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The Pleistocene Glaciations as One of the Major Factors Having Impact on the Current Range of Occurrence and Species Diversity of Mites from the Suborder Uropodina (Acari: Mesostigmata) in Poland

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Abstract: On the basis of data collected since 1961, the authors of the current article conducted an analysis of the distribution of Uropodina (Acari: Mesostigmata) species in Poland. The areas of occurrence of the species were compared with the range boundaries of the successive Pleistocene glaciations in Poland. The second aim of the study was to establish the importance of the former nunataks (paleonunataks) for the preservation of biodiversity of this group of mites in Poland. The study has revealed that there are six types of distribution of Uropodina species in the area of Poland: (i) species distributed consistently in the whole area of the country, (ii) species having their northern range of occurrence in Poland, (iii) species having their north-western range of occurrence, (iv) species having their north-eastern range of occurrence, (v) species of boreal-mountainous distribution with evident disjunction in central Poland, and (vi) Carpathian species migrating northwards along the Vistula River. The analyses of the species composition of Uropodina communities on nunataks shows that the concave nunatak in Jura Krakowsko-Czestochowska, described in the literature as the "Jurassic Inland Oasis", turned out to be the location with the highest Uropodina diversity, whereas on the nunatak of the Ślęża Massif, which was covered by two glaciations, the Uropodina diversity was the lowest.

Keywords: biodiversity; geographical parthenogenesis; glaciations; range of occurrence; refuge; zoogeography

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1. Introduction

Poland is an excellent testing ground for research into the distribution of invertebrates. The area of Poland was covered by the ice sheet several times (Figure 1). The glaciers retreated in different periods in different parts of the country, and some areas were covered by the ice sheet several times. The oldest of the glaciations, which took place roughly 800,000 or 600,000 years ago, is called the Podlaskie (or Günz) glaciation, and it affected north-eastern Poland and some parts of Pobrzeże Szczecińskie (Figure 1, (1)). During the second glaciation—the South-Polish glaciation (Mindel)—the ice sheet reached the northern slopes of the Carpathians and Sudetes at an altitude of about 400 m above sea level (Figure 1, (2)). The next glaciation, the Middle-Polish glaciation (Riss), covered central Poland, and the ice sheet again reached the Sudetes and the northern areas of Małopolska and the Lublin Uplands, covering the Racibórz Basin and most of the Silesian Uplands and the Nida Basin. During this glaciation, the Ślęża Massif once again became a nunatak (Figure 1, (3 and A)). During the fourth glaciation—the North-Polish glaciation (Würm)—the ice sheet covered the area of Poland northwards from Zielona Góra, Konin, Augustów

(Figure 1, (4)). The southern part of Poland (along the cities of Kraków, Przemyśl) was never covered by the glaciers, and therefore it remained a kind of refuge, whence the soil mesofauna spread northwards as the glacier receded (Figure 1 (D)) [1–6].

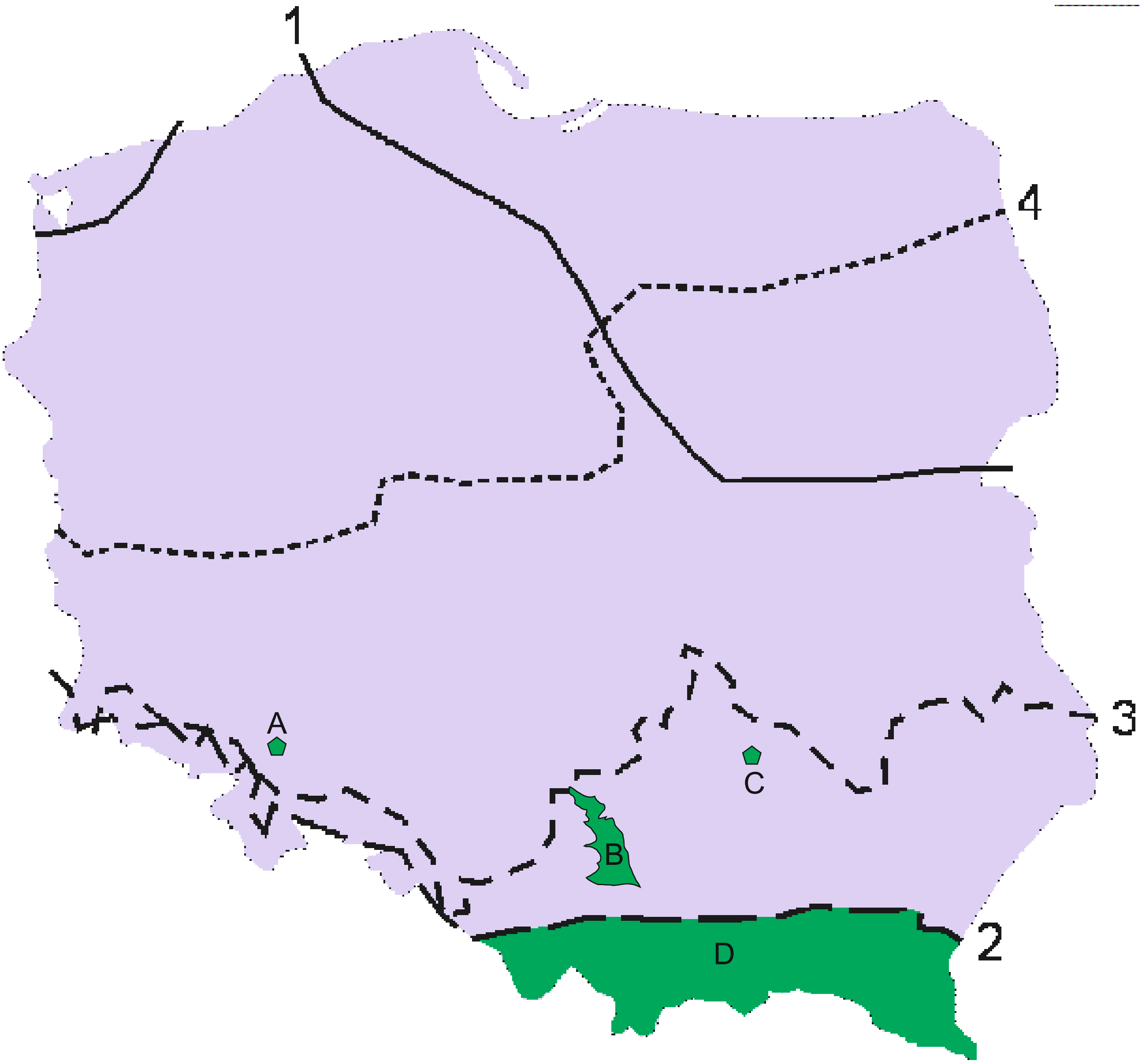

Figure 1. Maximum ranges of glaciations in Poland: 1—Podlaskie glaciation (Günz), 2—South-Polish glaciation (Mindel), 3—Middle Polish glaciation (Riss), 4—North-Polish glaciation (Würm) [1]. The green colour was used to mark areas never affected by the glacier: A—nunatak Ślęża Massif, B—"Jurassic Inland Oasis", i.e., concave nunatak, C—Świętokrzyskie Mountains nunatak, D—area not affected by glaciations in Poland along the cities of Kraków and Przemyśl.

Any research into the geographical range of occurrence of soil mesofauna species, especially mites (Acari), is very difficult from the methodological point of view. Mites are tiny arachnids that are usually less than 1 mm in size and are very common [7], but it is very hard to observe them in the field. The only effective method of ascertaining their ranges of occurrence is to analyse the content of soil samples from different locations and determine the most distant sites where the species occurs. However, this method also has some drawbacks, and its effectiveness depends on the number of collected samples and their density. In many cases, especially for older surveys, the location of the sampling site is described in very vague terms (often referring only to a country or a large administrative unit) [8–10]. Another problem is the "spurious endemism" of the species, as has been shown in earlier studies [11]. In such cases, the found species give the impression of being very rare or even endemic, but this is only due to the poor information on their distribution or wrong species designation and not due to their real ranges. Nevertheless, thorough analysis of the data available in publications was, and still is, mostly the only source that allows to determine, with a greater or lesser approximation, the geographical range of a given species.

Uropodina (Acari: Mesostigmata) belong to the group of saprophagous mites, which are best known in terms of their habitat requirements and geographical distribution in Poland [12–15]. The number of species of these mites in Poland varies between 130 and 150 [14,16,17]. Uropodina mites have two strategies of dispersion and reproduction, which are dependent on the type of habitat in which they live. Species which inhabit unstable microhabitats live in populations which consist of specimens of both sexes and reproduce sexually [14,15,18–20]. In this group of species, deutonymphs have developed the ability of passive dispersion by means of phoresy [21–24]. They can be carried by various groups of insects, e.g., by myriapods, as well as by fur mammals and in bird feathers [25–28], whereas the communities inhabiting soil are often dominated by parthenogenetic species, which are characterized by immense reduction of males in their populations. This strategy enables more effective colonisation of new areas [19,29].

However, despite the intensive research and apparently large number of publications focusing on this group, the information on the exact geographical distribution of many species, especially those that are rare, is still fragmentary and obscure. However, in the course of many years of research into Uropodina mites, it has been observed that many Uropodina species have their range of occurrence in Poland, most often the northern or western range [14,15,30]. It has also been observed that the modern range boundaries of some species in this group of mites overlap with the range boundaries of particular glaciations or correlate with the modern range of occurrence of some tree species (e.g., beech *Fagus sylvatica* or spruce *Picea excelsa*). These observations encouraged the authors to analyse these relationships in more detail.

The major aim of this study was to ascertain if and how the Pleistocene glaciations influenced the current ranges of occurrence of Uropodina mites in Poland. The authors of the study have also attempted to establish the importance of the prior nunataks for the preservation of biodiversity of this group of organisms in Poland. The study rests upon the analysis of extensive material from Poland collected since 1961. The article also contains the maps showing the current distribution of species which have their range of occurrence in the area of Poland (Figures 2–7). The analyses were possible due to the collection of precise data on the distribution of the analysed species in the "Invertebrate Fauna Bank" project, conducted for many years [31]. The project assumes collecting soil samples from all over the world and creating a computer database of the specimens from these samples, which provided the basis for the analysis of the spatial distribution of individual taxa of soil fauna.

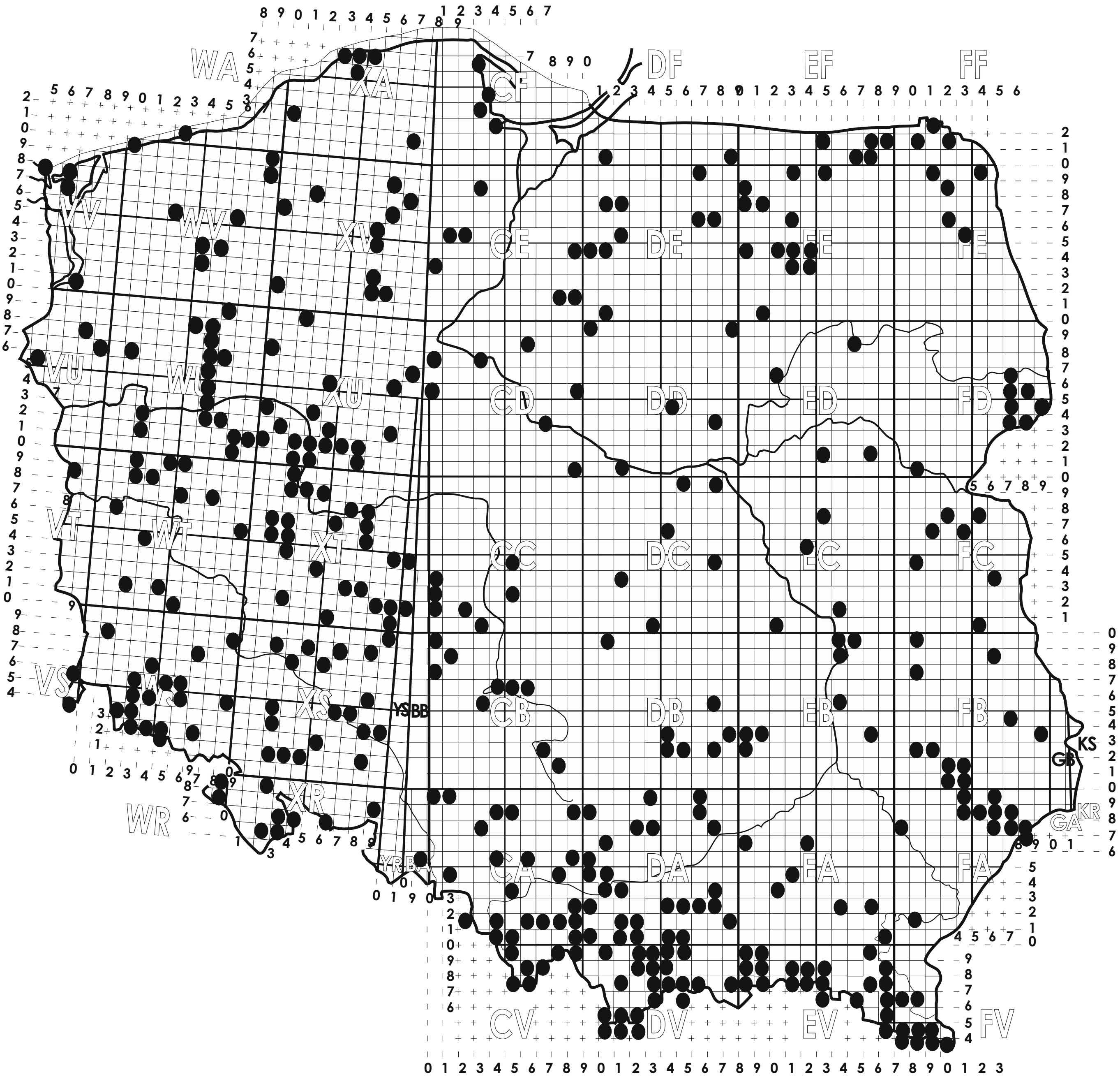

Figure 2. Geographic distribution of *Trachytes aegrota* as an example of a species with even distribution in the whole area of Poland (the black dots mark the locations in which the species was found).

2. Material and Methods

The materials analysed in this study contained over 22,000 samples collected between 1961 and 2022 from different types of habitat and microhabitat, collected in the whole area of Poland. The soil samples were both qualitative and quantitative [32]. They were mainly sieved litter and soil, as well as non-sieved samples from various types of unstable microhabitats (merocenoses) such as dead wood, hollows, anthills, and bird and mammal nests. The samples were extracted with Tullgren funnels, and then the extracted specimens were preserved in 75% ethyl alcohol. The mites were sorted from the samples with a stereoscopic microscope and were then identified after they had been cleared in 80% lactic acid by means of an Olympus BX51. The specimens were identified using the morphological criteria from the original descriptions and later accounts [12,14,18,33,34]. The identification of the species was carried out by the first author.

Each sample was tagged with UTM co-ordinates, which later allowed to ascertain their special localisation. The visualisation (in the form of a map) of the distribution of individual species in the area of Poland was made on the basis of a UTM grid, consisting of squares with sides of 10 × 10 km. The images presented here were all original and generated with Corel Draw 2020 computer graphics software. The community similarity of the species composition for Uropodina mites inhabiting Jura Krakowsko-Częstochowska (the Polish Jurassic Highland), Świętokrzyskie Mountains, and the Ślęża Massif nunataks was calculated by means of the Marczewski–Steinhaus species similarity index: $S = c/(a + b/c)$, where c is the number of species present in both compared communities, whereas a and b stand for the total number of species in each community [35]. The full joining analysis, which uses the most distant neighbours, was used to draw the dendrogram. The analyses were calculated with AnalizaTor 2.0 software (Poznań, Poland).

The following categories of species abundance were discerned for all the analysed samples:

>30,000 specimens—very high abundance
5001–30,000 specimens—high abundance
1001–5000 specimens—moderate abundance
100–1000 specimens—low abundance
<100—recedent

The following categories of frequency of occurrence were also discerned:

>2000 samples—very frequent species
501–2000 samples—frequent species
101–500 samples—rare species
10–100 samples—very rare species
<10—sporadic species

3. Results

3.1. Abundance and Frequency of Uropodina Species in Poland

The tabulation presented below (Table 1) shows 85 species (almost 204,000 specimens) of mites from the suborder Uropodina which were found in the analysed materials, including the information about their abundance and frequency of occurrence in the area of Poland.

Table 1. Abundance and frequency of occurrence of Uropodina species in analysed materials.

Species Name	Number of Specimens	Abundance in Samples	Number of Occurrences in Samples	Frequency in Samples
Trachytes aegrota (C. L. Koch, 1841)	38,396	very high abundance	6630	very frequent
Olodiscus minima (Kramer, 1882)	18,273	high abundance	4896	very frequent
Oodinychus ovalis (C. L. Koch, 1839)	38,538	very high abundance	3127	very frequent
Urodiaspis tecta (Kramer, 1876)	10,843	high abundance	2812	very frequent
Trachytes pauperior (Berlese, 1914)	8588	moderate abundance	2510	very frequent
Oodinychus karawaiewi (Berlese, 1903)	12,684	high abundance	1060	frequent
Dinychus perforatus (Kramer, 1882)	4635	moderate abundance	1041	frequent
Trachytes irenae (Pecina, 1970)	11,709	high abundance	969	frequent
Urodiaspis pannonica (Willmann, 1952)	2163	moderate abundance	861	frequent

Table 1. *Cont.*

Species Name	Number of Specimens	Abundance in Samples	Number of Occurrences in Samples	Frequency in Samples
Pulchellaobovella pulchella (Berlese, 1904)	6044	moderate abundance	449	rare
Polyaspinus cylindricus (Berlese, 1916)	1777	low abundance	401	rare
Cilliba insularis (Willmann, 1938)	1554	low abundance	318	rare
Uroobovella obovata (Canestrini et Berlese, 1884)	1782	low abundance	313	rare
Dinychus carinatus (Berlese, 1903)	2865	moderate abundance	308	rare
Olodiscus misella (Berlese, 1916)	916	low abundance	306	rare
Trichouropoda polytricha (Vitzthum, 1923)	2873	moderate abundance	292	rare
Trachytes lamda (Berlese, 1903)	672	recedent	270	rare
Oodinychus obscurasimilis (Hirschmann et Z.-Nicol, 1961)	1355	low abundance	224	rare
Cilliba rafalskii (Błoszyk Stachowiak et Halliday, 2008)	622	recedent	220	rare
Dinychus arcuatus (Trägårdh, 1922)	777	recedent	207	rare
Trematurella elegans (Kramer, 1882)	4327	moderate abundance	203	rare
Leiodinychus orbicularis (C. L. Koch, 1839)	3024	moderate abundance	190	rare
Uropoda orbicularis (Muller, 1776)	2147	moderate abundance	190	rare
Nenteria breviunguiculata (Willmann, 1949)	1773	low abundance	175	rare
Discourella modesta (Leonardi, 1889)	389	recedent	167	rare
Dinychura cordieri (Berlese, 1916)	542	recedent	150	rare
Dinychus woelkiei (Hirschmann et Zirngiebl-Nicol, 1969)	1269	low abundance	146	rare
Phaulodiaspis rackei (Oudemans, 1912)	1628	low abundance	142	rare
Dinychus inermis (C. L. Koch, 1841)	1034	moderate abundance	139	rare
Uroobovella pyriformis (Berlese, 1920)	4731	moderate abundance	125	rare
Apionoseius infirmus (Berlese, 1887)	1848	low abundance	102	rare
Phaulodiaspis borealis (Sellnick, 1940)	3231	low abundance	101	rare
Trachytes minima (Trägårdh, 1910)	601	recedent	80	very rare
Discourella baloghi (Hirschmann et Z.-Nicol, 1969)	1750	low abundance	72	very rare
Olodiscus kargi (Hirschamann et Z.-Nicol, 1969)	262	recedent	66	very rare
Cilliba erlangensis (Hirschmann et Z.-Nicol, 1969)	225	recedent	44	very rare
Polyaspis patavinus (Berlese, 1881)	689	recedent	44	very rare
Oodinychus spatulifera (Moniez, 1892)	804	recedent	39	very rare
Urodiaspis stammeri (Hirschmann et Z.-Nicol, 1969)	475	recedent	37	very rare
Metagynella paradoxa (Berlese, 1919)	291	recedent	35	very rare
Uropolyaspis hamulifera (Berlese, 1904)	79	recedent	35	very rare
Trichouropoda calcarata (Hirschmann et Z.-Nicol, 1961)	61	recedent	34	very rare
Iphiduropoda penicillata (Hirschmann et Z.-Nicol, 1961)	85	recedent	29	very rare
Polyaspis sansonei Berlese, 1916	259	recedent	29	very rare
Cilliba cassidea (Herman, 1804)	212	recedent	25	very rare
Nenteria stylifera (Berlese, 1904)	61	recedent	22	very rare
Cilliba selnicki (Hirschmann et Z.-Nicol, 1969)	174	recedent	18	very rare

Table 1. *Cont.*

Species Name	Number of Specimens	Abundance in Samples	Number of Occurrences in Samples	Frequency in Samples
Urotrachytes formicarius (Lubbock, 1881)	23	recedent	18	very rare
Trachytes montana (Willmann, 1953)	23	recedent	17	very rare
Oplitis minutissima (Berlese, 1903)	26	recedent	16	very rare
Trachyuropoda coccinea (Michael, 1891)	152	recedent	16	very rare
Uroplitella paradoxa (Canestrini et Berlese, 1884)	26	recedent	16	very rare
Allodinychus flagelliger (Berlese, 1910)	299	recedent	14	very rare
Polyaspinus schweizeri (Hutu, 1976)	43	recedent	14	very rare
Uroobovella marginata (C. L. Koch, 1829)	55	recedent	14	very rare
Uropoda undulata (Hirschmann et Z.-Nicol, 1969)	39	recedent	11	very rare
Uroplitella conspicua (Berlese, 1903)	31	recedent	10	sporadic
Fuscouropoda appendiculata (Berlese, 1910)	22	recedent	9	sporadic
Uroseius hunzikeri (Schweizer, 1922)	23	recedent	9	sporadic
Phaulodiaspis advena (Trägårdh, 1922)	1063	low abundance	6	sporadic
Trachytes splendida (Hutu, 1973)	12	recedent	6	sporadic
Trachyuropoda willmanni (Hirschmann et Z.-Nicol, 1969)	18	recedent	6	sporadic
Trichouropoda sociata (Vitzthum, 1923)	200	recedent	6	sporadic
Trichouropoda patavina (G. Canestrini, 1885)	50	recedent	5	sporadic
Nenteria floralis (Kardg, 1986)	17	recedent	4	sporadic
Trichouropoda tuberosa (Hirschmann et Z.-Nicol, 1961)	14	recedent	4	sporadic
Uroobovella nova (Oudemans, 1902)	6	recedent	4	sporadic
Uroseius geieri (Schweizer, 1961)	6	recedent	4	sporadic
Nenteria pandioni (Wiśniewski et Hirschmann, 1985)	10	recedent	3	sporadic
Trichouropoda structura (Hirschmann et Z.-Nicol, 1961)	5	recedent	3	sporadic
Dinychus septentrionalis (Trägårdh, 1943)	2	recedent	2	sporadic
Oplitis alophora (Berlese, 1903)	8	recedent	2	sporadic
Oplitis franzi (Hirschmann et Zirngiebl-Nicol, 1969)	2	recedent	2	sporadic
Oplitis philocenta (Trouessart, 1902)	1	recedent	1	sporadic
Oplitis schmitzi (Kneissl, 1908)	1	recedent	1	sporadic
Oplitis stammeri (Hirschmann et Zirngiebl-Nicol, 1961)	1	recedent	1	sporadic
Oplitis wasmanni (Kneissl, 1907)	1	recedent	1	sporadic
Protodinychus punctatus (Evans, 1957)	2	recedent	1	sporadic
Trachyuropoda poppi (Hirschmann et Z.-Nicol, 1969)	1	recedent	1	sporadic
Trichouropoda bipilis (Vitzthum 1921)	1	recedent	1	sporadic
Uroobovella baloghi (Hirschmann et Zirngiebl-Nicol, 1962)	2	recedent	1	sporadic
Uroobovella fimicola (Berlese, 1903)	2	recedent	1	sporadic
Uroobovella ipidis (Vitzthum, 1923)	1	recedent	1	sporadic
Uropoda italica (Hirschmann et Z.-Nicol, 1969)	1	recedent	1	sporadic
Total	203,871			

As can be seen, most of the found Uropodina species (79%) were rare, very rare, and sporadic species. Most of them were found in very few locations, which does not allow researchers to ascertain the exact range of geographical occurrence of these species. For this reason, the further analyses presented include only the more common and more abundant species.

3.2. Range of Occurrence of Selected Uropodina Species in Poland

Species such as *Oodinychus ovalis*, *O karawaiewi*, *Trachytes aegrota*, *T. pauperior*, *Olodiscus minima*, *Urodiaspis tecta*, *Pulchellaobovella pulchella*, *Dinychus perforatus*, *D. carinatus*, and *Trematurella elegans* are among those which have even geographical distribution in Poland (Figures 2 and A1). These are usually the most abundant and common species in mite communities (Table 1).

The analysis of the collected materials shows that three species from the genus *Trachytes*, such as *T. irenae*, *T. minima*, and *T. montana* (Figure A1) have their northern range of occurrence in Poland [14,15]. The exact boundary lines of the ranges for these species are presented in Figure 3.

The East Carpathian species, which have the north-western limit of their range in Poland (Figure 4), are an interesting group from the zoogeographical point of view. They occur only in the south-eastern part of the country, in an area that has never been glaciated. These species are *Trachytes splendida*, *Polyaspinus schweizeri*, and *Urodiaspis stammeri*. The western range of the dense occurrence of most of them is at the Ropa River near Uście Gorlickie. On the western bank of the river, the occurrence of these species is sporadic, while in the eastern areas of the river, the species in question are rather frequent.

Such species as *Polyaspinus cylindricus*, *Olodiscus misella*, *Cilliba erlangensis* (Figure 5), *Neodiscopoma splendida* (Figures 6 and A1), and *Oodinychus obscurasimilis* (Figures 7 and A1) have a specific geographical distribution in Poland [14,15]. The first three species are abundant and frequent in southern Poland, and their range of occurrence overlaps with the natural occurrence of the beech (*Fagus sylvaticus*) (Figure 5, (1, 2, 3)). However, in the north-western areas and in the north, the local populations of these species are rare. The range of *N. splendida* is disjunctive (Figure 6). This species is also relatively abundant and frequent in the southern part of the country. It also occurs, albeit less frequently, in the north-eastern parts of Poland.

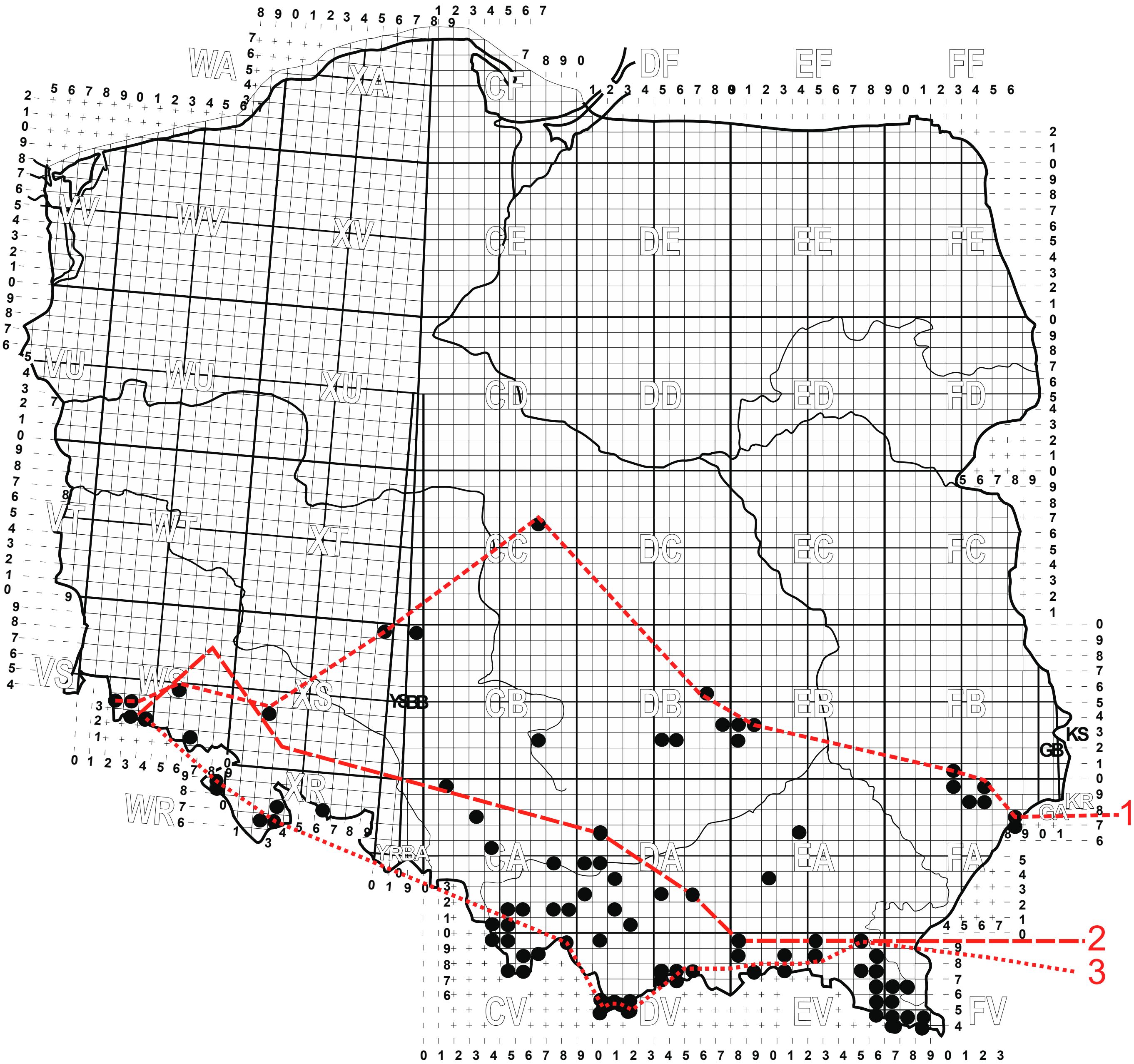

Figure 3. Geographical distribution of species from the genus *Trachytes* which have their northern range of occurrence in Poland: 1—*Trachytes irenae*, 2—*Trachytes minima*, 3—*Trachytes montana*.

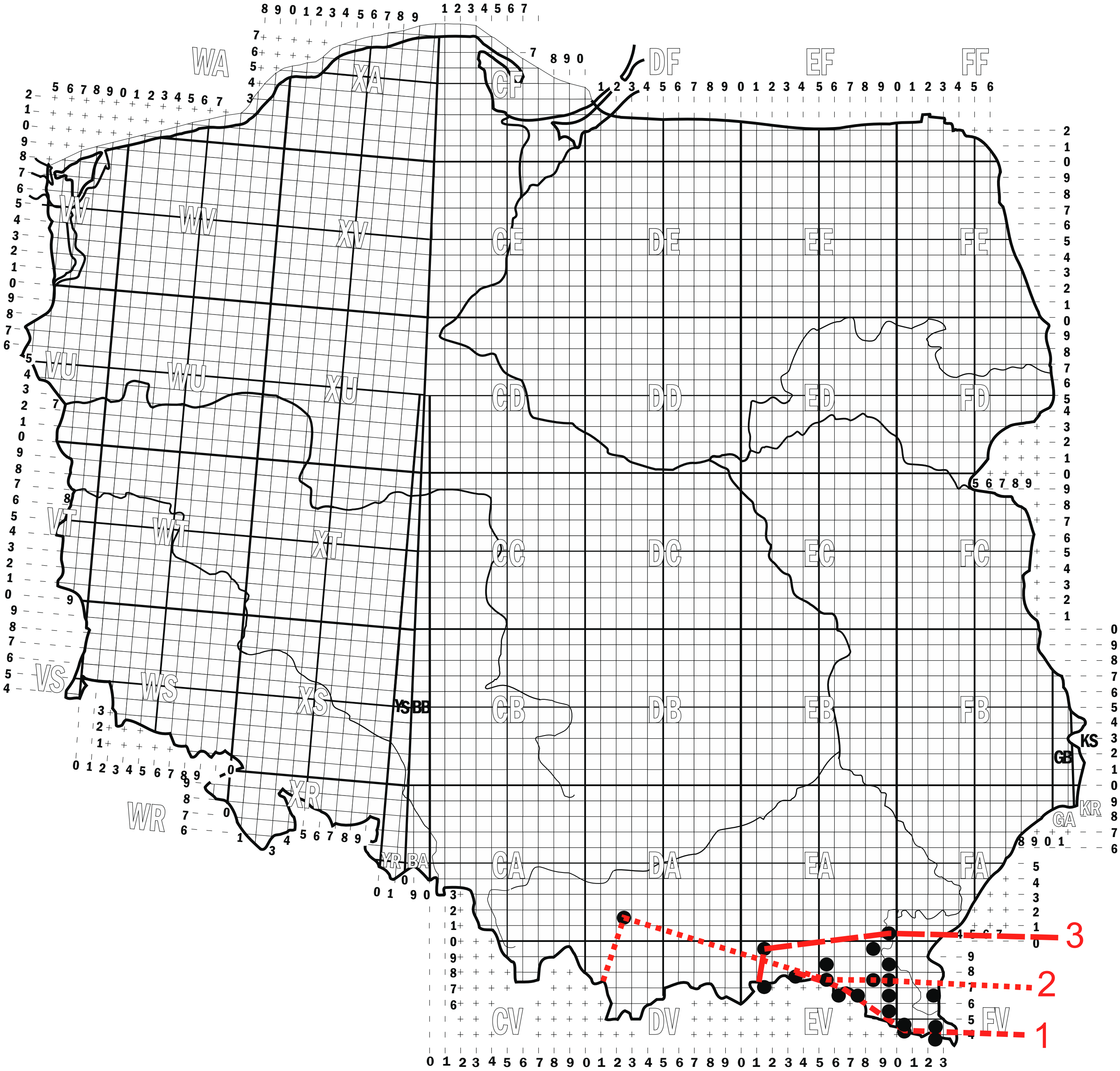

Figure 4. Geographical distribution of species which have their north-western range of occurrence in Poland: 1—*Trachytes splendida*, 2—*Polyaspinus schweizeri*, 3—*Urodiaspis stammeri*.

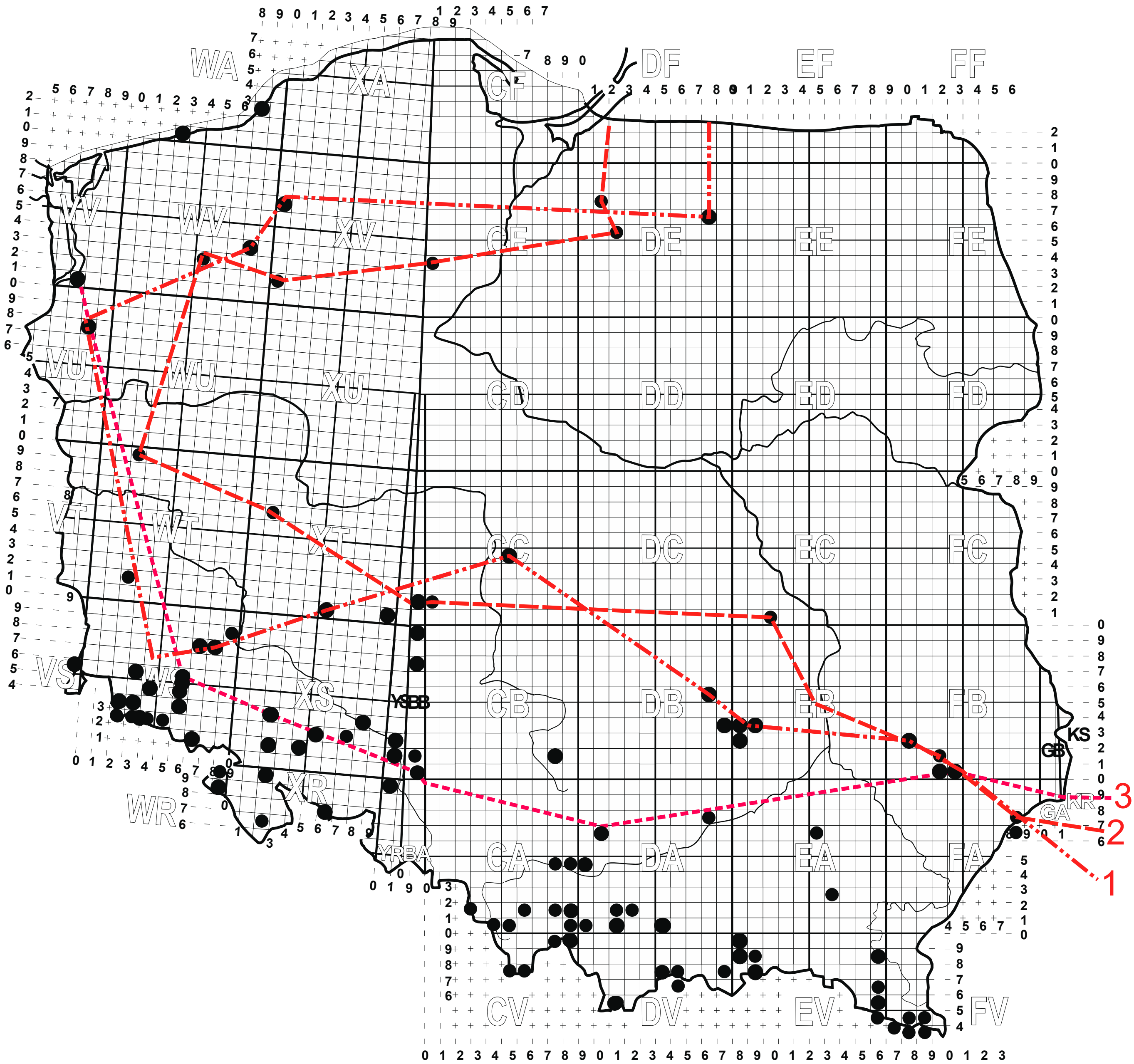

Figure 5. Geographical distribution of species which have their north-eastern range of occurrence in Poland: 1—*Polyaspinus cylindricus*, 2—*Olodiscus misella,* 3—*Cilliba erlangensis*.

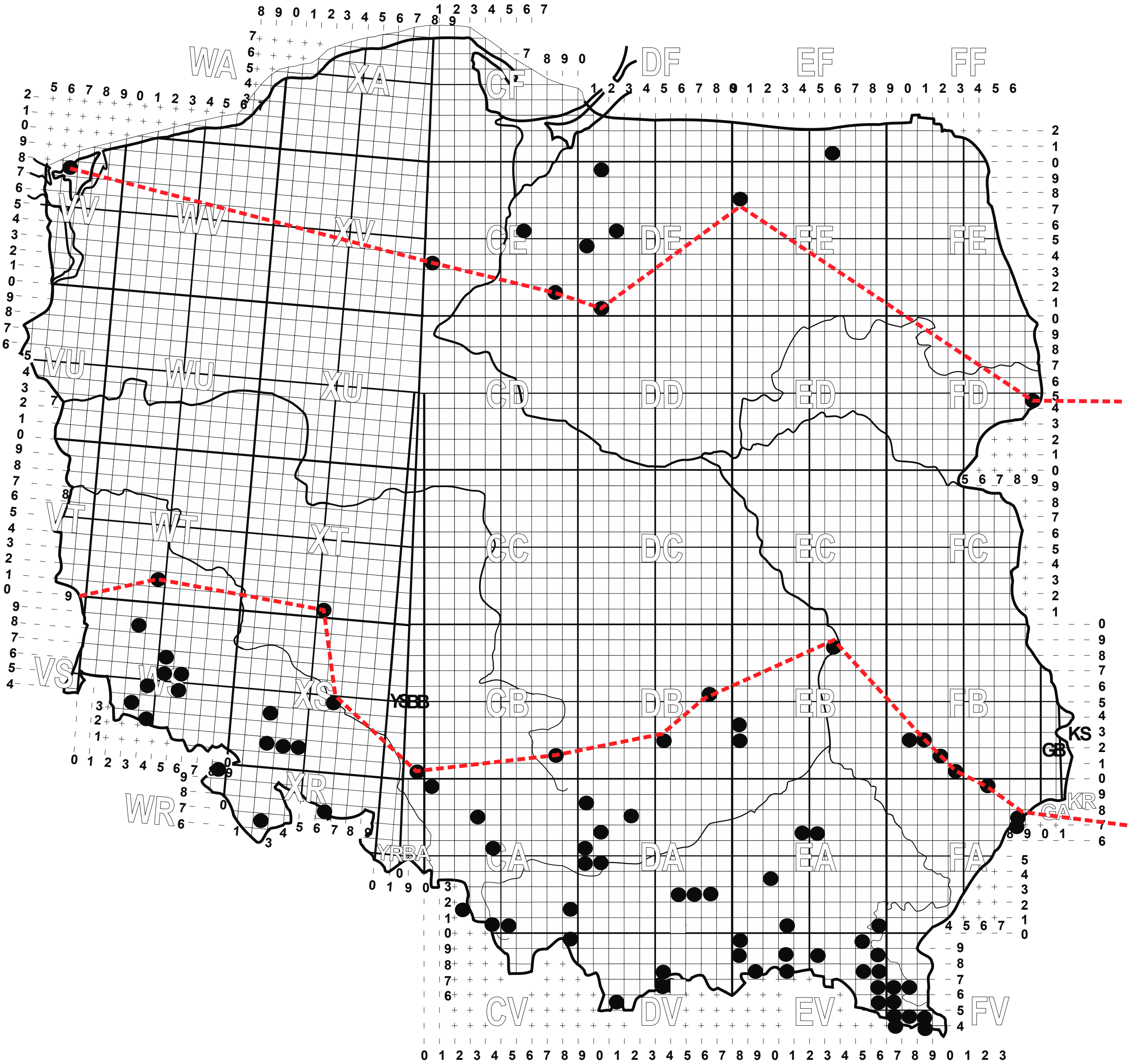

Figure 6. Geographical distribution of *Neodiscopoma splendida*; the red dashed lines mark the boundaries of the southern and northern populations.

However, in the other regions and in central Poland, it has not been found thus far (Figure 6). Meanwhile, *O. obscurasimilis*, which is a Carpathian species, has been extending its range of occurrence northwards along the Vistula river (Figure 7).

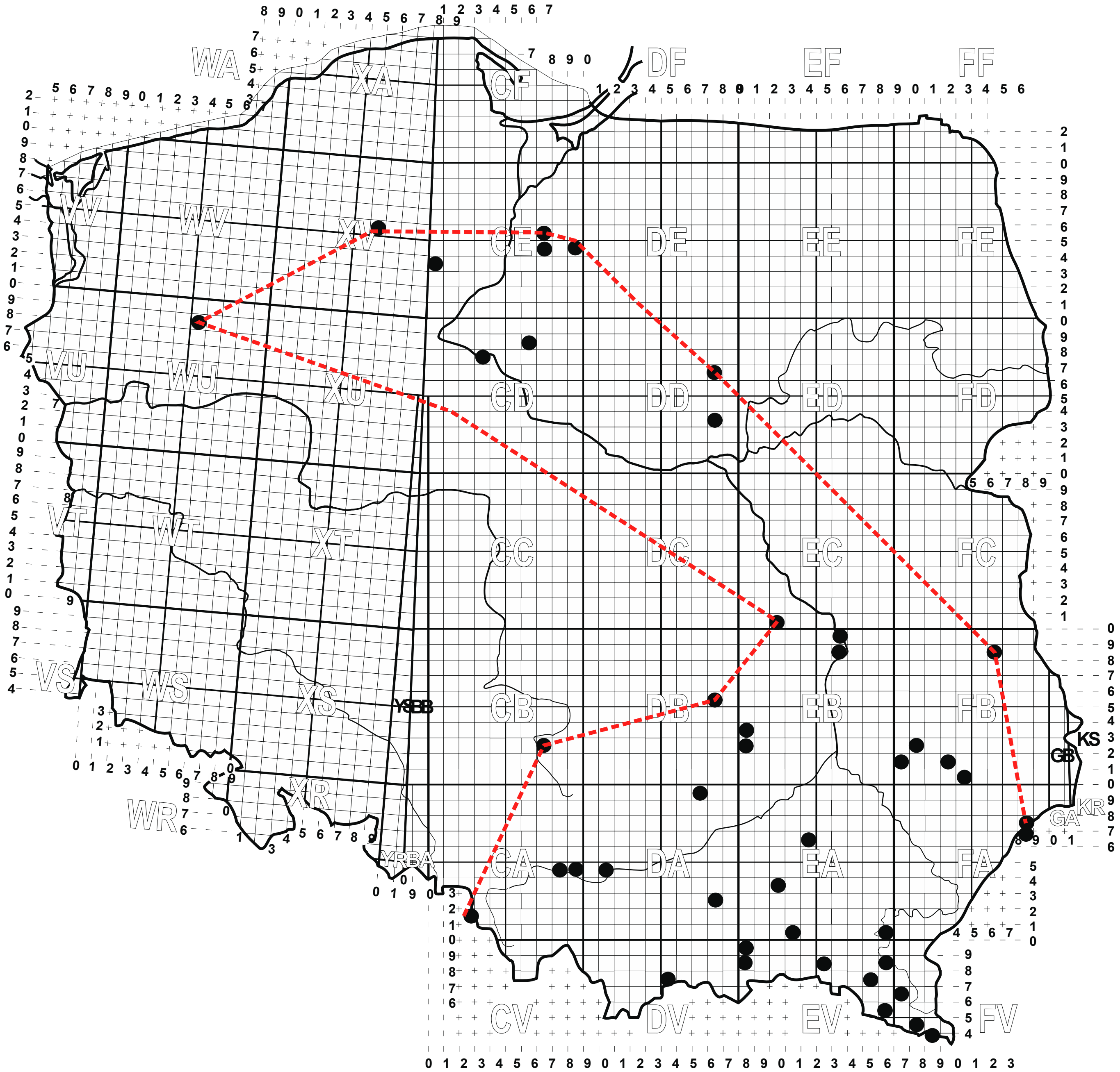

Figure 7. Geographical distribution of sites with *Oodinychus obscurasimilis* in Poland; the red dashed line marks the potential areas of occurrence of the species.

3.3. Fauna of Nunataks in Poland

A nunatak is a rocky hill or peak rising above the surface of the ice sheet, surrounded by an ice sheet [36]. The ice sheet covering the Polish territory had a considerable thickness, and few objects protruded above its surface. The nunatak during the South-Polish glaciation was the Ślęża Mountain (Figure A2), as well as the higher peaks of the Świętokrzyskie Mountains, where frost weathering developed, which in turn produced today's non-forest areas. In 1960, a hypothesis was put forward that during the Cracow (South-Polish) glaciation, a significant area of Jura Krakowsko-Częstochowska (the Polish Jurassic Highland) constituted the "Jurassic Inland Oasis", i.e., the so-called concave nunatak [37]. This hypothesis was also confirmed by the results obtained by Lewandowski [38].

The species diversity of Uropodina communities on the examined nunataks in Poland varies considerably (Table 2). Only 9 species occurred on all three nunataks, and these were *T. aegrota*, *T. irenae*, *D. perforatus*, *Cilliba insularis*, *O. minima*, *N. splendida*, *U. pannonica*, *U. tecta*, and *O. ovalis*. The concave nunatak in Jura Krakowsko-Czestochowska turned out to be the location with the highest diversity, which is another area in Poland that has never been glaciated. So far, 43 species of Uropodina have been found in this area. The lowest species diversity (in terms of the number of species) that has been observed was on the Ślęża Massif in Lower Silesia. Only 11 species from this group of mites have been found there so far. The Świętokrzyskie Mountains had two times more species than the Ślęża Massif, where 22 species of Uropodina have been found. The species composition of Uropodina in the Świętokrzyskie Mountains was more similar to that observed in Jura Krakowsko-Częstochowska, with an index of similarity (S) of 64% (Figure 8).

Table 2. Uropodina species found on nunataks in Poland; MS—Ślęża Massif, GS—Świętokrzyskie Mountains, JKC—Jura Krakowsko-Częstochowska.

Species	MS	GS	JKC
T. aegrota	+	+	+
T. irenae	+	+	+
D. perforatus	+	+	+
C. insularis	+	+	+
N. splendida	+	+	+
O. minima	+	+	+
U. pannonica	+	+	+
U. tecta	+	+	+
O. ovalis	+	+	+
C. erlangensis	+		+
D. cordieri	+		+
P. cylindricus		+	+
T. pauperior		+	+
D. arcuatus		+	+
D. carinatus		+	+
D. modesta		+	+
U.paradoxa		+	+
U. formicarius		+	+
O. kargi		+	+
O. misella		+	+
U. obovata		+	+
P. pulchella		+	+
D. karawaiewi		+	+
D. obscurasimilis		+	+
A. infirmus			+
T. lamda			+
T. minima			+

Table 2. *Cont.*

Species	MS	GS	JKC
P.sansonei			+
D. woelkei			+
O. alophora			+
T. coccinea			+
N. pulherrima			+
U. undulata			+
U. orbicularis			+
U. advena			+
U. rackei			+
U. fracta			+
U. pyriformis			+
T. curtipilis			+
T. penicilata			+
T. polytricha			+
T. sociata			+
T. swietokrzyskii			+
Number of samples	35	42	47
Number of species	11	22	43

+—occurence of the species.

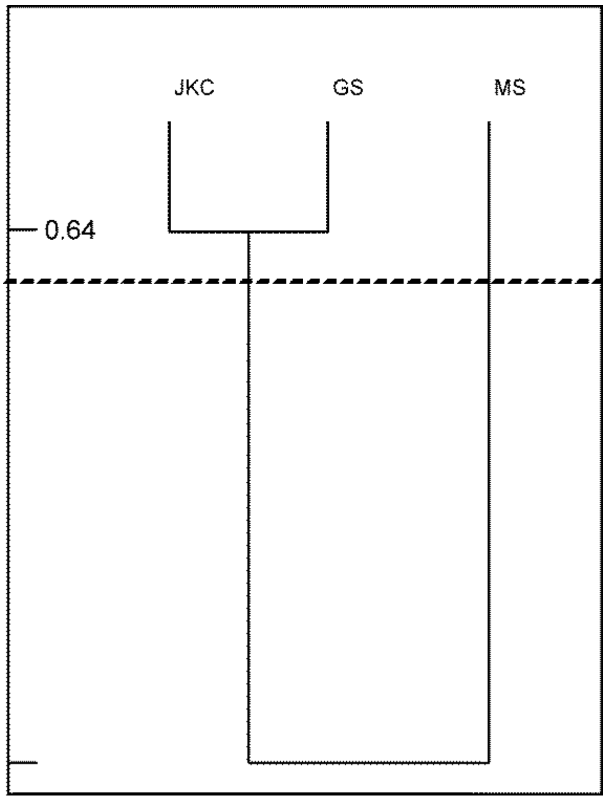

Figure 8. Species similarities of Uropodina communities on nunataks; JKC—Jura Krakowsko-Częstochowska, GS—Świętokrzyskie Mountains, MS—Ślęża Massif.

4. Discussion

Most species of Uropodina occurring in Poland are European species with wide distribution. Some of them occur consistently in the whole area of the country, while the ranges of others are restricted to certain areas only. The first group includes mainly common and numerous soil species (i.e., *O. ovalis*, *O. karawaiewi*, *T. aegrota*, *T. pauperior*, *U. tecta*, *O. minima*, *D. perforatus*) and species commonly found in unstable microhabitats, such as *P. pulchella* and *D. carinatus*. These species, due to their wide range of ecological tolerance (eurytopic species), have the best ability to colonise different types of environments. In contrast, the group that colonised the areas where the glacier retreated most rapidly are the species with a specific reproductive strategy. The geographical parthenogenesis observed in such cases [14,39–41] allows for a rapid increase in population size, and therefore, for the fastest colonisation of the area exposed by the retreating glacier. Notably, in the case of the genus *Urodiaspis,* one can also observe species substitution (vicariance) in Poland. The common *U. tecta*, which is found almost across the entire country, was replaced in the south-eastern part of the country by the related species *U. stammeri* [14]. The latter has so far successfully competed with *U. tecta* by blocking its eastward expansion in the Low Beskids and Bieszczady Mountains. This process is probably associated with the habitat and microclimatic conditions of the area, which are more favourable for *U. stammeri*. As can be seen, the species that successfully colonised the area earlier on competes with a related species, which arrived there much later.

As has already been shown in earlier studies, many of the species discussed in this article have their range of occurrence in the area of Poland [14,15,30]. In the case of species from the genus *Trachytes*, this is the northern range (*T. irenae*, *T. minima*, *T. montana*, and probably also *T. lamda*). The north-western range has also been marked for such species as *T. splendida*, *P. schweizeri*, and *U. stammeri*, whereas the north-eastern range has been revealed for *P. cylindricus*, *O. misella*, and *C. erlangensis*. The distribution of the last three species, considered by many as an Atlantic element, is quite interesting as their ranges overlap with that of the beech (*Fagus sylvatica*). In contrast, the range of *N. splendida*, which is typically a boreal-mountain species, is related to the natural range of the spruce (*Picea excelsa*) in Poland. As demonstrated by Błoszyk [13], a very important factor limiting the occurrence of species of the discussed group of mites is also the altitude. The vast majority of Uropodina species are lowland species (occurring in areas up to 500 m a.s.l.), and only *T. montana* can be regarded as a high-mountain species, whose abundance increases above 1300 m a.s.l.; hence, the range of this species is confined to mountain areas. On the other hand, *T. aegrota*, which is common in the whole area of Poland, should be considered an alpine species, as it occurs both in the lowlands and high in the mountains.

It is also noteworthy that during the long-term research focusing on changes in Uropodina communities in the area of two oak-hornbeam nature reserves in Wielkopolska (Greater Poland), which lasted over 40 years, the researchers managed to observe possible changes in the range of two species, i.e., *O. obscurasimilis* and *N. splendida* [42]. These two species did not occur in the examined areas in the first phase of the research, that is, at the end of the 1970s and the beginning of the 1980s, but they were found in 2014. This could stem from the global warming effect, which in turn resulted in a broadening of the ranges of these species. This phenomenon will be monitored in the future because such research is still being conducted.

The analysis of the geographical ranges of the Uropodina species discussed here indicates that the south-eastern part of Poland was a refuge from which some species spread northwards after the glacier receded. This is also confirmed by the analysis of the communities on the nunataks. The retreating glacier exposed further areas which could be easily colonised by mites. However, this was possible only due to certain conditions which had to be fulfilled, namely the formation of a humus layer in the soil. Saprophagous mites, which include most of the Uropodina species, could only occur in areas abandoned by the ice sheet after they had been colonised by plants. This is also confirmed by more recent research carried out directly in front of the glacier edge in Norway in 2000–2001.

Trachytes aegrota was found in patches of initial vegetation [43], which confirms this thesis. The analysis of the Uropodina communities of the three nunataks showed that the area of Jura Krakowsko-Częstochowska not covered by glaciation, which is known as the "Jurassic Inland Oasis" [37], exhibited the highest diversity in Uropodina species. In this area, it was possible for the species previously found there to survive the glaciation period. Thus, after the glacier receded, the area became a refuge from which they could migrate northwards to other areas released by the ice sheet. Of course, some species arrived in the area to join the existing mite communities later on, after the glacier had receded. However, such a high prevalence of the number of species found there (43 (Table 2)), compared with the other nunataks, suggests that a large percentage of them certainly survived the area's glacial period. Further research is required to specifically determine which species survived the glaciations and which of them got into the area of Jura Krakowsko-Częstochowska later. At the same time, the species composition of the Uropodina community in the Ślęża Massif clearly shows that the double glaciation of this mountain up to the height of 500 m has resulted in a much lower number of species in the area. It is also dominated by common, widely distributed species (Table 2), most of which colonised the Ślęza Massif only after the glacier had receded. The glacier retreated from the Świętokrzyskie Mountains earlier than from the Ślęża Massif; hence, more species are found there.

The rapid colonisation of areas exposed by the retreating glaciers was favoured by the life strategy of some Uropodina species, which consisted in switching to parthenogenetic reproduction, manifested by a reduction in males in populations which culminated in their entire loss [19,44]. Nowadays, the soil Uropodina species, widely distributed and usually abundant in Poland, are often parthenogenetic [14,19,45]. Among them, there are such species as *T. aegrota*, *T. pauperior*, *T. lamda*, *P. cylindricus*, *O. minima*, *O. misella*, *C. erlangensis*, *U. tecta*, *U. pannonica*, *P. pulchella*, and *D. modesta*. That the reduction in males took place relatively recently can be inferred from the sporadic occurrence in local populations of some species [46]. The switch to the parthenogenetic mode of reproduction gave these species an advantage through a rapid increase in the size of their populations facilitating a more efficient dispersal into areas not covered by the ice sheet. A similar phenomenon was also observed in butterflies [39] and diplopods [40]. So far, this problem has been considered in more detail for mites from the family *Labidostommidae* [47–49]. The studies on these mites discuss the impact of glaciation on the modern distribution of three species from the genus *Labidostomma* and the occurrence of geographic parthenogenesis in *Labidostomma luteum* in Europe in the context of glaciations. It was shown that sexually reproducing populations currently occur only in south-western France, from where the species has spread to eastern and northern Europe, but already as parthenogenetic populations [49]. Furthermore, the phenomenon of conversion to non-sexual reproduction in populations at the northern boundaries of the range has also been observed in other organisms, such as the myriapods from the genus *Polyxenus* [50], and in plants [51].

5. Conclusions

Geographical distribution of mites depends on many factors, which can be related to both the biology and ecology of the species and to external factors associated with the climate and type of soil. The Pleistocene glaciations were one of the key factors determining the geographical ranges of the fauna in Poland and Europe. The results presented here show, for the first time, the influence of Pleistocene glaciations on geographical distribution of the discussed group of mites at the species level. The analyses also show the great importance of data collection focusing on species because only such data can be helpful in determining geographical distribution of species and reconstructing their colonisation trajectories of inhabited areas. Further research into the communities of these mites in Scandinavia are also planned, which may shed more light on the colonisation of the post-glacial areas by Uropodina. These areas of Europe were the last regions where the glaciers retreated, and the glaciers that still exist in Norway are natural laboratories that allow researchers to better understand the processes involved in the colonisation of areas exposed by the ice sheet by mites.

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Data Availability Statement: The data presented in this study are stored in a computer database called AMUNATCOLL and are openly available at: https://amunatcoll.pl/ (accessed on 16 January 2023).

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

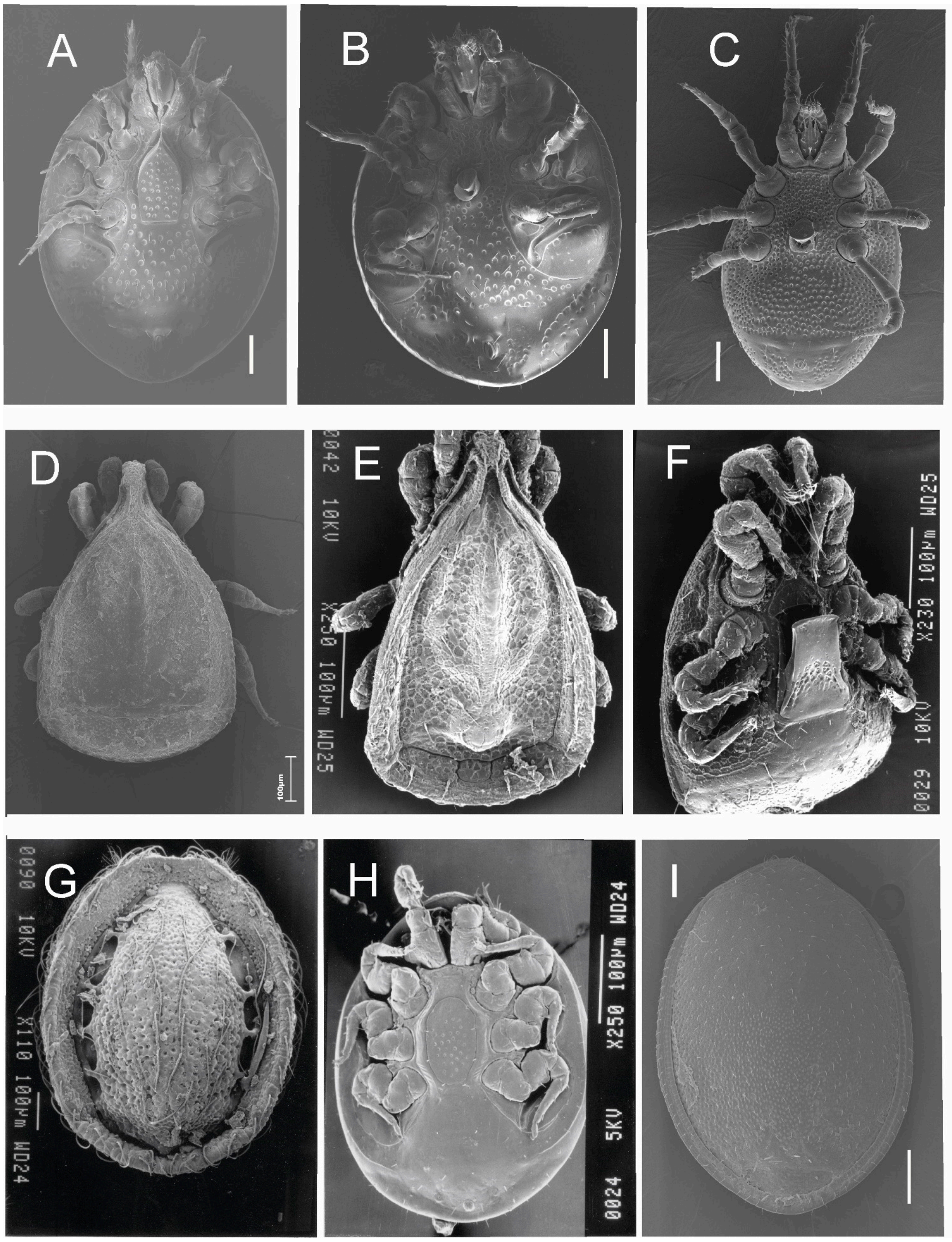

Figure A1. Species with different ranges in Poland: species occurring throughout the whole country—*Oodinychus ovalis*, female (**A**) and male (**B**) ventral side; *Dinychus perforatus*, male ventral side (**C**); species reaching the northern limit of its range in Poland—*Trachytes irenae*, female dorsal side (**D**); *Trachytes minima*—female (**E**) and male (**F**) dorsal side; a species with a boreal-mountain range—*Neodiscopoma splendida*, female dorsal side (**G**); species reaching the north-eastern limit of occurrence—*Olodiscus misella*, female ventral side (**H**); Carpathian endemic, migrating north along the Vistula River—*Oodinychus obscurasimilis*, female dorsal side (**I**).

Figure A2. Paleonunatak—Ślęża Mountain (718 m n.p.m.).

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