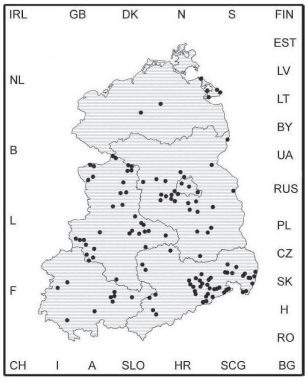
17 *Glomeris tetrasticha*



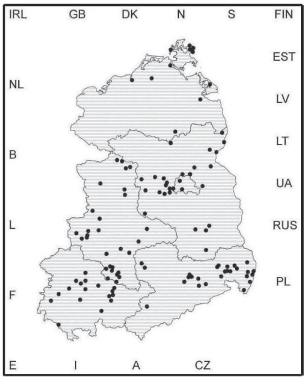
18 *Glomeris marginata*



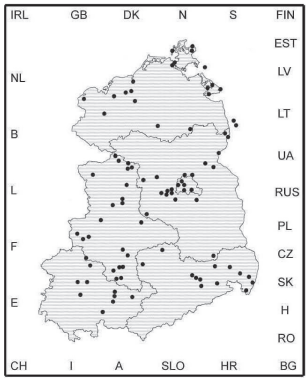
19 *Craspedosoma rawlinsii*



20 *Polydesmus denticulatus*



21 *Polydesmus inconstans*

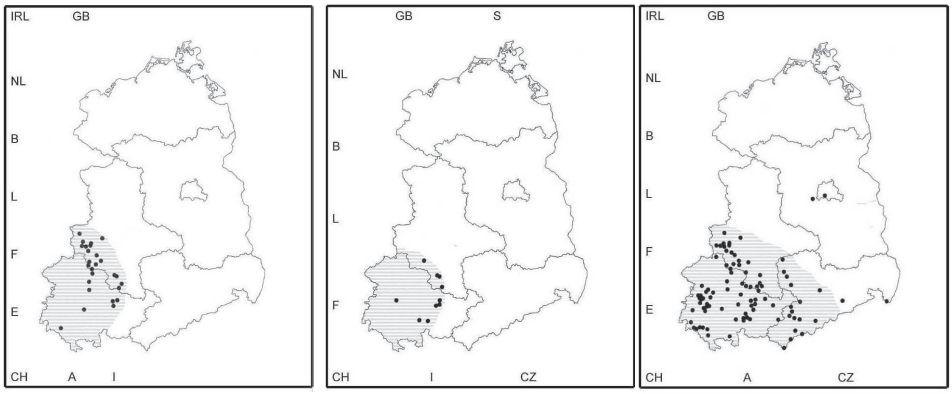


22 *Brachydesmus superus*

Figs 17–22 Widely distributed species.

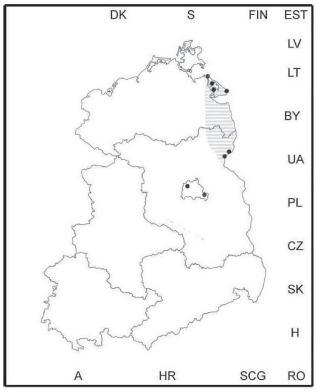
Isolated findings of some eastern German species, like that of *A. nitidus* in the Czech Republic (Lang 1951) and *M. germanica* in the Netherlands (Berg 2002), are not regarded as indicating active expansion of range in the sense of de Lattin (1967), and are likely to be due to anthropochory.

Assumed present postglacial expansion. The range of the western species *P. angustus* may be expanding. According to Schubart (1934) the eastern range limit of this species was in Thuringia, and there were no records from the well-investigated state of Saxony. Newer records, mostly from natural habitats, especially in the woods of the Ore Mountains (Hauser coll. 2007, unpubl.), the woods around Tharandt (Hauser & Voigtländer 2008) and, as the most eastern record, the Elbe Sandstone Mountains (Hauser & Voigtländer 2008) suggest a continuing postglacial expansion of this species. Whereas the parapatric boundary between *P. angustus* and *P. complanatus* crosses the centre of the area, the eastern range limit of *M. gallica* only just reaches eastern Germany. According to Schubart (1934) the western species *M. gallica* lives 'only west of the river Rhine', but there are newer records from more eastern parts of Germany, in central and northern Hesse (Spelda 1999, Hauser coll. 2006, unpubl.) and western Thuringia (Voigtländer coll. 2007, unpubl.). The 'eastern' *M. voigtii* has now been found on the British Isles, albeit synanthropically (Corbet 1996).

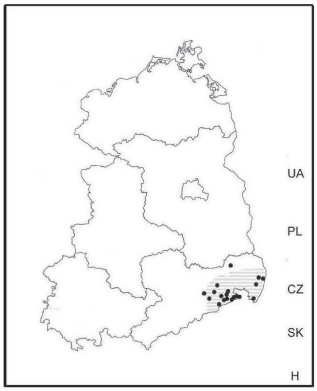


23 *Leptoiulus belgicus* 24 *Prolydesmus testaceus* 25 *Tachypodoiulus niger*

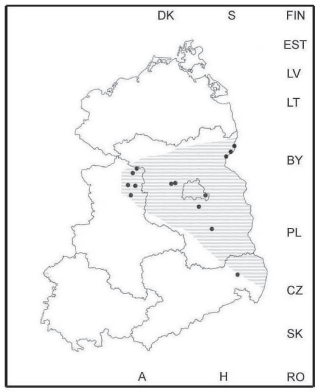
Figs 23–25 Atlantic species with eastern limits in eastern Germany.



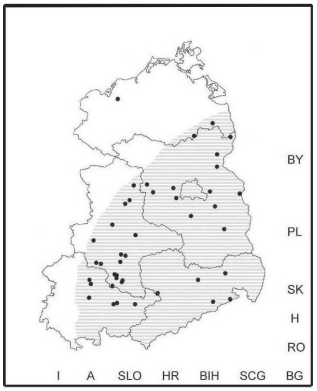
26 *Julus terrestris*



27 *Leptoiulus trilobatus*



28 *Leptoiulus cibdellus*



29 *Megaphyllum unilineatum*

Figs 26–29 Species with western limits in eastern Germany.

Historical biogeography of the millipede fauna north of the Alps. During the last glacial period, changes in climate as well as the ice movements must have caused fundamental changes in the structure of the eastern German millipede fauna. Most species would have been displaced from the area north of the Alps by glaciers. We can ask: Where did the different millipede species survive the long cold periods, what changes did the fauna experience in refugia, and by what routes did millipedes enter the eastern German area after the last glaciation?

Present-day distributions can be used to generate hypotheses about directions of postglacial migration into eastern Germany, which is illustrated in Tab. 2. Because the Alps have a west-east orientation, it seems likely that species of the pre-glacial fauna would have migrated south-east or south-west of the Alps to areas with a warmer climate. Based on this hypothesis, we see the following possible historical scenarios for species currently occurring in Central Europe. Most cases involve eastern German millipedes. All the scenarios are speculative although some look more likely than others.

Tab. 2 Species distribution in Europe and dispersal tendencies. E – Spain, F – France, B – Belgium, NL – Netherlands, EG – eastern Germany, ▸ / ◂ = direction of the assumed completed or continued dispersal, PL – Poland, SK – Slovakia, H – Hungary, RO – Romania, BG – Bulgaria, X = Records, data after Berg 1995, Enghoff & Kime (2004), Geoffroy (1996), Kime (2004), Mock (2001), Tajovský (2001) and Wytwer (2008).

	E	F	B	NL	EG	PL	SK	H	RO	BG
Brachychaeteuma bagnalli Verhoeff, 1911		X	X		▸					
Chordeuma sylvestre C. L. Koch, 1847		X	X	X	▸			?		
Melogona gallica (Latzel, 1884)		X	X	X	▸					
Propolydesmus testaceus (C. L. Koch, 1847)		X	X	X	▸					
Macrosternodesmus palicola Brölemann, 1908		X	X	X	▸					
Glomeris marginata (Villers, 1789)	X	X	X	X	▸					
Polydesmus angustus Latzel, 1884	X	X	X	X	▸					
Leptoiulus belgicus (Latzel. 1884)	X	X	X	X	▸					
Tachypodoiulus niger (Leach, 1815)	X	X	X	X	▸					
Cylindroiulus punctatus (Leach, 1815)	X	X	X	X	▸	X				
Ophiodesmus albonanus (Latzel, 1895)		X	X	X	▸	X				
Allajulus nitidus (Verhoeff, 1891)		X	X	X	▸	X				
Julus scandinavius Latzel, 1884		X	X	X	▸	X	X			
Polydesmus inconstans Latzel, 1884	X	X	X	X	▸	X	X			
Leptoiulus trilobatus (Verhoeff, 1894)					◂	X	X	X		
Leptoiulus proximus (Němec, 1896)					◂	X	X	X	X	
Leptoiulus cibdellus (Chamberlin, 1921)					◂	X	X	X	X	
Julus terrestris Linnaeus 1758					◂	X	X	X	X	
Kryphioiulus occultus (C. L. Koch, 1847)					◂	X	X	X	X	
Unciger foetidus (C. L. Koch, 1838)					◂	X	X	X	X	
Glomeris hexasticha Brandt, 1833					◂	X	X	X	X	X
Trachysphaera costata (Waga, 1857)					◂	X	X	X	X	X
Mastigona bosniensis (Verhoeff, 1897)					◂	X	X	X	X	X
Polydesmus complanatus (Linnaeus, 1761)					◂	X	X	X	X	X
Strongylosoma stigmatosum (Eichwald, 1830)					◂	X	X	X	X	X
Megaphyllum unilineatum (C. L. Koch, 1838)					◂	X	X	X	X	X
Cylindroiulus arborum Verhoeff,1928					◂	X	X	X	X	X
Polyzonium germanicum Brandt, 1831		X			◂	X	X	X	X	X
Mastigophorophyllon saxonicum Verhoeff, 1910					◂	X			X	
Ommatoiulus vilnense (Jawłowski, 1925)					◂	X			X	

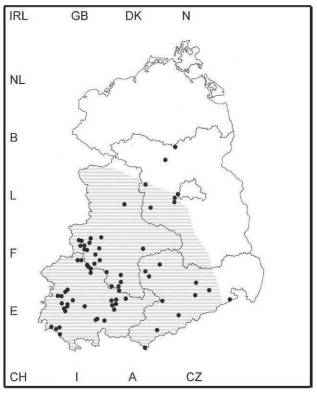
1. Some species may have survived the ice age either south-west or south-east of the Alps, and dispersed into the area north of the Alps during the Holocene. This may apply to the 18 western and 19 eastern European species, respectively (Tab. 1).

2. Some species may have survived the ice age both south-west and south-east of the Alps. In isolation they differentiated into two new species, which dispersed post-glacially from the west and the east into Central Europe.

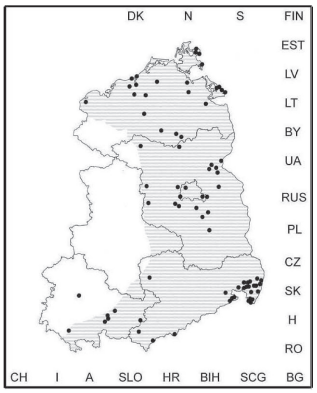
This may the case for the west/east distributed species *Melogona gallica* and *M. voigtii* as well as *Polydesmus angustus* and *P. complanatus* (Figs 30, 31). The two pairs have almost parapatric distribution in Central Europe. But from this, the conclusion cannot be drawn that both were subspecies. There is no evidence that *P. angustus* is the closest relative of *P. complanatus*, and that *M. voigtii* is the closest relative of *M. gallica*. Several other species are more closely related than these. There is also no evidence for hybridisation in the overlap zones of either species pair.

3. Some species may have survived the ice age both southwest and southeast of the Alps, but did not become genetically incompatible in isolation. When the distributions of the possibly evolved subspecies met postglacially in Central Europe, hybrids appeared.

For this scenario one possible example has been noted in Europe, namely the complicated and interesting situation with *Craspedosoma rawlinsii* (Leach, 1815). There are two morphologically distinguishable forms, '*Craspedosoma alemannicum*' Verhoeff, 1910 (western) and '*C. rawlinsii*'(eastern). Since *C. rawlinsii* is a very expansive species, it entered the distribution area of *C. alemannicum* in many places, thus producing the hybrid '*C. germanicum*' Verhoeff, 1910 over wide areas of Germany where the two subspecies came into contact (Hauser 2004). This interpretation explains previously incomprehensible distribution patterns (Verhoeff 1938, 1939). Since the taxa are known to hybridise, they are regarded today as subspecies, *C. rawlinsii rawlinsii* (Leach, 1915) and *C. rawlinsii alemannicum* Verhoeff, 1910. The subspecies status of *germanicum* being provisional because of its hybrid nature: *C. rawlinsii* X *germanicum* Verheoff, 1910.



30 *Polydesmus angustus*



31 *Polydesmus complanatus*

Figs 30–31 Example of a west/east-distributed species.

4. In cooler periods, some more stenotopic alpine species may have dispersed into ice-free parts of the Central Uplands, where they survived into warmer periods as small populations in suitable habitats. A likely example of such a glacial relict is *Pachypodoiulus eurypus,* which occurs outside of its otherwise alpine distribution area only as a small population in one very cool and wet ravine in Saxony (Richter 1967).

5. In cooler periods, some more eurytopic alpine species may have dispersed into ice-free parts of the Central Uplands, where they were able to maintain large, continuous, extra-alpine distributions when the glaciers withdrew. There are three species, widely distributed in the Alps, for which this case is likely to be true. *Haasea flavescens*, *Ochogona caroli* and *Haploporatia eremita* all extend north to the south of eastern Germany and adjacent regions. *H. flavescens* and *H. eremita* have their northern distribution limit near Dresden/Saxony (Hauser & Voigtländer 2008, Hauser & Voigtländer 2009), *O. caroli* in Upper Lusatia/Saxony (Hauser & Voigtländer 2008).

6. Some alpine species may have migrated into the Uplands during the glacial period and may have differentiated as isolated populations into new species. This may be the case with the non-alpine species *Haasea germanica*, a rare endemic of the German-Czech Central Uplands (Hauser & Voigtländer 2008) which occurs sympatrically with the closely related and much more widespread *H. flavescens*, a species also found in alpine areas. If *H. germanica* arose from *H. flavescens* in this manner, then the record of *H. germanica* in Romania (Ceuca 1992) is doubtful.

7. Some species may have survived the glacial period in ice-free areas between the alpine and northern glaciers. *Mycogona germanica* is unique in having a clearly defined centre of distribution in the Central Uplands, and may be an example of in-situ survival (Malicky et al. 1983). Another example may be *Proteroiulus fuscus* which ranges north in Europe up to arctic-alpine habitats.

For millipedes with large ranges across Europe, e. g. euryoecious species like *Ommatoiulus sabulosus* or *Polydesmus denticulatus* (Fig. 20)*,* it is more difficult to guess from present-day distributions where the species were during the last glacial, and how they expanded their ranges afterwards.

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