

***Lithobius curtipes* (Chilopoda: Lithobiomorpha), a centipede with an enigmatic distribution**

Anthony D. Barber

7 Greenfield Drive, Ivybridge, Devon PL21 0UG, UK.

Email: abarber159@btinternet.com

Abstract

Lithobius curtipes is one of Britain's less common centipedes and is apparently absent from Ireland. It is, however, widespread across Northern Europe to the Urals and as far east as Mongolia and occurs far north to inside the Arctic Circle. In Britain it is known from a variety of habitats including up to 1,000m in Snowdonia but is unrecorded from Scotland apart from two records from the south. As well as being able to survive, and in some cases, be, the only lithobiid present in northern latitudes in Europe, overwintering in the frozen state. Amongst other habitats, *L. curtipes* is also associated with floodplains, notably in Central Europe, and may co-exist there with *Lamyctes emarginatus* on the basis of their different life-cycles.

Introduction

Lithobius (Monotarsobius) curtipes C.L.Koch, 1847 is a relatively small (11mm), chestnut brown species of *Lithobius* distinguished from a number of other British species of that genus by its 2+2 teeth on the forcipular coxosternite, the lack of posterior projections on its tergites and single claws on the last pair of legs. Along with *Lithobius crassipes* L. Koch, it is one of the two British representatives of the sub-genus *Monotarsobius*, recognised, amongst other characteristics, by having only about 20 antennal articles. *Lithobius (Sigibius) microps* Meinert has about 25 (23-27) and other British & Irish species (subgenus *Lithobius*) rather more (26-34 in *Lithobius lapidicola* Meinert to 49-54 in *Lithobius piceus* L.Koch). Although Ganske *et al.* (2021) indicate that these subgenera are not monophyletic, it is convenient to see these two *Monotarsobius* as distinct from the remainder of the British *Lithobius* species.

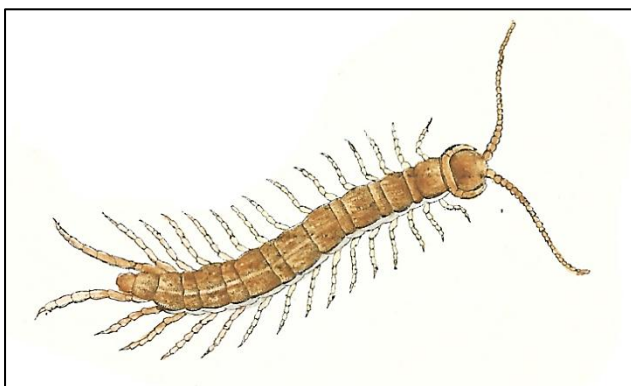


Figure 1: *Lithobius curtipes* C.L. Koch
(From C.L. Koch, Die Myriapoden, 1863)

Lithobius curtipes and *L. crassipes* are not always easy to distinguish and it is quite possible that in the past the former has been occasionally overlooked although, even allowing for this, the total numbers of records of the two species obtained by the BMIG Centipede Recording Scheme for Mainland Britain up to the end of 2018 are strikingly different. There are only 171 for *L. curtipes* compared with more than 2,500 for *L. crassipes* and no records of the former from Ireland. Adult males are fairly easy to distinguish by the flattened projection on the posterodorsal extremity of the tibiae of the ultimate (15th)

legs in *L. curtipes* (Figs. 2 & 3). There are also differences in the arrangement of the ocelli, 1, 1 + (usually incomplete) rosette compared with 1 + 2 or 3 straight rows, of the forcipular coxosternal teeth and the gonopods but these characters are not always clearly definitive so spinulation might need to be looked at. In addition to these morphological characters, *L. curtipes* also has a reputation for a much greater tendency for curling up when disturbed (as in *L. microps*). The distribution of *L. crassipes*, both in Britain and in Mainland Europe, very much overlaps with that of *L. curtipes* and extends to both Ireland and to Southern Europe.

Once regarded as a lowland, possibly ancient woodland, species in Britain (Barber & Keay, 1988) further records of *L. curtipes*, including its discovery by Richard Gallon at 1,000m asl in Snowdonia (Barber & Gallon, 2020) along with its apparent absence from most of Scotland even though its range extends far north in Europe, prompted a review of aspects of its distribution and ecology by reference to some of the sources in which it is listed. Reports of some other non-British sites from which centipedes were collected but from which *L. curtipes* was not found are included also as part of the context. It must be emphasised that this account does not attempt to be a comprehensive survey of all the literature relating to the species but refers to some of the available published sources from across its known distribution area, notably from the Nordic countries, Germany, Poland and Russia and from Austria, Hungary, the Czech Republic and Slovakia.

Nomenclature

The species was first described by Koch from Nuremberg (Nürnberg), Germany and its status reviewed by Eason (1972) from specimens in the Natural History Museum (London). He also reported specimens from Lithuania and the (present) Czech Republic. A list of synonyms and the names of three subspecies are given in Chilobase (Bonato *et al.*, 2016). Of these latter, *Lithobius curtipes turkestanicus* Attems, 1904 and *Lithobius curtipes taurica* Ellingsen, 1910 are, apparently, synonyms of *Lithobius ferganensis* (Trotzina, 1894) and *Lithobius curtipes diversipes* Verhoeff, 1901 is identified as *L. curtipes* (probable but uncertain synonymy).

There has been some confusion in the past regarding the name of the species that we currently know as *Lithobius curtipes*. In 1947, Loksa, as cited in Chilobase (Bonato *et al.*, 2016), described a species *Lithobius (Monotarsobius) baloghi* from Romania and in a subsequent paper (Loksa, 1955a) listed both *M. curtipes* and *M. Baloghi*, the latter of which he described as a high-alpine type, recording it at 1800m in the Carpathians. However his drawings (p 10; Abb. 96 & 97) of the tibia of a *L. curtipes* ♂ show a tubercle as is characteristic of *L. ferganensis* which his *L. Baloghi* ♂ (now known to be synonymous with *L. curtipes*) does not have (Abt. 98; see previous comments). From Russia, he subsequently described a subspecies *Monotarsobius baloghi rybinskianus* (= *L. curtipes*) from Rybinsk, at the confluence of the Volga and Sheksna Rivers, NNE of Moscow (Loksa, 1962).

Matic (1966) in his account of the anamorph centipedes of Romania (1966) described and illustrated *L. curtipes* under the name *L. (Monotarsobius) baloghi* Loksa, 1947 and *L. ferganensis* under the name *L. (Monotarsobius) curtipes* C.Koch 1847 (see Dányi, 2006; Eason,

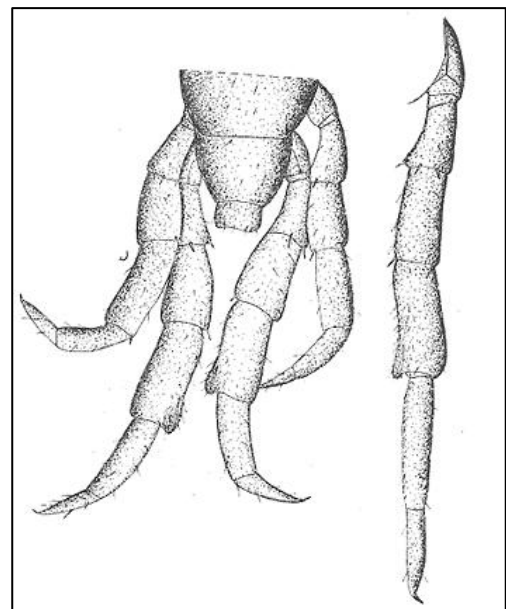


Figure 2: *Lithobius curtipes* ♂ posterior region (dorsal) & 15th leg
(From Matic, 1966, as *Monotarsobius baloghi* Loksa)

1972, 1997). It also seems likely that the drawing of the ♂ ultimate leg in *Pareczniki Polski* (Kaczmarek, 1979: Fig. 35) was based on that of Matic and shows the features of *L. ferganensis*. However, the description of *L. curtipes* in that key (p 55) is correct (M. Leśniewski *pers.comm.*). Zalesskaja (1978) treats *L. baloghi* as a synonym of *L. curtipes*.

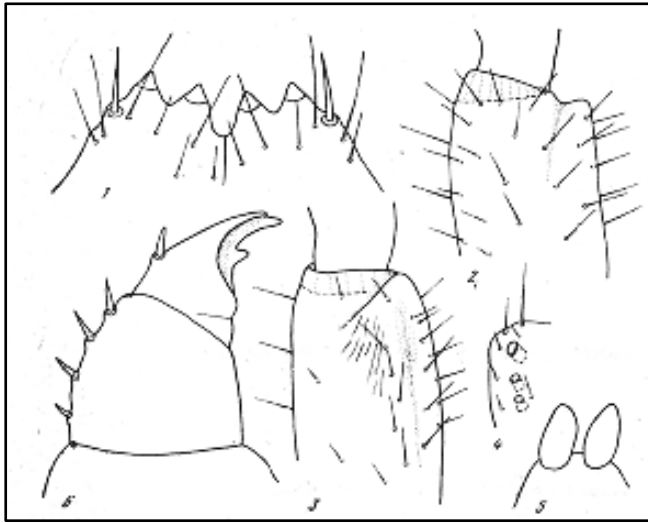


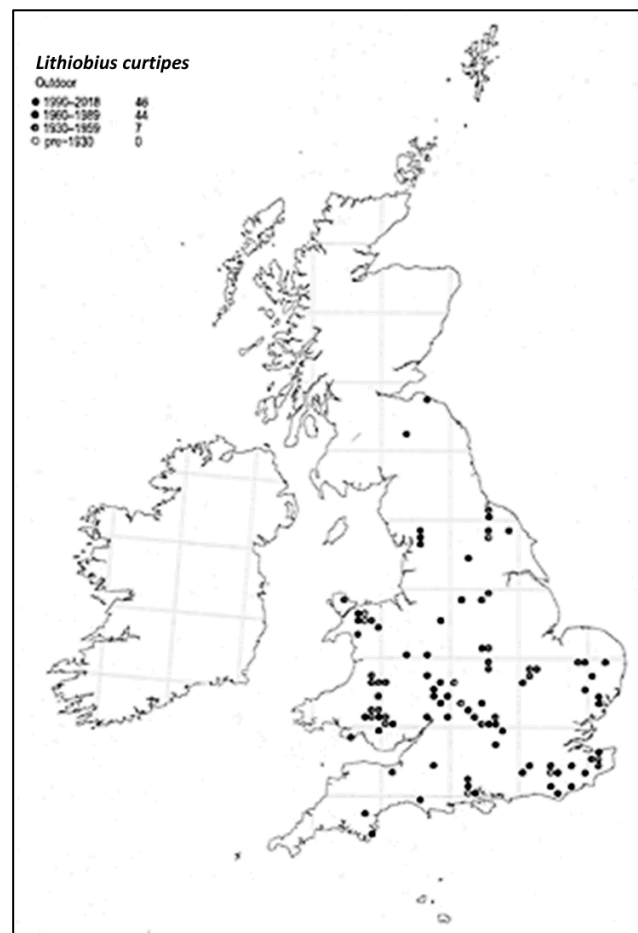
Figure 3: *Lithobius curtipes* (after Zalesskaja, 1978)

1. Forcipular coxosternite teeth
2. Femur of 15th leg ♂, distal end (ventral)
3. Femur of 15th leg ♂, distal end (dorsal)
4. Coxal pores, 15th leg
5. Gonopod spurs ♀
6. Gonopod claw ♀

Status in Britain

The first published report of *Lithobius curtipes* in the British Isles was by Brade-Birks (1934): “This species has been collected in Cambridgeshire by Dr F. Barton Worthington, but this is the first published record of the fact”. No further details seem to be available. It was later reported from Coughton Park, Warwickshire by E.H. Eason (1951). There are scattered subsequent records, often from woodland, right across England and Wales but only a few records from Dorset, Somerset and South Devon, and none, so far, from Cornwall. To the north, it is recorded from south Westmorland (2 locations) and NE Yorkshire. From Scotland there are single records from Woodhall Dene (VC 82) and Wester Kershope (VC 79) only. No records have so far been obtained for Ireland, the Isle of Man or the Channel Islands (Map 1).

During the 1950s there were two studies of centipedes in the New Forest by research students at Southampton University. H. Roberts (1956) looked at lithobiomorphs in Burley Wood, an area of mixed beech woodland. Although *Lithobius variegatus* Leach reached a peak density in summer of 10m⁻² and over the period of a year he collected 238 identifiable individuals of *Lithobius microps* (known at the time as *L. duboscqui*), there



Map 1: Hectad (10km grid square) map for *L. curtipes*, pre 2019.
(From BMIG Centipede Recording Scheme)

were only four records of *L. curtipes* and a single isolated individual later. S. Vaitilingham (1960) worked at the Denny-Matley Nature Reserve and also at Chilworth Woods, Southampton Common and the University Grounds. As far as *L. curtipes* was concerned, he found it in five habitats (Table 1). For comparison, his results for his *Geophilus carpophagus* (*G. carpophagus* s.l. in the modern sense, most likely *G. easoni* Arthur *et al.* in this case, almost certainly so at Denny and Chilworth) are included in the table.

Table 1: Occurrence of *Lithobius curtipes* and “*Geophilus carpophagus*” in Denny Reserve and other sites (after Vaitilingham, 1960)

Sycam = Sycamore, Pine Plant’n = Pine plantation, CW = Chilworth Woods (Mature Birch).
 Soton Comm = Southampton Common, Univ Gr’ds = University Grounds
 Key: + = Litter, - = Soil, o = Cryptozoic

Species	Heath	Oak	Beech	Sycam	Ash	Birch	Conifer	Pine Plant’n	CW	Soton Comm	Univ. Gr’nds
<i>L. curtipes</i>		+	+	- o	o +		+				
“ <i>G. carpophagus</i> ”	- o +	- o +	- o +	- o +	- o +	- o +	o +	- o +	- o +	- o +	- o +

Vaitilingham also showed frequency indices for the centipede species he found, calculated as:

$$\frac{\text{Number of samples where species is present}}{\text{Total number of samples}} \times 100\%$$

An extract from this is shown in Table 2:

Table 2: Frequency indices for 6 species of centipedes in Denny Reserve & Chilworth Woods (after Vaitilingham, 1960)

Species	Heath	Oak	Beech	Sycam	Ash	Birch	Conifer	Pine Plant’n
<i>L. curtipes</i>	0	21	17	98	66	5	22	0
<i>L. borealis</i>	0	0	18	8	7	42	28	5
<i>L. microps</i>	0	0	0	6	0	0	0	52
<i>L. variegatus</i>	13	100	100	100	80	84	100	79
<i>L. forficatus</i>	35	58	55	50	46	73	83	68
“ <i>G. carpophagus</i> ”	35	100	100	100	80	79	83	100

Table 3: Occurrence of *L. curtipes* in Whitley Wood samples, March 2002 to May 2014. (from Soil Biodiversity Group data)

Dates	Mar. 2002	July 2004	Sept. 2004	July 2005	Aug. 2005	July 2008	May 2014
No. specimens	Start Date	1	1	1	1	1	End Date

A much more recent New Forest study was that by the Soil Biodiversity Group (SBG) at the (London) Natural History Museum (Angela Lidgett, *pers. comm.*). At Whitley Wood, 1m² litter samples were taken every 7m along a 98m transect (15 samples) and sieved before being subjected to a three-day Winkler bag extraction at the museum. Over a period from March 2002 to May 2014 (126 monthly samples) only five specimens of *L. curtipes* were found.



Figure 4: *Lithobius curtipes* C.L. Koch, Britain.

Photo © Paul Richards

Over the same period, excluding undetermined lithobiomorphs (including damaged & juveniles), some 320 specimens of *Lithobius variegatus*, 230 *L. muticus* C.L.Koch, 117 *L. microps* along with various numbers of *L. borealis* Meinert (6), *L. crassipes* (28), *L. maci-lentus* L.Koch (5), *L. melanops* Newport (1) and *Lamyctes emarginatus* Newport (2) were recorded. The only apparent pattern of occurrence for *L. curtipes* seems to be that all specimens were all found over the months of July to September.

A further study, using litter sampling, soil pits and pitfall trapping in another New Forest habitat Ocknell Inclosure, in 2010/2011 yielded two further examples of *L. curtipes*.

The same group also surveyed a variety of woodland types in Berks, Bucks, Cambs, Devon, Essex, Lancs and East Sussex variously designated under the National Vegetation Classification (Hall *et al.*, 2004); 10 of these were classified as wet woodland (Types W1 – W7) and 12 as dry (Types W8 – W17). A similar procedure to that at Whitley Wood was used with the woodlands being surveyed at around five yearly intervals between the years 2003 and 2016. In only one of these further woodlands was *L. curtipes* recorded and that in both survey years, 2005 and 2010. This was at Abbots Wood, East Sussex, a designated W10 (*Quercus robur* - *Pteridium aquilinum* - *Rubus fruticosus*) woodland type with a total of 22 *L. curtipes* identified out of 85 centipede specimens collected in 2005 and 5 out of 58 in 2010. Also recorded there were *L. variegatus* and *L. muticus*. None of the other 8 NVC Type W10 sites yielded *L. curtipes* although there were various combinations and numbers of the two larger *Lithobius* (*L. variegatus*, *L. forficatus* (Linn,)) and the “smaller” *L. muticus*, *L. borealis*, *L. crassipes* and *L. microps*.

The results of the British Myriapod Group / British Myriapod & Isopod Group Centipede Recording Scheme, which included historical as well as recent records, showed that, up to the end of 2018, *L. curtipes* had been found in 97 10km grid squares (hectads) in a total in 45 of the 111 vice-counties of Mainland Britain. The regional distribution of these hectads is shown in table 4 and the overall distribution pattern in Map 1. There are no records from Northern Scotland, the Isle of Man, Channel Islands or Ireland.

Lithobius curtipes is very distinctly a rural animal - of the 129 records with appropriate data, nearly 95% (weighted) are reported as from rural sites with the remainder (two records) from suburban/village ones and none at all from sites described as urban, a rural:other sites ratio higher than that for any other British centipede. 88.8% (weighted) of the 89 records with appropriate data were recorded as being more than 1km from the sea, the remainder less than 1km with no splash zone / seashore ones. It was recorded in all months of the year.

Table 4: Regional occurrence of hectads from which *L. curtipes* has been recorded (weighted percent). (Taken from the Centipede Recording Scheme data).

Key: SE = South-east England, SW = South-west England, East = Eastern England, W&N Midl's = West & North Midlands, Yk, La, Wm = Yorkshire, Lancashire &, Westmorland, NE & SS = Northern England & Southern Scotland, NS = Northern Scotland

Region	SE	SW	Wales	East	W&N Midl's	Yk, La, Wm	NE & SS	NS	IOM	Ireland	CI
Weighted percent	16.1	7.3	25.9	14.6	14.8	2.1	2.9	0	0	0	0

With less than 200 records from less than 100 hectads over a period of eighty years since Eason's 1951 report, the data suggests that it is not a common animal in Britain and Lee (2015) gives its GB Rarity Status as "Nationally Scarce". As can be seen from the from the SBG data, however, it could, in fact, be most likely present in a site over a period of years without necessarily being found in a survey at any particular time. It seems difficult to predict its occurrence and specimens may turn up, apparently at random in surveys. On the other hand, as for instance in Vaitilingham's work and in the SBG collection from Abbots Wood (above) relatively large numbers might be found in a particular site at the time of a survey.

Lithobius curtipes in Britain seems to be found in a variety of rural habitats, both lowland and upland, and recent studies by Richard Gallon (Barber & Gallon, 2020) reveal it as being characteristically present in upland sites in scree and felsenmeer in Snowdonia between 700 m and more than 1,000 m (1,024 m, Carnedd Dafydd). The following table indicates the actual numbers or records at different altitude ranges collected by the recording scheme. Because of the relatively small number of records for the species and the small numbers of overall centipede records for higher altitudes, weighting the data is of limited value and could be misleading so such data is not presented and similarly for the principal habitats data where there are very limited records from certain types of habitat.

Table 5. Records for *Lithobius curtipes* for different altitude ranges.

(Taken from the Centipede Recording Scheme data).

Altitude range (m)	0-49	50-99	100-149	150-199	200-249	250-299	300-349	350-399	400-499	500-599	600-699	Over 699
Records (Actual)	19	15	13	225	12	2	1	2	3	1	2	9

Table 6. Records for *Lithobius curtipes* for different types of habitat.

(Taken from the Centipede Recording Scheme data).

Key: Decid WL = deciduous woodland, Conifer WL = coniferous woodland, Mixed WL = mixed woodland, Woodl NS = woodland (not specified/other).

Habitat	Wet land	Heath / Moor	Grass-land	Decid WL	Conifer WL	Mixed WL	Woodl NS	Rock	Exca-vation	Waste	Various
Records (Actual)	4	7	1	31	2	9	6	10	3	1	1

It will be noted that woodland of various types has been the habitat with most records (48) but woodland is a habitat that is probably the one most frequently sampled by recorders.

Distribution in Europe and elsewhere

Latzel (1880) refers to 125 adults with other stages all collected in Bohemia, Moravia and Silesia. According to Porath, he says, the animal, which inhabits the highest points and the gorges of the Sudeten and Reisingebirge Mountains, is common in Sweden, while it had not yet been found in the Alpine region. He also notes that L. Koch had said that it especially loved moorland/peat soil and was often found in quite wet sphagnum. Porath (von Porat, 1889) described *L. curtipes* as among the most common species in central Sweden; otherwise found in the Scandinavian peninsula as far north as the Varangerfjord, as far west as Kristiana (Oslo), and as far south as northern Skane. He also lists Belgium, Bavaria, Silesia and Austria. However, Würmli (1972a) in his account of Middle European and South Italian cryptozoic macro-arthropods does not refer to *L. curtipes* at all.

Zapparoli (2009) shows a distribution map by country of its European occurrence from France to South European Russia although this does not include its currently known occurrence in North European Russia, Latvia, Lithuania, Austria or Slovenia. Chilobase (Bonato *et al.*, 2016) currently lists *L. curtipes* from within Europe as from Austria; Belgium; Czech Republic; Denmark; France; Germany; Great Britain; Hungary; Lithuania; Netherlands; Norway; Poland; Romania; Slovakia; Sweden; Switzerland and Ukraine. It is also reported from Slovenia (Kos, 2001), Latvia and Belarus (Maksimova, 2014; Tuf *et al.*, 2015), Estonia (Sammet *et al.*, 2018), Finland, Moldova, Bulgaria, Luxembourg, Georgia, Armenia, Azerbaijan, European Russia as far east as the Caucasus, the Russian Caucasian Republics and the Urals, western and eastern Siberia, the Near East (Egypt, Israel, Jordan, Lebanon, Syria, Turkey) and the Arabian Peninsula (Nefedief *et al.*, 2016) and Kazakhstan (Bragina *et al.*, 2020). There are no records of it from Ireland or Iceland and I have been unable to locate any relevant papers referring to the Kalinigrad Oblast (Russia) but it would be reasonable to assume that *L. curtipes* would be found there in suitable locations as it is in the adjacent states of Poland and Lithuania. The furthestmost east records seem to be from Mongolia (Doboruka, 1960; Loksa, 1978; Poloczek *et al.*, 2016).

Lithobius curtipes has been variously referred to as mainly a central and East European species (Sammet *et al.*, 2018), a Trans-Palaeartic polyzonal species (Bragina *et al.*, 2020), Centralasiatic-European (Zapparoli, 1999, Stoev, 2002) and a polyzonal eurytopic (Zenkova, (2016).

Northern Europe

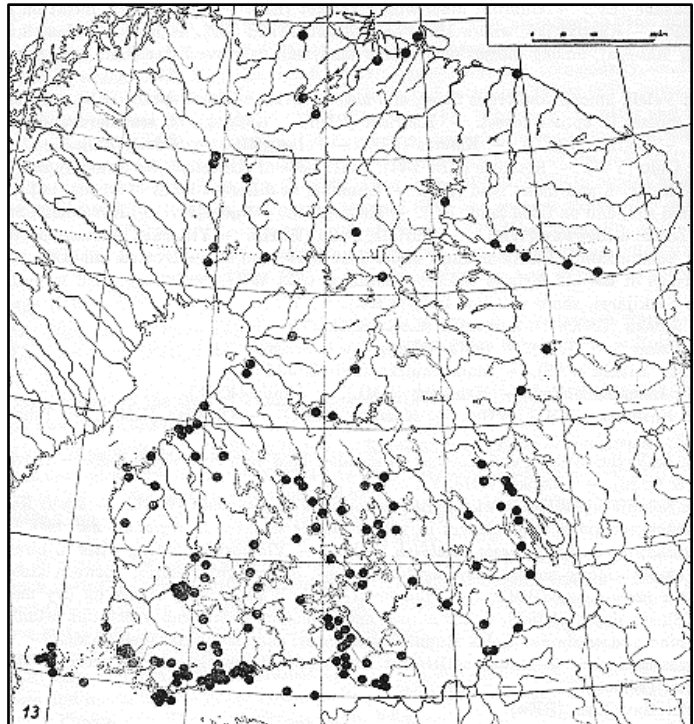
Lithobius curtipes appears to be relatively limited in its occurrence in NW Europe. In France, it has been recorded from only seven départements, mostly in the northern half of the country and, of these, only three are post-1980 records. It is described from there as a species “sténoèce très hygrophile” (Iorio, 2014). In Belgium, where it occurs in humid to very humid woodland and peat swamps, it is noted as a fairly rare species although the map shows records from most provinces (Lock, 2000) but it was not recorded from the forests of Flanders (Lock *et al.*, 2001) or the inland dunes of East Flanders (Lock & Dekoninck, 2001). In the Netherlands, according to the distribution map, most records seem to be from mid and eastern areas and it is recorded from 7 out of 12



Map 2: Distribution of *L. curtipes* in Europe by country (Britain and France only are shown with a regional pattern)

provinces (Berg *et al.*, 2008). For the Grand Duchy of Luxembourg, Remy & Hoffmann (1959) had described *L. curtipes* as “parait être rare”, only knowing it from two localities and Spelda (2001) did not record it from the mountainous, sandy woodland Muellertal region. In Denmark it has been recorded from six out of eight provinces but, seemingly, from only two of these post-1949 (Andersson *et al.*, 2008). On the map of Andersson *et al.* (2005) it is shown as on the western part of the Danish mainland plus one outlier, much as in the more detailed map of Enghoff (1983) where that author’s map also shows *Lithobius borealis* Meinert as present in the east by contrast. In the northern part of Sweden (Norrland) it is described as the most common *Lithobius* in all provinces, a woodland and inland species and significantly more common in localities with no human influence (Andersson, 1985).

In his classic study of the centipedes of Eastern Fennoscandia, Palmen (1949) had more than 130 mapped records of *L. curtipes* from right across Finland and adjacent areas of Russia including the Kola Peninsula (Map 3). He remarked that, among northern chilopods, *L. curtipes* was least restricted in its choice of habitats. It was very abundant in the luxuriant groves occurring occasionally in southern Finland but also seemed to be rather abundant in the subalpine and alpine regions of the fjelds in the northernmost parts of Eastern Fennoscandia and clearly it could survive a great climatic range. It was a very characteristic species of almost all woodland types and, although pine heaths had only scattered populations, on moist land and in groves it was an almost regular inhabitant. It also occurred on various types of bogs, especially on wet pine peatmoors. It occurred in the moss and lichen cover of rocks where they were surrounded by forest vegetation, in decaying wood, at shore localities where there is a well-developed layer of drift or wrack, and when overlying loose stones cover the soil surface. It seemed not to be favoured by cultivation or to occur in greenhouses.



Map 3: Palmen’s records of *L. curtipes* in Eastern Fennoscandia, 1948 (Finland & NW Russia)
(from Palmen. 1949)

Zalesskaja (1978) in her account of the Lithobiomorpha of the, then, USSR had written about *L. curtipes* (as *Monotarsobius curtipes*) and listed a number of localities although, she did not include a distribution map. Zalesskaja & Golovatch (1996) note the species as Palearctic and occurring from the tundra to the mountainous lands south of the Russian Plain.

Germany

Schubart (1964) listed the species as an eastern one that penetrated to France as far as the Seine and in North Germany, but from Hanover and Schleswig-Holstein not reported. He described it as missing in Mid and South Germany with the exception of a relict occurrence at Badener Höhe. The first published records from NW Germany appear to be those of Jeekel (1964) where he records it from two locations in 1932 & 1935.

Verhoeff (1925, cited by Vossel & Aßmann, 1995) had said that the main occurrence was moist or even boggy forests and these authors, noting Jeekel’s reference to its hygrophilia, commented that perhaps in the NW German lowlands it was a typical species of oak-hornbeam forests whilst in the German

Mittelgebirge (mid-range mountains/upland) it is a widespread and common species of different types of forest. In this 1995 study they looked at areas of wood pasture and planted oak-hornbeam forest in SW Lower Saxony, recording it from the former and describing it as a relic species of ancient woodlands in the lowlands of NW Germany.

Albert (1976) investigating at a 150 year-old woodrush/beechness woodland at Solling (NW of Göttingen) calculated the mean annual abundance of *L. curtipes* there as 32 individuals m⁻² and noted a generally inverse relationship between biomass of this species and that of spiders. Other German locations for the species include forest nature reserves, sampled by a combination of pitfall traps and litter samples, in Hessen (Central Germany) where 11 species of *Lithobius* were recorded (Spelda, 1999a), Oberreichenbach, Landkreis Calw, Baden-Württemberg, (Spelda, 1993) and the Brocken area (Voigtländer, 1999). In the latter, the author comments that *L. curtipes* prefers deciduous and coniferous forests, but is also found in open sandy and meadow areas, as well as in bogs and that, according to laboratory experiments (Rossolino & Rybakov, 1997), *L. curtipes* is a hygro- and thermophilic species.

Jabin *et al.* (2004) investigating the influence of dead wood in a managed oak-beech forest in Rhineland-Palatinate, reported the dominant centipedes as *L. crassipes*, *L. curtipes* and *Lithobius mutabilis* (L. Koch) with geophilomorphs being represented only by *Strigamia acuminata*. Reip & Voigtländer (1996), in their list for Thuringia, listed *L. curtipes* from Thüringer Becken and Thüringer Wald, describing it as having a central Asiatic-European distribution. A study of myriapods in twelve sites in the vicinity of Lebus near Frankfurt/Oder where there were remnants of flood-plain forest (Voigtländer, 2010) showed *L. curtipes* to be present in only two of these. Voigtländer & Lindner (2017) in a nature park in Lower Saxony, from 13 habitat types found *L. curtipes* only in deciduous woodland and alder swamp forest.

Voigtländer (1996) commented that *Lithobius curtipes* is in Germany widely distributed and not uncommon (is widespread and not uncommon in Germany). There are, however a number of reports of collections been made in different parts of Germany where the species was not reported. These include a study in the Bausenbergs and Östlichen Eifel (Becker 1982), a survey of river bank and stream islands in the northern Upper-Rhine using pitfall traps and stem collectors (Decker & Marx, 2017), investigation of ecological differences of SW German lithobiids (Spelda, 1999b) and a combination of pitfall trapping, hand-sorted quadrat samples and ground-photoelectors in beech forest (Stadtwald Ettingen) during 1977 to 1985 (Fründ, 1991). Karin Voigtländer, herself, has published reports on studies, often from Eastern Germany, where *L. curtipes* was apparently not found including effects of pollution on a spruce forest at Dubringer Moor NR (Voigtländer, 1995), dry grassland near Halle (Voigtländer, 1996), North Hesse basalt area (Voigtländer, 1998) and the Leutratl NR near Jena (Voigtländer & Dunger, 1998). In all of these various other species of *Lithobius* were found. Unsurprisingly, given its apparent avoidance of synanthropic sites, *L. curtipes* does not feature in a study of primary colonisation of reclaimed land by Dunger & Voigtländer (1990)

Poland

Jadwiga Kaczmarek in her monograph on Polish centipedes (Kaczmarek, 1979), describes *L. curtipes* as an East European subspecies, known from all over Poland, living in various types of forests, staying in litter and under stones. In a companion volume (Kaczmarek, 1980), of the 25 divisions and sub-subdivisions of the country as mapped, she has definite records of the species from 16.

There have been a number of studies of various habitats in Poland including various types of woodland (including riparian forests), urban greens and forest steppe. A comparison of linden-oak-hornbeam with thermophilous oak forests in the Mazovian Lowland (Wytwer, 1990) found *L. curtipes* in two sites in one of the five former but not at all in the oak-woods. The same author (Wytwer, 1992), looking at

approximately hundred year-old stands in natural sites of fresh pine in three forest complexes in different regions found only four centipede species in all regions, *Lithobius lapidicola*, *L. forficatus*, *L. erythrocephalus* and *L. curtipes* with the latter being found in all stands examined and occurring abundantly in all study sites. *L. curtipes*, when sampled by sieving or soil sampling gave much higher values of dominance structure percentage than from pitfall-trapping whereas *L. mutabilis*, in the two areas where it occurred, showed very much the reverse. Comparing forests in Mazovia and urban greens in Warsaw, by the same author (Wytwer, 1995), dominance structure charts show *L. curtipes* as 14.1% in edaphic communities, the second most abundant centipede, in linden-oak hornbeam forests (*L. mutabilis* was 70.3%), in pine forest 12.2% but not in oak forest. In Puszcza Białowieska in Eastern Poland (Wytwer, 2000) a study of centipede communities in forest habitats (fresh pine, pine-spruce, mixed, lime-oak-hornbeam, ash-alder floodplain, bog alder), the edaphic component of each community was dominated by *L. curtipes* with *L. mutabilis* dominant in the epigeic except in bog alder where *L. curtipes* had that role.

In qualitative and quantitative studies in the Roztocza Upland, Kaczmarek & Leśniewska (1998), found *L. curtipes* to be the second most frequent centipede species, being found in almost all habitats but in a beech forest in the (Carpathian) Magura National Park (Leśniewska & Taborska, 2003), *L. curtipes* appears to be absent. However, this particular paper also tabulates differences between centipede species occurrence in beech woodlands between Wielkopolska, Pieniny, Roztocze and Beskid Niski with total species numbers of 19, 17, 13 and 24 respectively with *L. curtipes* only present in Wielkopolska and Rostocza.

A comparison of four alder stands in wetlands of three national parks in NE Poland, only four species of centipede in total were found and only one, *Lithobius curtipes*, was present in all four, at a density of 3.2 to 28.8 m⁻². (Tajovský & Wytwer, 2009). Comparing this with data obtained on the same type of swampy alder habitat in Slovakia by Guliča (1960, cited by the authors), only one species was common to both (*L. mutabilis*) and *L. curtipes* was replaced there by *Lithobius aeruginosus* L. Koch.

In the Ojców National Park (predominantly beech) *L. curtipes* was recorded from a single specimen in hornbeam forest out of six woodland types (Leśniewska *et al.*, 2011). In 15 sites in the Bielinek reserve on a calcium rich escarpment on the Odra River (Leśniewska & Leśniewski, 2016), 7 species of *Lithobius* were recorded but no *L. curtipes* whereas in a beech forest, in the Buckzyna reserve in Western Poland following wind-damage (Leśniewska & Skwierczyński, 2018), *L. curtipes* was one of the most frequently found centipedes and (with *L. forficatus*) was found in all the sampled sites.

The Baltic Republics

In the Baltic Republics (Lithuania, Latvia and Estonia), *L. curtipes* is widespread. As noted earlier, material in the Natural History Museum contains four specimens from Lithuania (Eason, 1972). Trauberg (1929) recorded it from Latvia, reporting it as often being found unter verwesenden Blättern, Gras, verwesenden Bäumen, z.B. an den Ufern des Flusses (under decomposing leaves, grass and decomposing trees, for example on river-banks).

Tuf *et al.* (2015) in their checklist for Lithuania list 8 sites for *L. curtipes*, some associated with the Curonian Spit, others inland with habitats including old-growth mixed forest, replanted pine plantation, bog, wet forest and hornbeam forest. Sammet *et al.* (2018) map *L. curtipes* as occurring in all areas of Estonia and comment that it is one of the two most common centipede species in different habitats, favouring more fresh habitats than *L. forficatus*.

Belarus

Lithobius curtipes was recorded from Belarus by Zalesskaja (1978) and is listed by Maksimova (2014) who describes it as the most common and numerous species, abundant on the forest floor, in stumps and under the bark of trees. Detected in pines and spruce, birch and black alder.

Austria

Würmli (1972b, cited in Szucsich *et al.*, 2011) had recorded *L. curtipes* at the exit of the Zillertal at Straß-Schlittens, a record that seems to date from Attems' (1949) *Myriopoden der Ostalpen* but, as already indicated, not referred to in Würmli's (1972a) paper on the cryptozoic fauna of Central Europe and South Italy. Neither is it included in Moser's (1999) account of the Innsbruck area, by Koren (1992) in his account of the chilopod fauna of Carinthia and East Tyrol, by Voigtländer *et al.* (1994) from Western Styria or in Zapparolli's (2009) Fauna Europaea. However, Zulka (1991, 1992) studied its biology and life cycle in floodplains of the River Morava near Vienna.

Hungary

Szalay (1940) did not record *L. curtipes* amongst the 11 lithobiids that he listed from the Kőszegi mountains. Loksa (1955a), as previously noted, had described *L. curtipes* under the name *Monotarsobius Baloghi*, remarking of it "Interessant ist sein Vorkommen in Bátorliget, wo er wahrscheinlich den Charakter eines Reliktes hat" (Interesting is its occurrence in Bátorliget, where it probably has the character of a relic). He did not include it in his account of the centipedes and millipedes of the environs of Lake Velence (Loksa, 1955b).

Dányi & Korsós (2002), reporting what they described as only the third Hungarian record of *L. curtipes*, noted that at Szigetköz (NW Hungary) it occurred in 6 sites, in both hard and softwoods, sometimes as a dominant species. It is reported from two Hungarian National Parks, Fertő-Hanság and Aggtelek (Korsós & Dányi, 2002; Novak & Dányi, 2010). In the first of these it was found in small numbers in every locality but in the second from only one site. However, in a survey of the Hungarian "lower mountains" (c400-1,000m asl), Dányi (2006) did not find *L. curtipes* which, he says, occurs more frequently in the plains although, he comments, there is no support in the literature that it avoids mountainous regions anywhere else.

Czech Republic

Already referred to are specimens from what is now the Czech Republic (Eason, 1972) in the Natural History Museum and the report of it from Bohemia and Moravia by Latzel (1880). Referring to the latter, Folkmanova (1928), who had included *L. curtipes* in his monograph, commented that "although this species was found abundantly by Latzel in Bohemia and Moravia, I myself have never found it".

Using pitfall traps, heat extraction, sieving and hand collecting Pavelcová, (2008) in nine types of Carpathian localities recorded a total of 31 species (48% of the Czech centipede fauna) but recorded *L. curtipes* (described as eurytopic) in only two of these. Pižl *et al.* (2013/2014), using pitfall traps, recorded it (amongst 24 centipede species) from one location in ravines in the Bohemian Switzerland National Park (České Svýcarsko).

Tajovský (1998), using a combination of hand-sorting, soil-sampling and pitfall trapping in the Labské Pískovce PLA in north Bohemia, in a variety of habitat types, recorded 23 species of centipede (1,104 individuals) but no *L. curtipes* and Božanič *et al.* (2013) sampling bryophytes in the Litovlvelské Luhy NNR recorded 5 species of *Lithobius* but not *L. curtipes*.

Tuf & Tuřová (2008) in their proposed ecological classification for habitat quality evaluation in the Czech Republic, classify *L. curtipes* as E (eurytopic species), species with widest ecological valence.

Slovakia

There have been several records of *L. curtipes* from Slovakia but, correspondingly, it is not reported in various surveys.

Using a combination of sifting and pitfall traps, Országh & Országhova (1995) monitored the impact of the hydroelectric structures Gabčivikovo on centipedes. Of 28 species, they observed a decline in some

but an increase in the dominance of eurytopic ones such as *L. forficatus* and *L. mutabilis* and the appearance of some not previously found. They found that the community of species of the Danubian floodplain forest represented by *L. curtipes*, *L. crassipes*, *L. aeruginosus* and *Pachymerium ferrugineum* (C.L. Koch) remained preserved and in a study of centipede and millipede communities of hedgerows of upland agricultural landscape in the Carpathians, Stašiov *et al.* (2017) recorded *L. curtipes* from two locations only (total 3 specimens) compared with *L. mutabilis* in all 20 sites.

Several studies of oak-hornbeam forest in Slovakia (Holecová *et al.*, 2005; Holecova *et al.*, 2012; Országh & Országhová, 2005) or in the Boky National Nature Reserve, also oak-hornbeam (Stašiov *et al.*, 2012) did not record *L. curtipes* and it was also not recorded in sub-mountain beech by Stašiov & Svitok (2014). This is despite the fact that Országh & Országhová (2005) had recorded 17 other species of *Lithobius* in the Malé Karpaty Mts and Trnavská Pahorkatina Hills and Stašiov & Svitok (2014) 13 in the Kremnickévrchy Mts.

Romania

There has been some lack of clarity about the status of *L. curtipes* in Romania. Matic (1966) described *L. curtipes* as a montane species, usually found at heights between 1,500-2,000m but Negrea (2006) commented that in Romania it was very rare (only in the reported sites and only a single male). As Dányi (2008) points out, *Lithobius (Monotarsobius) baloghi* Loksa, 1947, from a few locations, as included in Matic's account and mapped from five locations there, is a junior synonym of *L. curtipes* whilst Matic's drawings of *L. curtipes* (his Fig.86) show clearly the characters of *Lithobius ferganensis*.

Bulgaria

Kaczmarek (1975), in her account of lithobiid centipedes of Bulgaria, did not include *L. curtipes* amongst the species of *Monotarsobius* she referred to although *L. aeruginosus* and *L. crassipes* are both there. However, in Stoev's (1997) checklist of the centipedes of the Balkan peninsula, the only country of that region of Europe for which *L. curtipes* is listed is Bulgaria and in his account of Bulgarian species (Stoev, 2002), it is described as occurring at 400-700m in the East Stara Planina and the Sredna Gora Mountains. It is not recorded in the survey of the Rila or Central Balkan National Parks (Deltshev *et al.*, 1999a; b) nor that of the Myriapoda of Shumen City and Shumen Plateau (Bachvarova, 2011).

Slovenia

Kos (1988) did not include *L. curtipes* in his account of the Lithobiomorpha of Slovenia nor was it listed in his review of the centipedes of the then Yugoslavia (Kos, 1992) as being present in Slovenia, Croatia, Bosnia-Herzegovina, Montenegro, Serbia or Macedonia.

According to Kos (2001), in Slovenia the species has been preserved in relict populations and is known from three locations. It is not listed in a study of centipede diversity in different developmental phases of a beech forest near Ljubljana (Grgič & Kos, 2003).

Europe: far north

The occurrence of *L. curtipes* in the far north of Europe is notable, being found right up to the northern coastline of Norway (Finnmark) beyond the Arctic Circle (66° 34' N) with a record from Berlevåg at 70° 52' N (Andersson *et al.*, 2005, Bergersen *et al.*, 2006. Interestingly, its occurrence in that country, apart from Oslo and a few other records, is restricted to the northern part of Finnmark whereas it is common in both Sweden and Finland. The only other European centipedes extending regularly this far north are *Geophilus proximus* C.L. Koch and *Pachymerium ferrugineum*. These same three species extend across the Kola Peninsula and around the White Sea Area (Palmen, 1949, A. Przhiboro *pers. comm.*, I. Zenkova, *pers. comm.*). Zenkova (2016) described *L. curtipes* as a "polyzonal eurytopic" species on the Kola Peninsula; by comparison she cites but a single record of *L. forficatus* from taiga on the continental part of that area.

Korobushkin *et al.* (2016), citing Zalesskaja (1978), describe *L. curtipes* as the most common and abundant centipede species in the European part of Russia. According to Zenkova (2016) records from Vaygach (Вайра́ч) Island in the Arctic Ocean (69-70°N) and those from Finnmark are the northernmost records for centipedes. *L. curtipes* is the only species of myriapod found in arctic Finnish Lapland (69°45'N) where it inhabits birch forest-tundra 70km from the Arctic Ocean with an average annual temperature of +2.5° and the lowest recorded by local weather stations at -48°. It is widespread in natural and anthropogenic ecosystems on the Kola peninsula up to tundra ecosystems along the coast of the Barents Sea. On the Hibiny Mounts, in high mountain rocky desert with fragmentary moss and lichen cover at more than 1,000m asl the density is higher than in most lowland ecosystems. Here air temperatures above 0 °C are recorded on less than 40 days a year.

Zenkova & Petrashova (2008) studied the population structure and dynamics of *L. curtipes* in the Murmansk Oblast where it was dominant of the soil macrofauna; it completes several developmental stages within the short growing season and has a long development involving several overwinterings. Kolesnikova & Konakova (2021) from the Komi Republic (N European Russia) recorded *L. curtipes* as dominant in pine whilst Taskaeva *et al.* (2020) in mixed grass communities near hydrogen sulphide springs in the Adak Nature Reserve (Komi Republic) listed a single species of centipede, *L. curtipes*, which they record from four out of five sampling sites.

The Urals

Including the Cis- and Trans-Urals, *L. curtipes* is the only centipede common in all mountain provinces of the Urals up to the Polar Ural and it also occurs in the arctic tundra (Farzalieva & Esyunin, 2008, 2010, Konakova *et al.*, 2017, Zenkova, 2016). Farzalieva & Esyunin (2010) report on population structure of lithobiomorphs, notably *L. curtipes*, in Trans-Ural forest steppe where the population in forests was an order of magnitude higher than in the steppe and, in these, in birch-aspen groves, a mosaic distribution was demonstrated.

A situation where mountain density of centipedes is higher than the plains has also been reported for the Northern Urals (Farzalieva & Esyunin, 2008). From the Kozhym river basin in the sub-polar Urals (Konakova *et al.*, 2017) only two lithobiids are listed with *L. curtipes* recorded from mountain forests, larch forest, stunted birch, mountain tundra and other biotopes (coastal, sub-tundra meadows) whereas *L. crassipes* is reported at much lower levels and only from the mountain forest and the “other biotope” categories. Habitats for *L. curtipes* include elfin woodland, low-bush tundra, birch with grass, spruce-pine forest, alpine meadow, mountain tundra, dark coniferous mountain taiga, etc. In the Southern Urals it is reported from oak-lime, pine, and birch forest, birch wood-meadow, oak, birch and birch-oak forests, rocky steppe, birch forest with poplar, chalky plateau, deserted village, etc. The centipede fauna of the Urals and Cis-Ural area comprised 11 species in 4 genera, the number of species being 5-7 in all zones from steppe to southern taiga. Only *L. curtipes* reached to the forest-tundra and tundra. This compared with more than 50 species in the Caucasus and 48 in the Russian Plain.

A study of soil macroinvertebrates along a contamination gradient in the Central Urals (Vorobeichik *et al.*, 2022) recorded *L. curtipes*, along with *Arctogeophilus macrocephalus* (Folkmanova & Dobroruka) and *Polyzonium germanicum* Brandt as the dominant myriapod species; numbers declined as the smelter (copper) was approached but with centipedes common even in the heavily contaminated area.

Southern European Russia

In Southern European Russia, in the region of Rostov-on-Don, a region with considerable anthropogenic transformations, there had been several previous records of centipedes before the more recent ones of Zuev & Evsyukov (2016) who reported *L. curtipes* from various habitats including steppe (under stones), river & lake banks and island, plantations, nature park, etc.

There are also records from the Caucasus such as the area of Stavropol which include a number of records from different habitats including various forests (including mountain forest), steppe, pasture, conifer plantations, floodplain forest, a botanical garden and bird & mammal nests (Zuev, 2016). In the Abrau Peninsula, *L. curtipes* is reported only twice by Korobushkin *et al.* (2016), whereas there are 27 records for *L. ferganensis*; *L. curtipes* is described as being found in the upper soil layer (0-10cm) and litter in the Caucasus.

Ukraine

There are records of the species from Ukraine with Kunah (2013) describing *L. curtipes* and *L. forficatus* as the most typical centipede species in the Steppe Upper Dnieper area; Zhukov *et al.* (2018a; b) recorded a relatively low density of $1.52 (\pm 0.54) \text{ m}^{-2}$ in floodplain forest of the Dnipro River where *L. curtipes* and *L. aeruginosus* were found in litter and a beta density of $1.83 (\pm 0.59) \text{ m}^{-2}$ in deciduous woodland in the same river's arena terrace. However, it was not included in the list of 16 lithobiids in the paper by Kos'janenko & Chumak (2008) for primeval beech forests in the Carpathian Biosphere Reserve.

Asian Russia

In recent years there have been a number of publications dealing with aspects of the centipede fauna of various areas of Siberia and many of these (and probably others) include reference to aspects of *L. curtipes* with shorter or longer lists of locations and habitats. What emerges is not only its wide distribution but the wide diversity of habitats that it has been recorded from.

The lowland Altai are a transition zone between the plains of SW Siberia and the mountainous region of Southern Siberia (Nefediev *et al.*, 2018) and *L. curtipes* was recorded here from birch-aspen and bird cherry-birch from hand searching and soil extraction. An earlier paper had reported on the Lake Teletskoye area (434m asl) in the Altai State Biosphere Reserve (Nefediev, Farzalieva & Tuf, 2017) where it was found at a number of locations above 1,800m and in a diversity of habitats with a variety of tree types, pine (*Pinus sylvestris*, *P. sibirica*), larch (*Larix sibirica*), fir (*Abies sibirica*), birch, aspen and alder.

In the Omsk area, a part of the West Siberian Plain, bordering Khazakhstan with marshy taiga in the north, gradually replaced by forested or grassland in the south (Nefediev, Knyazev *et al.*, 2017), *L. curtipes* was found in aspen – birch - dark conifer forest, mixed herbaceous meadow, aspen-birch, flood meadow, edge of dark coniferous forest, pine (*Pinus sylvestris*) – birch, birch-grass and in birch stand. Sergeeva (2013) had previously looked at centipedes in the Irtysh River valley in this same area and reported *L. curtipes* from taiga, folious, meadow, meadow-field, xerophytic, grassy, overflowed meadows and river forests biotopes but not from river water meadows (from which no centipedes were recorded). In the Kemerovo area, also in SW Siberia (Nefediev, Farzalieva, Tuf & Efimov, 2020), a small sample of material yielded *L. curtipes* from mixed forest, lime (*Tilia sibirica*), birch-aspen forest, aspen and birch forests.

Nefediev & Farzalieva (2020) include an additional list of localities and habitats for *L. curtipes*, a map of its distribution and a list of references to other work. They list its known occurrence in Siberia as the Altai and Krasnoyarsk provinces, the Novosibirsk, Omsk, Tyumen and Tomsk and Kemerovo areas, the Khanty-Mansi and Yamalo-Nenets autonomous regions and the Republic of Altai. Reports of surveys where *L. curtipes* was not found include the Khakassia Republic, Central Siberia from a small sample taken there (Nefediev *et al.*, 2021)

Kazakhstan & Mongolia

Bragina *et al.* (2020) recorded *L. curtipes* from birch forest, in litter, in the Kostanay district in Kazakhstan and also referred to it from steppe landscapes and birch-aspen forest.

As noted, Mongolia seems to represent the furthestmost eastern known records for *L. curtipes*. Doboruka (1960) reported *L. crassipes baloghi* from Ulan Bator (Ulaanbataar), whilst Loksa (1978) recorded it, as *L. baloghi*, from a location north of there at 1,700m and from another site at 1,600m. Poloczek *et al.* (2016) looked at three locations in the Khentey Mountain Range where the vegetation was mostly “light taiga” (mostly *Larix* dominated), with “dark taiga” of shade tolerant trees such as *Pinus sibirica* and *Picea obovata* at higher altitudes and southern slopes having steppe-like vegetation. At one of the sites, Khonin Nuga, at 900-1,600m with light, dark and mixed taiga and riverine forest and the greatest species diversity, they collected 19 specimens of *L. curtipes*, 6% of the total number of centipedes found there.

Turkey (Anatolia)

In his 1990 paper on distribution patterns and taxonomic problems of the centipede fauna of the Anatolian Peninsula, Zapparoli (1990) commented that *L. curtipes* showed a scattered distribution there but that the geographical data was still very incomplete. In a subsequent paper (Zapparoli, 1999) he referred to it in his table as being a Centralasiatic-European chorotype, and recorded it from 5 out of 9 natural regions in Anatolia.

The (sometimes) apparent rarity of *L. curtipes*

As noted, even in countries where *L. curtipes* appears to be widespread, it is not always collected in every apparently favourable habitat/location sampled. There are a number of possible reasons for this, including the fact that rarer species are less likely to turn up in samples than common and abundant ones and that, in any case, there is always a certain element of chance. Andersson (1983) remarked that, in a certain site, if there had been no change in species composition over the period 1970–81, then, using a combination of hand sorting and sieving, on average, 50% of the species in the locality were being found each time. In addition, anyone who has collected myriapods to any extent will be aware of the effect of seasonal changes and present and recent past local weather conditions.

Christian (1998) commented on possible aspects of apparent rarity in zoological and biospeleological records. Such aspects of apparent rareness could include local endemism, patchy distribution of habitat, regional stenotopy, a misleading search image (“suchbild”), inadequate sampling, polymorphism and misidentification, regional stenotopy (regional stenoecy) resulting from a species’ ecological demands and the presence and extension of suitable habitats. A species which inhabits a variety of biotopes in one part of its area may find in another part, tolerable conditions solely in scattered special biotopes. The author observed that increasing stenotopy is typically observed beyond the border of the more or less evenly populated area and in exclaves.

There is always the possibility that, although there has been extensive collecting in an area, the sampling method used is not the best for the species concerned and/or the local conditions or of appropriate microsites or that the population was low such that the likelihood of it being found in small number of samples was correspondingly low. For example, Vaitilingham’s (1960) study gave different results for *L. curtipes* depending on both the sampling technique and the litter type (Table 2) and looking through much of the habitat data listed gives an impression that although *L. curtipes* may be found in pitfall traps, it tends to be a litter animal, most likely to be collected by extraction, hand sorting or sieving. The situation described in Whitley Wood by the Soil Biodiversity Group (SBG) where 126 monthly samples yielded only 5 specimens of the species (Table 3) would suggest that there was clearly a population of the species, however small or dispersed, present throughout the year. Five specimens of *L. curtipes* in 126 months means that, apparently, the chance of finding it at all in any particular month in the area studied would be about 4%, and in any particular sample about 0.26%.

In practice, one of the most commonly used sampling method in the past for work on centipedes has been pitfall trapping. However, Iorio & Petillon (2020), referring to the work of both Gerlach *et al.* (2009) and Tuf (2015) comment that this is not the most reliable method for assessing centipede diversity and numbers of individuals. Gerlach *et al.* on the basis of experimental work with pitfall traps and using various epigeic arthropods (including one centipede species, *Lithobius mutabilis*), concluded that, as a method, it was inappropriate for quantitative investigations of arthropods living at a site.

Thiele (1956, quoted by Albert, 1978), using pitfall traps (Fallenfänge) and quadrat sampling in Burgholz (Wuppertaler Wälden) found examples of *Lithobius piceus* only in the traps, *Lithobius macilentus* L. Koch and *L. dentatus* C.Koch in both and *L. crassipes*, *L. curtipes*, *Lithobius microps* Meinert and *Lithobius tricuspis* Meinert only in the quadrat samples. In a subsequent paper, (Albert, 1982) she used extraction to collect seven species of *Lithobius* (including *L. curtipes*) plus *Lamycetes emarginatus* from Solling (NW of Göttingen) habitats, including both *L. curtipes* and *L. emarginatus* from meadow sites.

Pitfall trapping in selected ecotones in NW Poland by Tracz (2000) captured small numbers of centipedes with *L. curtipes* being found in those including rowan (15) and aspen (1) but not those with beech, broom or pine, a total of only 15 specimens compared with 47 for *L. mutabilis*. Much larger numbers of millipedes were collected e.g. 1,159 for *Julus scandinavicus* Latzel and 840 for *Ommatoiulus sabulosus* Linn.

In Tuf's (2000) study of centipedes in Litovelské Pomoravi (Czech Republic) he found no specimens of *L. curtipes* by pitfall trapping and a small number by soil sampling whilst *L. mutabilis* and *L. forficatus*, for example, were found by both methods. The same author (Tuf, 2015), using soil sampling, pitfall trapping, litter sifting and hand collecting in four localities in the same protected landscape area, assigned centipedes to five groups with *L. curtipes* being in the category "smaller soil lithobiomorphs", collected mostly by extraction and some in pitfall traps whilst *L. mutabilis* and *L. forficatus*, "larger abundant lithobiomorphs", were found by all techniques but more often in pitfall traps.

Fründ (1987) looked at the centipede community in a 140 year old beech forest near Würzburg and described *Lithobius lusitanus valesicus* Verhoeff as the most abundant species at the base of beech and oak trees but generally rare in litter whilst *L. crassipes* seemed to be confined to rotting logs (although known to inhabit a wide variety of habitats elsewhere). More than 95% of the centipedes in the litter belonged to the three species *Lithobius mutabilis* L. Koch, *L. curtipes* and *Strigamia acuminata* (Leach). Although *L. mutabilis* was mainly in the upper stratum of the litter and *L. curtipes* in the lower no spatial separation could be concluded as *L. mutabilis* was common in the litter too. Laboratory experiments showed all species having a preference for 100% humidity although a longer survival time in dry air for *L. mutabilis* than *L. curtipes* was recorded. *L. mutabilis*, which the author described as having a greater tendency to change resting places than *L. crassipes*, is also larger, 10-15mm as compared to 6.5-11mm as described by Brolemann (1930) for *L. curtipes*.

Habitats

As can be seen from the various accounts of collections from different areas of Europe and Asia, *L. curtipes* can be found in a wide diversity of habitats from arctic tundra and taiga to various types of coniferous and broad leaved woodland, mixed grass and trees, meadow and in montane situations up to 2,000m but no obvious preferences emerge other than the fact that it can be found in certain situations where few other centipedes survive, notably at high altitudes and in flood plains and associated with this is its tolerance of freezing over winter and its ability to survive immersion.

Floodplains & “wet” habitats

It is notable that there are a number of references in the literature to *L. curtipes* in floodplains and similar areas, including those in Middle Europe. These types of locations are subject to fast changes of flood and drought conditions (Marx *et al.*, 2012) and pose particular problems for survival of terrestrial arthropods. High levels of tolerance are shown by certain millipede species and by the overwintering eggs of *Lamyctes emarginatus*.

In looking at the lithobiomorphs, isopods and millipedes in meadows and forests of the floodplain of the River Morava in Eastern Austria, Zulka (1991, 1992) noted that in non-flooded areas, the widespread *Lithobius forficatus* was found whereas in two flooded forests the species composition was completely different and the main species were *Lamyctes emarginatus* and *L. curtipes*. He studied the life-cycles and submersion tolerance of these two species, animals of similar size but with very different life history strategies, the former with a life cycle of several years and the latter an annual one.

In the floodplain of the Lower Oder Valley, Zerm (1997), using pitfall traps, 7 lithobiomorph species were collected but in the temporarily flooded locations *L. curtipes* was virtually the only lithobiid found and only in small numbers. However *L. fulvicornis* was caught in almost every study site although in higher numbers in the temporarily flooded ones. It seemed most likely that the latter survived the winter and inundation period in the egg stage.

Voigtländer (2005) notes that in Central Europe, *L. curtipes* shows a clear preference for wet and humid habitats with high vegetation cover whilst *L. emarginatus* is an inhabitant of humid to very wet habitats with low vegetation cover, later commenting (Voigtländer, 2011) on *L. curtipes*' occurrence in the litter layer of floodplain forests and its co-existence with *L. emarginatus*., the latter surviving unfavourable seasons in the egg stage. In a later publication, (Voigtländer, 2016) she notes that in recent years, an increasing number of surveys in floodplain forests have yielded a large number of new records of *L. curtipes*.

In the Litovelské Pomoraví Protected Landscape Area (Czech Republic) with floodplain forest, field, fallow, etc., Tuf and Ůzanová (1998), using both pitfall trapping and litter extraction collected a number of specimens of *L. curtipes*, especially from litter with all but one from floodplain. Tuf (2000), used pitfall-trapping and soil sampling looked at centipede communities in three successional stages in floodplain forest in the same PLA. There was a larger number of species and greater abundance in older forest but a higher percentage of lithobiomorphs in the younger area but *L. curtipes* was only found in soil samples and only from the areas of 30 and 80 year-old trees. In a subsequent study, the same author (Tuf, 2003) looked at successional changes over four years following a disastrous summer flood lasting several weeks. He recorded *L. curtipes* by both pitfall trapping (epigeic part of the community) and soil sampling (endogeic) and concluded that the species was dominant in long-term flooded forest whereas in forest with regular brief flooding, *L. mutabilis* had that role. Tajovský (1999) had described *L. curtipes* and *L. emarginatus* as characteristically present in the fauna of the most flooded forests in a study of seven of these in the Dyje River alluvium.

Tufová & Tuf (2005, citing other authorities), note *L. curtipes* as dominant in a softwood floodplain in Litovelské Pomoraví and in forests exposed to long lasting inundation near the confluence of the Rivers Morava and Dyje and typical of floodplain forests along the middle stretch of the Danube as well as of non-forested Central European floodplain areas. However, Grinvald (2011), using pitfall traps to study myriapods in different forest growths in a fragmented forest environment in the same PLA (87 y-o. oak/elm, 10 y.o. oak, 2 y.o. clear cut with seedlings, 127 y.o. oak/elm floodplain forests and the ecotones between them) failed to record the species although four other *Lithobius* species were recorded.

In Hungary, *L. curtipes*, (as *M. baloghi*), was described as the dominant species amongst the Chilopoda from Ócsa (Kiskunság National Park; swamp forest with ash and alder) (Sallai, 1993a, b). A previous study by the same author (Sallai, 1992) of Nagy-Szénás with grassland, mixed and hornbeam-oak woodland on dolomite near Budapest and using pitfall-trapping had failed to record *L. curtipes*, although finding five other species of *Lithobius*. Novák & Dányi (2010) reported *L. curtipes* from alder forest in the Aggtelek National Park. They note that Spelda (1999c) had found the species characteristically in wet habitats which is supported by their data.

In a comparative study of four alder stands in wetlands of three national parks in NE Poland, only four species of centipede in total were found and only one, *L. curtipes*, was present in all four, at a density of 3.2 to 28.8 m⁻² (Tajovský & Wytwer, 2009). In the Bug River valley in the east of the same country, using pitfall trapping, Leśniewska *et al.* (2015) found that *L. curtipes* was one of the four most common and most numerous species. It was found in five out of seven habitat types with the highest number of specimens in riparian forest. This habitat was dominated (dominance value 87.8%) by *L. curtipes*, a species, according to the authors, that prefers wet and humid habitats with high vegetation.

This occurrence in flooded areas is not confined to Central Europe. In Estonia, Sammet *et al.* (2018) provide a graph showing relative abundances in different types of habitat. In this, carrs & swamp forests and bogs show the highest values followed by mesophilic boreal forests, broad-leaved (nemoral) forests, fens & waterlogged meadows and dry heathland forests. Lowest values are for coastal meadows & alvars (shallow alkaline soils) and arable fields. Ivask *et al.* (2019), reporting on centipedes and millipedes of semi-natural flooded meadows in Matsalu, mapped *L. curtipes* from the area furthest from the sea where floodplain meadow prevailed and not at all from the coastal/floodplain transitional area or locations closest to the sea.

Kolesnikova *et al.* (2016), referring to European NW Russia, comment that river floodplains are “oases of life” in the northern regions due to the warming effect of the river waters giving rise to highly productive meadows and deciduous forests with grassy groundcover. In their study of the Systola River valley in the middle taiga (Komi Republic, White Sea basin), they reported only two species of myriapod, *L. curtipes* and the millipede *Polyzonium germanicum* which have underwater survival times of 126.3 and 688.2 hours respectively (Tufova & Tuf, 2005). The authors comment on the paucity of species compared with alluvial soils in Central Europe.

Not all collections made from “wet” areas in Central Europe necessarily report the presence of *L. curtipes*; one such is that by Decker & Marx (2017) as already referred to, from the floodplain of the Rhine near Ingelheim.

Humidity tolerance & survival under water

Vaitilingham (1960) in looking at humidity tolerances and immersion in water showed that after 72 hours only those specimens of *L. curtipes* at 100% RH all survived with none at all at 50 or 66% RH being still alive after this time. He obtained rather similar results for both *Lithobius crassipes* and *Brachyophilus truncorum* (*Geophilus truncorum* (Bergsö & Meinert)) whereas “*Geophilus carpophagus*” (almost certainly *G. easoni* Arthur *et al.*) had much better survival rates. He commented that the RH of litter was 90-100% and that *L. curtipes*, *L. crassipes* and *G. truncorum* required a saturated atmosphere. Immersed in tap water at 19-21°C, his geophilomorphs (*G. truncorum*, “*G. carpophagus*”) showed much better survival rates than *Lithobius* species (*L. variegatus*, *L. forficatus*, *L. curtipes*, *L. duboscqui* Brolemann = *L. microps*) with the two latter, smaller, species performing better than the two larger ones (which, because of their size, could possibly move relatively quickly out of unfavourable situations). The mean survival time for *L. curtipes* obtained by Vaitilingham according to Tufova & Tuf (2005) was one day at c20°C.

According to Adis & Junk (2002, cited in Leśniewska *et al.*, 2015) *L. curtipes* was found alive after 34 days of inundation. Tufová & Tuf (2005) investigated survival of centipedes, millipedes and woodlice in a young floodplain forest in the Litovel'ské Pomoraví PLA. In water at 10°, 95% O₂, *L. curtipes* had the highest mean survival time of the three centipede species studied (5.3 days) compared with 43.6 hrs for *Lithobius mutabilis* and 23.0 hrs for *Lithobius agilis*. These were lower than the two isopods and a number of the millipedes; In the case of *Polyzoniium germanicum* Brandt the last individual survived 72 days The respective dominance of the three *Lithobius* species in the community concerned were 35.0, 25.0, 25.0% and there was a significant positive correlation between dominance and time of survival. Two specimens of *Lithobius forficatus*, excluded from the statistical test, survived for 32 and 47 hours.

As Zulka *et al.* (1996) pointed out, in neither Vaitilingham's or Tufová & Tuf's' procedures was the water aerated during the course of their experiments.

Altitude

L. curtipes is not listed in Beron's (2007) account of high- altitude Isopoda, Arachnida and Myriapoda in which species of *Lithobius* are listed as up to 5,545m in Nepal and a highest altitude on Earth for myriapods at 5,700m. However, Pavelcová, (2020) reported *L. curtipes* up to 1,994m at in Rozpadliny in the High Tatras, Negrea (2006, citing records from Loksa, 1947) refers to *L. curtipes* (described as *L. baloghi*) from 1,800m at Pitrosu in the Rodna Mountains, Romania and in the Altai Reserve, SW Siberia, Nefediev *et al.* (2017) recorded it at 2,030m in a sparse *Pinus sibirica* stand with *Betula rotundifolia* & *Salix glauca* bushes below scree in litter.

Mikhailov and Moiseev (2017) discuss the response of alpine biota to climate change using evidence from the Polar Urals summits. They report on the dominance structure of arthropods on Slantseveya summit (417m) as in 2008 and 2015 and show that *L. curtipes*, a "dominant" in 2008 no longer has that status in 2015, its place being taken by a mirid bug.

Table 7. Dominance structure of herpetobiotic arthropods on Slantseveya summit at species and family levels. (from Mikhailov and Moiseev, 2017)

	2008		2015	
Dominance class	Species	Family	Species	Family
Eudominant	<i>Chlamydatus opacus</i> <i>Calacanthia trybomi</i>	Miridae Saldidae	<i>Calacanthia trybomi</i>	Saldidae
Dominant	<i>Lithobius curtipes</i>	Lithobiidae	<i>Chlamydatus opacus</i>	Miridae
Subdominant	<i>Carabus truncaticollis</i> <i>Alopecosa hirtipes</i>	Carabidae Lycosidae	<i>Alopecosa hirtipes</i> <i>Pardosa septentrionalis</i> <i>Oedostethus simularius</i>	Lycosidae Lycosidae Elateridae
Number of Species	21		24	

Temperature adaptations

Survival of freezing conditions in animals depends upon one of two mechanisms, either avoiding freezing by supercooling of body fluids or by tolerating extracellular ice. In the latter case, freeze tolerant animals, freezing of extracellular fluids is promoted by protein nucleators and up to 50% or more of body water may be converted into ice (Block, 1990; Storey & Storey, 1996). Berman & Leirikh (2017), looking at cold-hardiness in common soil invertebrates in NE Asia, a region with winter temperatures extreme for the Northern Hemisphere, found that 34 species of insects overwintered in the supercooled state whereby they withstand temperatures of -12 to -35° but 13 other species (insects,

myriapods, slugs, earthworms and an amphipod) spend winter in the frozen state and survive temperatures from -5 to -46°C.

Rybalov *et al.* (2000) who determined thermopreferences of three species of centipede in the Yenisey Region of Siberia found that individuals of *L. curtipes* (the most numerous species) from forest-tundra, had a wide range of temperature preferences from 14 to 25°C, the majority in the range 17 to 22° in summer (mean 18.2°). In the autumn their preferences were similar at 13-25° (majority 16-21°, mean 17.9°). Individuals from taiga populations had preferences of 16 to 26° (July) and 15 to 25° September with, at both times, the most preferred temperature being 16 to 24°. All the species of lithobiomorph examined were frost tolerant and overwintered in the frozen state. The mean supercooling points (freezing points) for *L. curtipes* collected in forest-tundra was -4.5° (July), -3.9° (September) and -3.1° (February); for specimens from middle taiga the values were -4.9°, -3.2° and -3.1°. Because it overwinters in the frozen state, this may explain these very small changes in supercooling ability due to their particular nucleators remaining active all year round. The authors comment that relatively high freezing temperatures are common in animals surviving in sub-zero temperatures with extracellular ice in their bodies.

Urban areas

A fairly consistent pattern runs through records of *L. curtipes* in relation to rural as opposed to urban habitats with the species rarely being recorded from the latter – in other words, a strongly “urban avoider” as suggested by the British data. There are, however, a few papers that seem to specifically refer to *L. curtipes* in urban areas and Zalesskaya & Golovatch (1996) actually describe it, along with *Lithobius forficatus*, as known to very often occur in purely synanthropic habitats with this accounting for [their] vast distribution very recently, during the last few decades/centuries.

Zenkova (2016) refers to the species as being widespread in natural and anthropogenic ecosystems on the Kola peninsula. However, Palmén (1949) referring to Eastern Fennoscandia, had remarked that it seemed not to be favoured by cultivation or to occur in greenhouses. In the Bulgarian catalogue and key (Stoev, 2002) habitats are given as “urban habitats: yard”. It seems that this latter location, which is from Ribarov’s original record reads (in Bulgarian) *under rotten logs in the museum’s yard* and presumably refers to the Regional History Museum of Panagyurishte, a settlement not large, situated at the foot of the mountain so the rural influence is significant (Pavel Stoev, *pers.comm.*).

In the “urban greens” of Warsaw (wooded areas, parks, street lawns) it was not recorded at all by Wytwer (1995, 1996) even in the five wooded areas, from one of which *L. crassipes* was listed. However, in a study on the effect of urbanisation in the Wielkopolska-Kujawy lowlands of western Poland, maximum altitude 200m, most of the area being under cultivation (Leséniewska *et al.*, 2008), *L. curtipes* was found both in Poznań and in one other built-up area as well as in deciduous forest areas. The rural area habitats for it were alder, beech, marshy, oak-hornbeam and oak but not oak-pine. In the city of Poznań it was collected only from wooded areas (Leséniewska, 1996).

In a paper on centipedes of urban areas in SW Siberia (Nefediev *et al.*, 2016) only a relatively few locations and habitats are listed; *Pinus sylvestris*, river bank (*Betula* & *Populus tremula*), river bank (*Betula* – in litter), “Nagornyi Park” (pitfall), “Izumrudnyi” Park (*Acer*, *Populus*), “Tomsknefteknim” (near acetylene plant, *Populus tremula*). All but the last (which is from the Tomsk area) are from Altai Province. A subsequent paper on Lithobiomorpha from anthropogenic habitats of Siberia (Nefediev, Farzalieva & Efimov., 2020) does not include reference to the species.

Habits and origins of the British population of *L. crassipes*

In comparison with many European and Asiatic countries referred to above, Britain, although having mountains up to 1,345m in Scotland lacks mountainous country comparable with that in many other

areas of Europe. It extends to a latitude of more than 60° N (Shetlands) / 58°N (Mainland Britain) and at its southernmost mainland point is only just under 50°N; for comparison, Oslo and St. Petersburg are both just under 60°N and Edinburgh is almost exactly the same latitude as Moscow. However, Britain and Ireland are surrounded by sea which with its moderating effect on climate and its warming by the Gulf Stream / North Atlantic Drift which, together with its weather systems, gives an oceanic climate. Given that *L. curtipes* extends northwards to inside the Arctic Circle around 70°N in both Scandinavia and NW Russia, its absence from Northern Britain, however, is notable.

There are not extensive seasonally flooded river floodplains as in Central Europe and elsewhere although there are areas alongside rivers in various parts of Britain where periodic or occasional flooding occurs and although *Lamyctes emarginatus* is generally considered a species favouring damp habitats (and has been recorded from river gravels in Wales), the sort of pattern described by Zulka (1991,1992) and Voigtländer (2011) has not yet been found in Britain. It will be noted, however, that there are a few British records from what are described as “wet” habitats. In vegetation terms, certainly there are no large areas of taiga or tundra comparable with those of Scandinavia or Russia. Clearly, however, as in the results from North Wales indicate, it can survive in relatively inhospitable upland environments here.

There has been much informal discussion amongst British myriapodologists over the years as to why particular species occur where they do. For any animal species there are a variety of factors that could influence their distribution patterns. Amongst others, these could include (a) lack of barriers (b) climate (c) acceptable habitats (d) competition (e) human activity. Centipedes are more or less generalist carnivores so presumably the presence or absence of possible prey, except in extreme conditions, might not be a major issue in most environments. What is much more likely is the presence of potential competitors, both other species of *Lithobius* or other arthropods in any particular habitat

So why does *L. curtipes*, an animal with a known wide choice of habitats and a high tolerance of extreme conditions, only occur where it does and not in other places? With our present knowledge of its current distribution and ecology in Britain, it is difficult to fit it into the pattern referred to by Christian (1998) since it does seem to occur in a variety of habitats here and does not presently clearly show the stenoecy predicted for a species on the edge of its range.

In mainland Europe, it is seemingly restricted to central and northern areas with apparently no records from southern France, Iberia, Italy, Croatia, Bosnia-Herzegovina, Serbia, Montenegro, Albania, Serbia, North Macedonia or Greece and, although it is recorded from Anatolian Turkey (and the Middle East), there seem to be no records from European Turkey. Its occurrence in Slovenia is described as “relict”, only two locations are noted for Bulgaria and in Romania it is “rare”. There have been a number of records of *L. curtipes* from Slovakia but, correspondingly, it is not reported in various surveys from there. In the Czech Republic, from where it has been found a number of times since its first discovery, there are surveys from possibly suitable sites where it has not been reported. All this suggests that conditions are more favourable to the species as one goes from south to north.

From west to east, it is not known from Ireland, is quite rare in France and its occurrence in Belgium and The Netherlands is patchy as also in Denmark and Norway as already described even though it is present in the north of the latter. Iceland, with its isolated location in relation to the rest of Europe has a very limited myriapod fauna (Andersson *et al.*, 2008) and Ireland has a smaller range of species than Britain, probably reflecting its earlier isolation from mainland Europe. The pattern we see suggest that there could be some factor, possibly climatic limiting the occurrence of *L. curtipes* (or favouring its competitors) in the West European “fringe” as we go from east to west and a similar situation in the south. As noted, its eastward limit extends as far as Mongolia and, again, suggests some limiting factor.

Barber & Jones (1996) reviewed the distribution pattern of British and Irish millipedes and how it might have originated following the last glaciation when, at its maximum, ice-sheets covered much of mainland Britain as far south as South Wales and Norfolk. Even outside the glaciated area, periglacial conditions would have tended to make the range of myriapod species very limited, if at all present. From about 10,000 years BP climatic improvement allowed the spread of forests and presumably with this the northward spread of myriapods from more southern areas, Britain and Ireland being joined to the European Mainland at the time. One might anticipate that *L. curtipes* with its tolerance of arctic conditions and the comparatively low-level of human activity (which the species seems not to favour) would make it one of the front-runners amongst colonisers or re-colonisers as far as our smaller lithobiids were concerned.

The breakdown of the land-bridge between Britain and Ireland could have been the factor that prevented *L. curtipes* (along with some other species such as *Lithobius calcaratus* C.L. Koch) being present there. Subsequently, the loss of the connection between Britain and the mainland would prevent further “natural” spread of species from there into England and beyond. It is clearly possible that colonisation by such a “northern adapted” species could occur in the time period between the retreat of the glaciers and the breakdown of the land connection with *L. curtipes* being able to spread across the island of Britain. What it does not explain is its present absence from most of Scotland (although not Wales) whilst other species of *Lithobius* (including *L. crassipes* and *L. borealis* are present there.

Certainly, once the land connection to the mainland was lost, a significant barrier would exist towards further colonisation unless some form of passive transport across the English Channel (minimum width about 33 km), North Sea or other ocean barrier. There are two categories of modes of transport permitting (non-flying) terrestrial animals to cross such a barrier, those not involving human activity and those in which, in some way, accidentally or deliberately, human activity provides the mechanism.

Non-human transport includes the possibility of transport by, for instance vertebrates, the proverbial “birds’ feet” of Blackburn *et al.* (2002). Certainly, attaching to birds’ feathers (e.g. Anastacio *et al.* (2013) indicates the possibility of this for e.g. aquatic invertebrates – in that case recently hatched crayfish. Possible transport across ocean has been discussed by Barber (2009) in relation to littoral myriapods with reference to zoochory, aerial transport and rafting (hydrochory). Clearly littoral species of centipedes are in by far the most likely habitat to be accidentally transported in plant debris in this latter case but *L. curtipes* certainly does not fit into this category.

Accidental transport by human activity has undoubtedly been going on for thousands of years and introduction of myriapods as well as other animals undoubtedly takes place via such things as building materials, food sources, etc. in which they are accidentally picked up and transported elsewhere. However *L. curtipes*, despite the few references to it having an anthropogenic tendency, comes out from an overwhelming majority of reports both for Britain and elsewhere, as an animal that avoids the effect of human activity. Nevertheless, the possibility exists that postglacial human immigrants into Britain could bring in *L. curtipes* amongst timber, foodplants, etc. on a short sea voyage to a land having a low density of human population and consequential limited impact on it after the retreat of the ice; a land into which the species with its marked tolerances could well spread widely.

There remains another intriguing possibility and that is, that instead of being completely wiped out during the last glaciation, the species, with its marked capacity for survival in arctic conditions, could survive in one or more glacial refugia, perhaps in Wales or SW England and then, with improving climate, spread out across the country. Its apparent absence from the Isle of Wight, Isle of Man and other offshore islands, if this proves to be genuine, could, perhaps, tend to support the idea that we might have here a pre-glacial relict but, as noted, it is an elusive species and might even simply not be being recorded because of low density, habits and the collecting methods used. Conditions at the top of

Snowdonia, where it occurs today though, must be pretty tough and indicate its capacity for survival in Britain in situations very different from lowland deciduous woodland where it is also recorded.

Whatever its origin, it is certainly possible that the range of *L. curtipes* in Britain may have changed since its first post-glacial maximum in response to climate change, competition and/or human activity. The scattered distribution that we see today may be, perhaps, that of a species in decline or, at least, one that is more or less stable following an historical decline.

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