Zoologischer Anzeiger 286 (2020) 90–99

Contents lists available at ScienceDirect

Zoologischer Anzeiger

journal homepage: www.elsevier.com/locate/jcz

Research paper

The influence of Pleistocene glaciations on the distribution of obligate aquatic subterranean invertebrate fauna in Poland

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ARTICLE INFO

Article history:
Received 22 November 2018
Received in revised form
3 April 2020
Accepted 13 April 2020
Available online 21 April 2020

Corresponding Editor: Joachim T. Haug

Keywords:
Stygobionts
Recolonization patterns
Faunal refugia
Endemisms
Biodiversity

ABSTRACT

Almost all the territory of Poland (except for the Carpathians, Sudetes and Kraków-Częstochowa Upland) was glaciated several times. Nevertheless, based on literature data, over 80 stygobiontic invertebrate species have been found there. Three reasons for such a richness have been hypothesized: survival in refugia situated either in non-glaciated areas or in sub-glacial areas, and re-settling of previously glaciated regions through different ways. The distribution of stygobiontic species in Poland is uneven (what was confirmed by statistical analysis) and connected mostly with the intensity of faunistic studies. The highest number of stygobionts was reported in the most intensively studied Carpathians, the largest non-glaciated area in Poland, well known as a faunal refugium. In other non-glaciated regions with distinctly smaller areas, the number of stygobionts is several times lower, but the presence of some endemic species indicates their origin and survival *in situ*. The occurrence of a few endemic species in glaciated regions could be explained by their surviving in sub-glacial refugia. Other stygobionts (probably except for water mites) recolonized glaciated areas through hyporheic waters of rivers flowing in pro-glacial valleys and currently active riverbeds. Migration of invertebrates through phreatic waters across groundwater divides (possible in two mountain ranges) played a minor role in the present distribution of stygobiontic species.

1. Introduction

Pleistocene glaciations played an important role in the morphogenesis as well as the composition of fauna and flora in the Northern Hemisphere (Benton & Harper 2009). The impacts of these climatic events on the distribution of aquatic invertebrates in Central Europe is much less known, though such studies have been conducted recently regarding crustaceans (Isopoda and Amphipoda) living in surface waters of Poland (Verovnik et al. 2005; Rewicz et al. 2015; Mamos et al. 2016) and previously pertaining to molluscs (*Dreissena polymorpha*) (Zieliński et al., 1996). However, surface waters are heavily influenced by local factors, what hinders our understanding of the role of glaciations in the current composition and abundance of aquatic fauna. Subterranean waters (especially ground waters) are far more isolated from both environmental influences and landscape changes (except for local water pollution) than are any other aquatic habitat; therefore, the composition of fauna could be much more stable and may indicate the effect of glaciations.

Obligatory aquatic subterranean species (named stygobionts) were for a long time considered to be non-existent in glaciated areas (Leruth 1939; Thienemann 1950; Vandel 1964), but this idea is no longer valid. However, the number of such species is distinctly lower in areas glaciated in the Pleistocene than in non-glaciated areas in both Europe (Deharveng et al. 2009; Gibert & Culver 2009; Martin et al. 2009) and North America (Strayer et al. 1995; Hobbs 2012).

At the end of the XX century there was a confidence that the majority of stygobiontic species living in the temperate climate zone found shelter in three main glacial refugia located in the Mediterranean Sea basin, i.e., the Iberian, Apennines and Balkan peninsulas (Hewitt 2000). However, in recent years, numerous phylogeographic and genetic studies have provided evidence for the existence of additional refugia (*sensu* Rull (2010)) situated in

European Water Mite Research www.watermite.org [7 March 2018]
Fauna Europaea https://fauna−eu.org [15 March 2018]
Slovak aquatic macroinvertebrates checklist and catalogue of autecological notes http://www.zoo.sav.sk/voda_pdf/voda_pdf.htm.

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https://doi.org/10.1016/j.jcz.2020.04.003
0044-5231/© 2020 Published by Elsevier GmbH.

higher latitudes, such as those in Central and Eastern Europe (see review by Provan & Bennett 2008; McInerney et al. 2014). Already in the 80-ties of the XX century Holsinger (1980) and Skalski (1982) hypothesised the possibility of stygobiontic species survival in subglacial refugia (deep groundwater beneath the ice) what was confirmed by e.g., Martin et al. (2009) and Kornobis et al. (2010).

In the Middle Pleistocene, the territory of the present-day Poland was glaciated several times during the South-Polish (Elsterian) (800-600 ka BP), Middle-Polish (Saalian) (380-160 ka BP) and Vistulian (Weichselian) (100-12 ka BP) groups of glaciations (Mojski 2005; Lindner et al. 2012; Marks et al. 2016). Only the Carpathians, part of the Sudetes Mts. and the Kraków-Częstochowa Upland were not glaciated (Fig. 1). The ice sheet of the Sanian 1 Glaciation occupied the largest part of the Polish territory, while the ice sheets of the successive South-Polish and Middle-Polish glaciations, such as Sanian 2 and Odranian (Lindner 2004; Marks et al. 2016), covered smaller areas (Fig. 1). Despite this geological history, approximately 80 stygobiontic species, which primarily inhabit interstitial and hyporheic waters of rivers, were found in Poland based on a recent literature review (Dumnicka & Galas 2017). However, it is difficult to determine the exact number of such species due to the various reasons e.g. validity of species determinations or recent taxonomic revisions. According to the Fauna Europaea database (https://fauna—eu.org), the presence of some of these species is not documented in Poland due to the publication of several records in local journals exclusively (published in Polish) or as a result of border changes after the Second World War.

The main objective of this paper is to infer which factors might be responsible for the observed stygobiontic species distribution and richness in various regions of Poland. Three working hypothesis have been discussed:

1. Stygobiontic fauna could have survived in non-glaciated areas of Poland
2. Stygobiontic fauna could have re-settled previously glaciated areas through different means:
   - Historical migration of species along proglacial river valleys situated latitudinally and by the Moravian Gate
   - Post glacial migration through hyporheic and interstitial waters of rivers existing at present
   - Migration through phreatic waters connected across groundwater divides
3. Stygobiontic species could have survived in sub-glacial refugia

2. Material and methods

2.1. Scope of the subject and sources of information

The stygobiontic species inhabit various types of subterranean waters that are located above and below the water table. The study of such fauna is possible in caves, mines, adits, wells, springs and interstitial waters, which fill the spaces among grains of sediments below river bottoms and along rivers or lake banks. Psammonic

Fig. 1. Map of Poland showing selected southern glaciation borders (after Marks et al. 2016). S1 – Sanian 1, S2 – Sanian 2, O – Odranian, V – Vistulian Glaciation, TV – Tatra Mts, partially glaciated during Vistulian. Non-glaciated regions: CA – Carpathians; SU – Sudetes; KC – Kraków-Częstochowa Upland; Other important regions mentioned in the text: 1 – Polish part of the East Carpathians; 2 – partially glaciated Kłodzko Basin; 3 – Małopolska Gap of Vistula River; 4 – the Moravian Gate.

fauna has not been included because it should not be treated as stygobiontic fauna (Botosaneanu 1986; Gibert et al. 1994; White & Culver 2012).

This paper was prepared on the basis of 99 publications that included studies of various groups of invertebrates with stygobiontic species (e.g., Annelida, Crustacea, Hydrachnidia, Turbellaria and Gastropoda) that were performed in Poland (see review by Dumnicka & Galas (2017)). The most intensive studies were conducted in the non-glaciated Carpathian region, and their results were summarized by Skalski (1981), Sywula (1981), Biesiadka (1997) and Dumnicka (2014). There are distinctly less publications concerning the invertebrate groups in glaciated parts of Poland, which explains why all results from the zone between the maximal extents of the Sanian 1 and the Vistulian Glaciations (Fig. 1) are presented together. The interpretation of the discussed results should be done cautiously, because the number of available data from various regions is heterogeneous. The full list of stygobiontic species as well as the bibliographic list has been already published (Dumnicka & Galas 2017), but additional species (Karpowicz 2016) and new localities have been added (Dumnicka et al. 2018).

2.2. Statistical analysis

Analyses employed SPSS ver. 24.0.0.1 (IBM Corp 2016). The data were analysed with the use of a generalized linear mixed model (GLMM). The Poisson probability distribution was used for numerical data. The model used post-estimation, Satterthwaite approximation and robust covariances.

The number of species was the target variable, and the fixed effect was the region. Calculations were made at the level of ATPOL squares 10 × 10 km (N = 102). The square distribution and the number of squares varied between the regions; therefore, the square ID was used as a random effect (covariance type: variance component). The pairwise contrasts for comparisons between the included regions (i.e., glaciated and non-glaciated) were used. The region covered by the Vistulian Glaciation (V) was excluded from the analysis because the sample size in this region was too low (see Fig. 2), while the areas of the Odranian (O) and Sanian (S1, S2) glaciations were merged.

3. Results

The stygobionts known from Poland belong to various taxonomic groups, such as Tricladida (1 species), Annelida (11), Crustacea (25), Hydrachnidia (45) and Gastropoda (1).

The distribution of stygobionts in regions with different glaciation history is uneven (Fig. 2, Table 1). The number of species calculated at the level of squares varied between the regions ($F = 3.04$, $p = 0.021$). This number was significantly higher in the Tatra Mts. (TV) which were partially glaciated during Vistulian, than in the areas covered by the Sanian and Odranian glaciations (OS1) (Fig. 3) (TV-OS1 contrast: $t = 2.11$, $df = 95$, $p = 0.038$). The number of species per square was also significantly higher in the non-glaciated area of the Carpathians (CA) than in the OS1 (CA-OS1 contrast: $t = 2.20$, $df = 95$, $p = 0.030$). The differences in the number of recorded species in the other comparisons (non-glaciated Sudetes (SU) and the Kraków-Częstochowa Upland (KC) and glaciated OS1) were not significant (Fig. 3).

To date, in the non-glaciated Carpathian region (excluding the Tatra Mts.), 56 stygobionts have been found (Table 1). A particularly high number of Hydrachnidia (40 species) have been found principally in interstitial waters in this region, especially in its eastern part (region 1 in Fig. 1). In other non-glaciated and glaciated regions in Poland, despite numerous studies, stygobiontic water mites were almost never found (Fig. 4). The majority of Hydrachnidia species as well as *Haber zavreli* (Oligochaeta) and crustaceans, including *Cyclocypris* sp., *Fabaeformiscandona latens*, *Pseudocandona mira,* and *Synurella tenebrarum*, were found solely in the Carpathian region.

In the Sudetes, the composition of stygobiontic fauna differs considerably compared to fauna from the Carpathian region. Only 13 stygobionts were found there, and among them, only one Hydrachnidia species was reported (Fig. 4) from the interstitial waters of the Nysa River in the Kłodzko Basin (region 2 in Fig. 1); in contrast, Annelida were represented by six species (Table 1). Stygobiontic fauna of this area is very specific, and five species (i.e., *Troglochaetus beranecki, Trichodrilus pragensis, Trichodrilus spelaeus* (Annelida), *Crangonyx paxi* and *Niphargellus arndti* (Crustacea)) are known exclusively from this region of Poland.

In the Kraków-Częstochowa Upland (region KC in Fig. 1) various types of subterranean waters (in caves, wells and springs) have been studied several times, but only nine stygobiontic species were found (Table 1). They are represented mainly by oligochaetes, two niphargids and one endemic species of Gastropoda; however, neither obligate subterranean species of Hydrachnidia (Biesiadka et al. 1990) nor Ostracoda (Matolicz et al. 2006) were reported.

From the area situated between the border of the Sanian 1 and Vistulian glaciations (OS1), 15 stygobionts were reported (Table 1), with the highest number (9 species) in the Małopolska Gap of Vistula (region 3 in Fig. 1), where more than one hundred wells and several springs were studied. In this area stygobiontic crustaceans prevailed and among water mites, stygobionts were not found (Fig. 4).

Despite the small number of studies conducted in the area covered by Vistulian Glaciation, which mainly focused on particular groups of invertebrates such as ostracods, copepods or oligochaetes, four species of stygobionts were found in this region (Table 1). In addition, two water mite species occurred in the marginal extent of this glaciation near Oder (Warsaw–Berlin ice-marginal paleo-valley) (Fig. 4).

In the Tatra Mts. (at the southern edge of the country) (TV in Fig. 1), only valleys were glaciated by mountain glaciers during the Vistulian and earlier glaciations (Marks et al. 2016). In a small area of this mountain range, 16 stygobionts were found (Table 1), mainly due to very intensive studies made by biospeleologists in various habitats and years. Among stygobionts, nine species of Hydrachnidia were found, and most of them are known from the non-glaciated Carpathians also. Moreover, four species of oligochaetes and three species of crustaceans were reported (Table 1) in this area.

The results of these studies indicate that the majority of stygobiontic species have been found in one region only; specifically, 93.3% of water mite species have been found in the Carpathians and the Tatra Mts., while the remaining groups account for approximately 58% of the species.

4. Discussion

Stygobiontic species form only a few percent of interstitial fauna (Martin et al. 2009), and frequently, only single specimens were caught in this habitat (Gledhill 1982). Sometimes, especially in deeper underground waters, invertebrates were not stated (Skalski 1982; Stein et al. 2012; Kur et al. 2016; Dumnicka et al. 2017) and usually they were scarce. Therefore such studies are constrained and the number of species recorded so far could be underestimated. Subterranean waters are frequently well colonised by invertebrates only in karstic areas, what was stated in the Tatra Mts and in French Jura (Dole-Olivier et al. 2009). Although the number of stygobiontic species decreases towards the North (Bănărescu 1991), finding of ca. 80 species in Poland indicates high species richness.

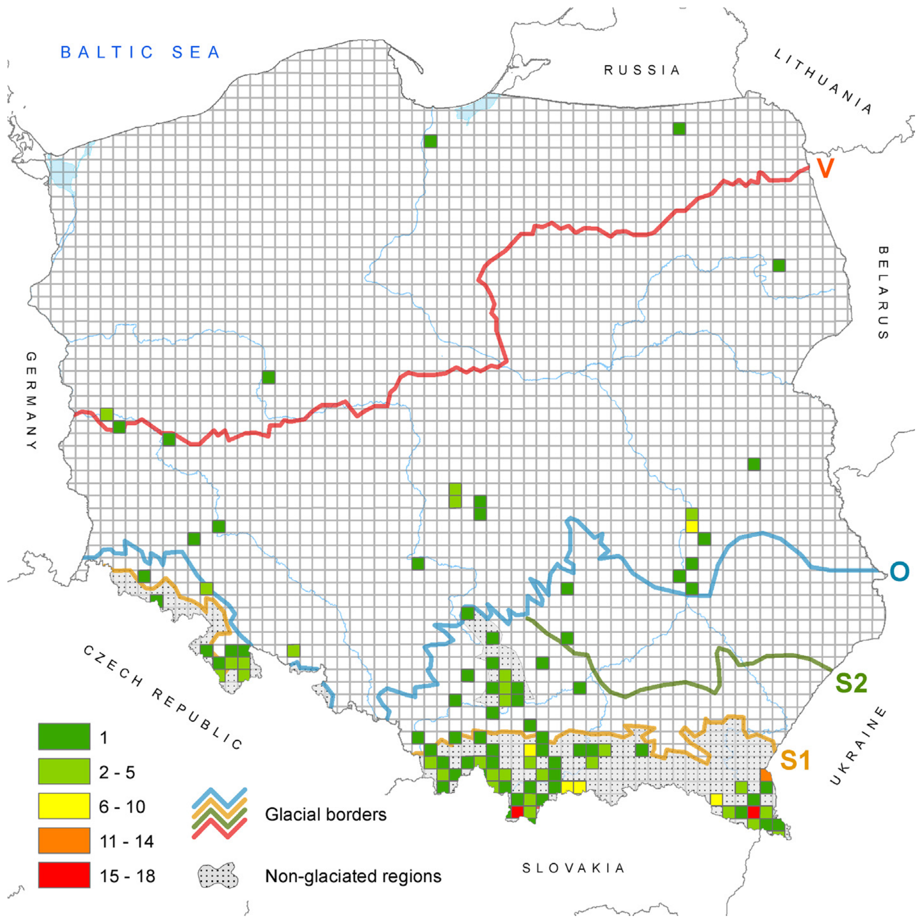

Fig. 2. The number of stygobiontic species recorded in various squares in particular regions. Glacial borders and non-glaciated regions – as in Fig. 1.

The number of stygobiontic species found in particular squares was the highest in the most intensively studied areas, the non-glaciated Carpathians (CA) and partly glaciated Tatra Mts. (TV) sites. Considerably fewer species were recorded in regions covered by the Sanian 1 and Odranian glaciations (OS1), and the number significantly differs between OS1 and both CA and TV. Our statistical analysis demonstrated that the intensity of the studies made in particular regions of Poland is the significant parameter influencing on the stygobiontic species distribution. This is in agreement with Hahn & Fuchs (2009) who stated, that the intensity of sampling strongly explains stygobiontic species richness.

4.1. *Stygobionts in non-glaciated areas*

When analysing data gathered from publications by various authors, it could be concluded that the composition of stygobiontic fauna differs strongly among three regions of Poland that were not glaciated in the Pleistocene, i.e., the Carpathians, Sudetes and Kraków-Częstochowa Upland. This may be explained by their different surface areas as well as different possibilities of recolonization due to different directions of proglacial outflows. The Carpathians (built from the flysch deposits and sandstones) are a long mountain belt that extends towards the South and are known as a refugium for species from various taxonomic groups (Provan & Bennett 2008; Mamos et al. 2016). The ice sheet of the largest extent (The Sanian 1 Glaciation), entered into the lower sections of the Carpathian valleys only (Fig. 1). During this glaciation (which lasted from several tens of thousands of years to one hundred thousand years), the waters from that area flowed down the Dnister River valley towards the Black Sea basin (Mojski 2005). In the Polish part of this mountain range, 56 stygobiontic species were reported, including seven species that are endemic to the Carpathians, i.e., an ostracod *P. mira*, water mites (*Atractides barbarae, Atractides gorcensis, Aturus petrophilus, Aturus pulchellus, Axonopsis cogitatus* - described by Biesiadka) and *Kawamuracarus chappuisi*. In this non-glaciated region stygobionts might survived in the peryglacial refugia situated mainly in foothills of mountains (Eme et al. 2013) or recolonised northern slopes mostly from the South-East (from the non glaciated Dnister River catchment), where many aquatic species (including stygobionts) could have existed.

In the Sudetes, the ice sheet of the Sanian 1 Glaciation entered the Kłodzko Basin and the Moravian Gate (regions 2 and 4 Fig. 1); however, glacial waters did not cross the main European watershed, and the ice sheet drained to the north (Lindner & Marks 1995; Tyráček 2011) or northwest. As is assumed for the western (German) part of the territory occupied by the Sanian (Elsterian) ice sheet (Ehlers et al. 2011; Cohen et al. 2014), the sub-glacial waters flowed westward towards the English Channel. The later glaciations (Sanian 2 and Odranian) also reached the Moravian Gate (Fig. 1) (Marks et al. 2016). Only during the Odranian Glaciation, waters from the Sudetes and the neighbouring regions flowed out through the Moravian Gate to the Danube basin (Lindner & Marks 1995; Tyráček 2011). Nevertheless, the number of stygobiontic species (including two endemic ones) found in Sudetic underground waters (mainly in the Kłodzko Basin built from karstified rocks) is relatively low, despite the fact that studies on subterranean aquatic

Table 1
List of stygobiontic species known from areas under different history of the Pleistocene glaciations.

Group/species	CA	SU	KC	OS1	V	TV
Tricladida						
Dendrocoelum cf. *carpathicum* Komarek 1919				+		
Annelida						
Cernosvitoviella parviseta Gadzińska 1974	+	+		+		+
Enchytraeus dominicae Dumnicka 1976 E		+	+	+		+
Enchytraeus polonicus Dumnicka 1977 E			+			
Gianius aquaedulcis (Hrabě 1960)			+			
Haber zavreli (Hrabě 1942)	+					
Rhyacodrilus subterraneus Hrabě 1963			+		+	
Trichodrilus cernosvitovi Hrabě 1937	+		+			+
Trichodrilus moravicus Hrabě 1937	+	+	+			+
Trichodrilus pragensis Vejdovsky 1876		+				
Trichodrilus spelaeus Moszyński 1936 E		+				
Trichodrilus sp. juv. Claparède 1862				+		
Troglochaetus beranecki Delachaux 1921		+				
Crustaceaa						
Acanthocyclops rhenanus Kiefer 1936				+		
Bathynella natans Vejdovsky 1882	+	+				
Crangonyx paxi[c] Schellenberg 1935 E		+				
Cryptocandona matris (Sywula 1976)	+			+		
Cyclocypris sp. Brady & Norman 1889	+					
Diacyclops clandestinus (Kiefer 1926)				+		+
Elaphoidella elaphoides (Chappuis 1924)				+		
Fabaeformiscandona latens (Klie 1940)	+					
Fabaeformiscandona wegelini (Petkovski 1962)	+			+		
Gammarus pulex polonensis Karaman & Pinkster 1977					+	
Graeteriella unisetigera (Graeter 1908)					+	
Nannocandona stygia Sywula 1976 E	+	+				
Niphargus ? *aquilex* Schiodte 1856					+	
Niphargus casimiriensis Skalski, 1980 E				+		
Niphargus inopinatus Schellenberg 1932						+
Niphargus leopoliensis Jaworowski 1893	+		+	+		
Niphargus puteanus[a] Koch 1836		+			+	
Niphargus tatrensis Wrześniowski 1888	+	+	+	+		+
Niphargellus arndti (Schellenberg 1933)		+				
Proasellus slavus (Remy 1948)	+					
Pseudocandona eremita (Vejdovsky 1882)				+	+	
Pseudocandona mira (Sywula 1976) E	+					
Pseudocandona szoecsi Farkas 1958	+			+		
Synurella tenebrarum (Wrześniowski 1888)	+					
Synurella coeca[d] Dobreanu & Manolache 1951				+		
Hydrachnidia						
Albaxona elegans Walter 1947	+					
Albaxona lundbladi Motas & Tanasachi 1947 = *A. gracilis* Schwoerbel 1962 (sensu Bogdanowicz et al. 2008)	+					
Albaxona minuta Szalay 1944	+					
Arrenurus corsicus Angelier 1951					+	
Atractides barbarae Biesiadka 1972 E	+					
Atractides gorcensis Biesiadka 1972	+					
Atractides latipalpis Motas & Tanasachi 1946						+
Atractides latipes (Szalay 1935)	+					
Atractides phreaticus (Motas & Tanasachi 1948)	+					
Atractides pilosus Schwoerbel 1961 = *A. tener* ? sensu Gerecke 2003	+					
Atractides pumilus (Szalay 1946) = *A. primitivus* (Walter 1947) sensu Gerecke 2003	+					
Atractides sokolowi (Motas & Tanasachi 1948)	+					
Aturus karamani Viets 1936						+
Aturus paucisetus Motas & Tanasachi 1946	+					
Aturus petrophilus Biesiadka 1979[b] E	+					
Aturus pulchellus Biesiadka, 1975 E						+
Axonopsis cogitatus Biesiadka, 1975	+					
Axonopsis inferorum Motas & Tanasachi 1947	+					
Axonopsis vietsi Motas & Tanasachi 1947	+					
Barbaxonella angulata (Viets 1955)	+					
Erebaxonopsis brevipes Motas & Tanasachi 1947	+					
Feltria mira (Motas & Tanasachi 1948)	+					+
Feltria subterranea Viets 1937	+					
Frontipodopsis reticulatifrons Szalay 1945	+					
Hungarohydracarus subterraneus Szalay 1943	+					
Kawamuracarus chappuisi Motas & Tanasachi 1946	+					
Kongsbergia alata Szalay 1954					+	
Kongsbergia arenaria Angelier 1951	+					
Kongsbergia clypeata Szalay 1945	+					
Kongsbergia dentata Walter 1947	+					+
Kongsbergia d-motasi Motas & Tanasachi 1958	+					
Kongsbergia lundbladi Szalay 1956	+					

Table 1 (*continued*)

Group/species	CA	SU	KC	OS1	V	TV
Kongsbergia pectinata Walter 1947	+					
Kongsbergia ruttneri Walter 1930	+					
Kongsbergia wroblewskii[b] Biesiadka 1997 E	+					
Lethaxona cavifrons Szalay 1943	+					
Lethaxona pygmea Viets 1932	+					
Loboharacarus weberi quadriporus Walter 1947	+					+
Neoacarus hibernicus Halbert 1944	+					
Neumania phreaticola Motas & Tanasachi 1948	+					
Parasoldanellonyx parviscutatus (Walter 1917)	+					
Sperchonopsis phreaticus Biesiadka 1975 E	+					+
Stygomononia latipes Szalay 1943	+	+				+
Wandesia thori Schechtel 1912	+					+
Wandesia stygophila Szalay 1944	+					
Gastropoda						
Falniowskia neglectissima Falniowski & Steffek 1989 E			+			
Number of taxa	**56**	**13**	**9**	**15**	**8**	**16**

E – endemic species; x – leg. A. Skalski 14.07.1977, det. E. Dumnicka.
Non-glaciated regions: CA – Carpathians; SU – Sudetes; KC – Kraków-Częstochowa Upland; Areas covered by various glaciations: OS1 – Sanian 1, 2 and Odranian glaciation; V – Vistulian glaciation; TV – Tatra Mts partially glaciated during Vistulian.
[a] False determination.
[b] Nomen nudum.
[c] Localization in Germany is false.
[d] Described as *S. coeca rafalskii* by Skalski (1981).

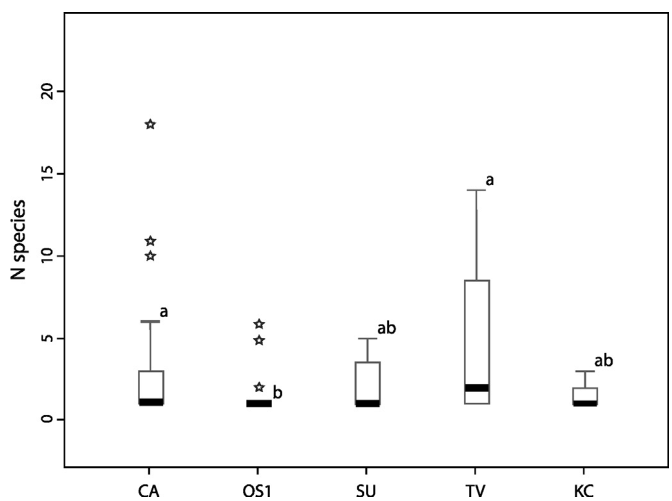

Fig. 3. Box plot of the number of species (±confidence intervals) in different regions. Non-glaciated regions: CA – Carpathians; SU – Sudetes; KC – Kraków-Częstochowa Upland; OS1 – area covered by Sanian 1, 2 and Odranian glaciations; TV – Tatra Mts, partially glaciated during Vistulian. Different letters (located above the T-bars) indicate significant differences between the regions. The dark line in the middle of the boxes is the median; the stars are outliers.

fauna have been conducted since the twenties of the XX[th] century in this basin (see bibliographic list in Dumnicka & Galas (2017)). The predominant northward outflow, such as that during the South-Polish Glaciation, probably limited the long-distance re-colonisation of Sudetic interstitial waters. Admittedly migration from the Danube catchment (rich in stygobionts) was possible during and after Odranian Glaciation, but this concept is not confirmed by the presence of many stygobionts. Without new studies of invertebrate fauna near the Moravian Gate this scenario is not valid. The present-day subterranean migration of water from the Kleśnica stream in Kłodzko basin, (catchment of the Baltic Sea) to the Morava stream (catchment of the Black Sea) was documented (Ciężkowski et al. 2009). In such situation the migration of species across the main European watershed is possible. It is probable that *T. pragensis*, a species unknown from other regions of Poland, reached the Kłodzko Basin through this route.

According to the recent state of knowledge, it is assumed that only ice lobes intervened certain northern and lower karstic areas of the Kraków-Częstochowa Upland (Fig. 1) during the Sanian 1 and Odranian glaciations (Knopik 2011; Lewandowski 2011). Relatively few stygobiontic species and only two endemic species (*Enchytraeus polonicus* and *Falniowskia neglectissima*) were reported from this small area. The lack of stygobionts representing crustacean groups (beside Amphipoda) and water mites from the area of the Kraków-Częstochowa Upland needs confirmation in future studies. Among amphipods, two species from the genus *Niphargus* were reported exclusively, i.e., *Niphargus leopoliensis* and *Niphargus tatrensis*. According to Skalski (1980), the distribution of *N. leopoliensis* is disjunctive because its localities in this Upland and neighbouring area (glaciated during Sanian 1) are isolated from its continuous geographic range. Specimens collected in areas of their regular distribution (Eastern Carpathians and *locus typicus* in Lwów City) differed morphologically from those found on the Upland (Skalski 1981); thus, we can presume that these populations were isolated for a long time. In cases of *E. polonicus, F. neglectissima* and disjunctive populations of *N. leopoliensis*, it is probable that they survived in the peryglacial or even sub-glacial refugia.

4.2. Stygobionts in glaciated areas

From Polish territory glaciated by the Sanian 1 and later glaciations (excluding the Vistulian Glaciation) 15 stygobiontic species were found with only one endemic taxon (*Niphargus casimiriensis*). This species is known exclusively (Skalski, 1980) from wells of a Cretaceous carbonate rock (marls) aquifer in the Małopolska Gap of the Vistula (region 3 in Fig. 1) which suggests its survival (maybe speciation also) in a sub-glacial refugium where temperatures were above zero, as was the case in temperate ice sheets (Jania 1993). Finding of a tricladid *Dendrocoelum cf. carpaticum* and crustacean *Synurella coeca* subsp. *rafalskii* exclusively in the Małopolska Gap speaks in favor of this theory. Proudlove et al. (2003) considered that such refugia might exist not only in karstic but also in non-karstic groundwaters. In Poland, most of the invertebrate groups with stygobiontic species (except for almost all water mites) were found in glaciated areas (Table 1). Probably, the post-glacial dispersion by hyporheic and interstitial waters, known for

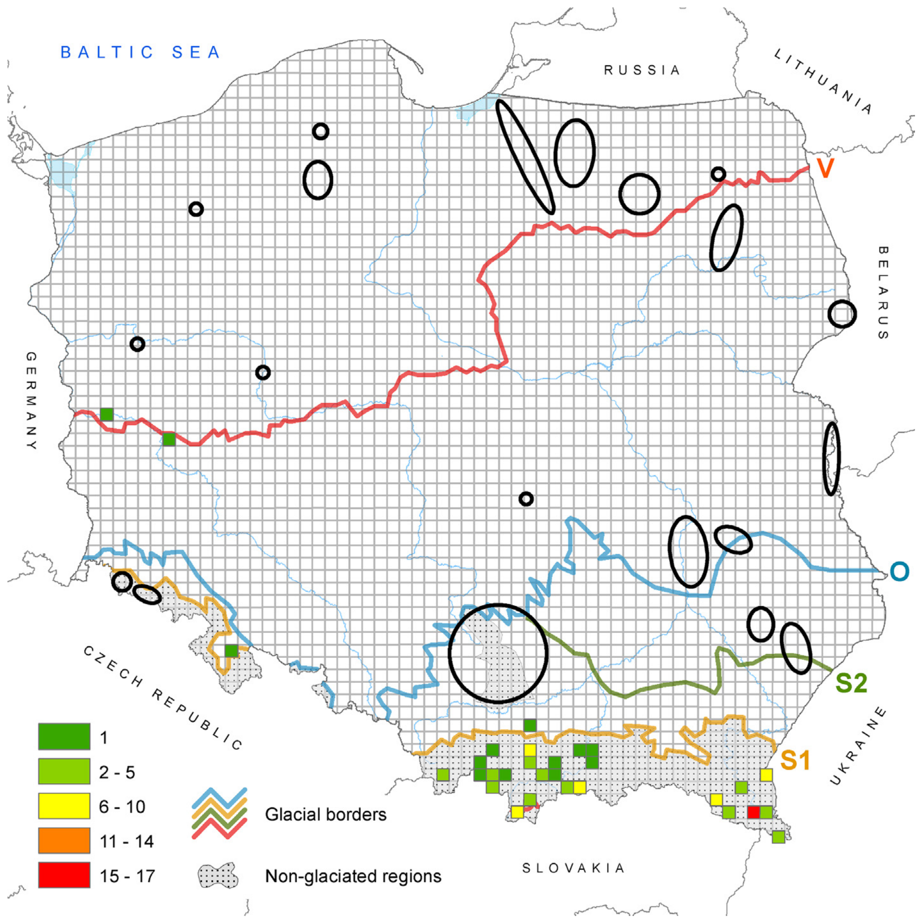

Fig. 4. The number of stygobiontic water mites recorded in various squares in Poland. Ellipses (or circles) represent areas in which water mite fauna was studied in various types of surface/subterranean waters (acc. to published data) but stygobionts were not found. Glacial borders and non-glaciated regions – as in Fig. 1.

stygobiontic species from various groups: oligochaetes (Dumnicka 2014), copepods *Elaphoidella elaphoides, Graeteriella unisetigera* (Galassi, 2001), ostracods *Cryptocandona matris*, *Pseudocandona eremita*, *F. latens* (Sywula, 1981) and an amphipod *N. tatrensis* (Skalski, 1978) allows such species to have wide ranges and penetrate the glaciated areas. Moreover, the long distance dispersal of species was possible during glaciations periods, when habitat connectivity increased, due to connections between the main north European rivers (including Vistula). Such a scenario was confirmed for stygobiontic isopods by Eme et al. (2013). Due to the scarcity of studies made in glaciated areas of Poland it is hard to decide whether a given species is absent on this area or just was not found.

The youngest Vistulian Glaciation covered principally north-west part of Poland. The water flowed from this region towards the west through several (4–5) ice-marginal paleo-valleys, among which the Warsaw–Berlin and Toruń-Eberswald "pradolinas" (paleo-valleys) are the best defined. These waters entered the lower section of the Elbe valley and eventually reached the North Sea (Mojski 2005; Ehlers et al. 2011; Marks et al. 2016). Even in this region the presence of endemic, eyeless population of *Gammarus pulex poloniensis* was stated in a subterranean water flow of the Warta River (Karaman & Pinkster, 1977). The occurrence of such population indicates the probable existence of a sub-glacial refugium in this area. The presence of a stygobiontic ostracod *P. eremita* near the mouth of Vistula to the Baltic sea (Namiotko, 1990) and *Rhyacodrilus subterraneus* in north-east of Poland (Dumnicka & Koszałka, 2005) might be the result of post-glacial migration or sub-glacial survival. The occurrence of two water mites (*Arrenurus corsicus* and *Kongsbergia alata*) (Biesiadka, 1975) and *Niphargus aquilex* in a small area situated in the Warsaw–Berlin ice-marginal paleo-valley suggests their postglacial migration to this area. The big part of Polish glaciated areas is situated in the belt of North Europaean Plains (Lowlands), where anoxic conditions were frequently stated in deeper subterranean waters due to the porous aquifer type (Stein et al. 2012), but in interstitial waters oxygen may be present (Zieliński & Jekatierynczuk-Rudczyk 2010). Moreover in Polish lowlands stygobionts were principally found in the wells situated in river valleys, where groundwater level is not deep. The high richness of subterranean fauna was also stated by Stein et al. (2012) in the Lower Rhine Valley. In such localities shallow subterranean waters are usually oxygenated. Furthermore stygobionts are well adapted to low oxygen availability, what was confirmed for the polychaete *T. beranecki* (Särkkä & Mäkelä, 1998) and many crustaceans (Hervant & Malard 2012).

When comparing glaciated areas, the number of stygobiontic species is the highest in the Tatra Mts, however studied caves and streams are situated in the valleys at a low altitude which were not reached by the mountain glaciers during last glaciations (the Vistulian) (Mamos et al. 2016). Moreover, species could have migrated from the nearby Carpathian rivers, what resulted in finding of nine water mites species (Biesiadka 1973). In addition, Gradziński et al. (2009) assumed the existence of the underground connection between the Vistula and Danube river catchments in the karstic part of the Tatra Mts. Such connection probably helped the migration of certain species, e.g., *Niphargus inopinatus* which is present in

Slovakia (south part of the Tatra Mts) (http://www.zoo.sav.sk/voda_pdf/voda_pdf.htm).

In Poland, the number of stygobiontic species (excluding Hydrachnidia) found in non-glaciated and glaciated regions is comparable, whereas Strayer et al. (1995), whose work was based on selected taxonomic groups only (Annelida, Crustacea) reported their higher richness in non-glaciated areas of the USA.

4.3. Hydrachnidia in non-glaciated and glaciated areas

Fauna of Carpathians stygobiontic water mites, which were principally studied in interstitial waters but have also been found in springs and streams (see Biesiadka 1973, 1975; Pešić & Chaniecka 2006), is especially rich. Such high species richness allows us to presume that not only endemic Carpathian Hydrachnidia survived cold periods in this refugium. In the case of species with wide geographic range, the long distance re-colonisation from the southeast through proglacial river valleys of Dniester River tributaries (Mojski 2005) was also possible. In the Sudetes only one species of stygobiontic water mite was found whereas in the Kraków-Częstochowa Upland their occurrence was not confirmed. Such results are difficult to explain, even when considering the smaller number of studies that have been conducted on this group in the Sudetes (Bazan-Strzelecka 1972a; Biesiadka 1975; Biesiadka & Cichocka 1993) and the Kraków-Częstochowa Upland (Biesiadka et al. 1990) in comparison to the number of studies performed in the Carpathians (see in Dumnicka & Galas 2017). According to data available from European Water Mite Research (www.watermite.org) the geographic ranges of many stygobiontic water mite species cover the Central European Uplands (including the Sudetes), and the range of some species even reaches much farther to the east. Anthropopression might be one of the reasons that explain the drastic reduction in stygobiontic water mite fauna in the Sudetes: stream beds have been modified by hydrotechnical constructions since the XIXth century (Witek & Latocha 2009; Witek 2010), and high pollution of running waters occurred during the XXth century (Florczyk et al. 1971; Fila et al. 1986), what could have resulted in lack of oxygen in interstitial waters. In glaciated areas of Poland, despite many studies (Fig. 4), stygobiontic water mites were almost never found, which seems to be surprising. Water mite fauna have been studied many times in various regions of glaciated areas, mainly in surface waters (Biesiadka & Kasprzak 1977; Cichocka 1996, Biesiadka & Cichocka 1997; 2004; Cichocka & Pakulnicka 2006; Zawal 2006; Stryjecki 2009; Cichocka & Biesiadka 2011; Stryjecki et al. 2012; Dumnicka et al. 2016) but some included the subterranean waters of the Małopolska Gap of the Vistula (Skalski 1982) and springs (Bazan–Strzelecka 1972b; Zawal & Sadanowicz 2012; Biesiadka et al. 2015).

The inability to find stygobiontic water mites in glaciated areas of Poland is hard to fathom, especially because these species live mainly in interstitial waters; thus, one would expect the re-colonisation of this habitat to be easy. In Scotland, which was glaciated during the last glaciation (Böse et al. 2012), ten stygobiontic water mites were found by Gledhill (1982). In Belgium, eight stygobiontic water mites were present in a karstic area of the Walloon region (Martin et al. 2009), which was located in the permafrost zone of the Younger Dryas (Isarin 1997). To elucidate the lack of stygobiontic water mites in glaciated areas in Poland further studies in hyporheic and other kinds of ground waters are needed.

When discussing distribution of stygobionts in Poland we consider that the presence of endemic species in both non-glaciated and glaciated areas indicates the possibility of their survival in peryglacial (in the Carpathians) and sub-glacial refugia. On the glaciated areas the presence of stygobiontic species was most frequently stated in the vicinity of proglacial or recent rivers, what indicates that migration of species along these valleys was possible. Current migration across groundwater divides is possible in the Tatra Mts and in the Kłodzko Basin (Sudetes) only. The discussion on the origin and distribution of stygobiontic fauna based on traditional faunistic studies conducted in Poland allowed us to extract the chief scientific problems, which may be solved using complex field, taxonomic and genetic studies of the collected species. Due to lack of genetic studies taxonomic status of species and subspecies endemic for Poland is not clear. Results of such studies elsewhere, which were performed principally on niphargids (Fišer et al. 2010; Meleg et al. 2013), but also on isopods (Eme et al. 2013) changed our knowledge about the geographic ranges of certain species due to the discovery of several cryptic species.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Declaration of Competing Interest

None declared.

References

Bănărescu, P., 1991. Zoogeography of Fresh Waters, vol. 2. AULA-Verlag Wiesbaden. Distribution and Dispersal of Freshwater Animals in North America and Eurasia.
Bazan-Strzelecka, H., 1972a. Wodopójki Hydracarina. Katalog Fauny Polskiej Catalogus Faunae Poloniae, vol. 34, p. 102. Warszawa PWN.
Bazan-Strzelecka, H., 1972b. Fauna of niebieskie Źródła springs. Water–mites (Acari, Hydrachnellae). Acta Univ. Lodz. Ser. II 46, 33–34 (in Polish with English abstract).
Benton, M.J., Harper, D.A.T., 2009. Introduction to Paleobiology and the Fossil Record. Wiley – Blackwell.
Biesiadka, E., 1973. Hydracariens nouveaux ou peu connus pour la faune de Pologne. Fragm. Faun. 18, 437–490 (in Polish with French summary).
Biesiadka, E., 1975. Contribution à la connaissance des Hydracariens des eaux souterraines de Pologne, avec la description de quatre espèces nouvelles. Fragm. Faun. 20, 75–113 (in Polish with French summary).
Biesiadka, E., 1997. Halacaroidea, Hydrachnidia. In: Razowski, J. (Ed.), Checklist of Animals of Poland, t. IV. Institute of Systematics and Evolution of Animals, PAS, Kraków, pp. 229–239.
Biesiadka, E., Cichocka, M., 1993. Habitat distribution of water mites in Karkonosze Mountains. In: Sarosiek, J. (Ed.), Geoekologiczne Problemy Karkonoszy. II. Ekologia Roślin I Zwierząt. Wrocław University, pp. 275–283 (in Polish with English summary).
Biesiadka, E., Cichocka, M., 1997. Hydracarina fauna in Lobelia–type lakes near. Bytów. Fragm. Faun. 40, 81–93.
Biesiadka, E., Cichocka, M., Warzecha, B., 1990. Water mites (Hydracarina) of the springs in the Kraków–Częstochowa and Miechów Uplands. Acta Hydrobiol. 32, 171–186.
Biesiadka, E., Kasprzak, K., 1977. An investigation on the macrofauna of the River Warta within the city of Poznań. Acta Hydrobiol. 19, 109–122.
Biesiadka, E., Kowalik, W., Ścibior, R., 2015. Water mites (Acari, Hydrachnidia) in three forest and landscape reserves in Roztocze. Annales UMCS Sec. C Biol. 70, 29–41. https://doi.org/10.1515/umcsbio–2015–0007.
Botosaneanu, L. (Ed.), 1986. Stygofauna Mundi. Brill, E.J, Backhuys., Leiden.
Böse, M., Lüthgens, C.H., Lee, J.R., Rose, J., 2012. Quaternary glaciations of northern Europe. Quat. Sci. Rev. 44, 1–25. https://doi.org/10.1016/j.quascirev.2012.04.017.
Cichocka, M., 1996. Water mites (Hydracarina) of peat lands in Bagna Biebrzańskie. Fragm. Faun. 39, 207–221 (In Polish with English Summary).
Cichocka, M., 2004. Water mites (Hydracarina). In: Kistowski, M., Mosdorf, J. (Eds.), The Resources and threats to the Natural Environment in the Ełk District and in Niemenczyn. Report 2004, Ełk, pp. 362–366.
Cichocka, M., Biesiadka, E., 2011. Water mites (Acari, Hydrachnidia) in aquatic habitats in the city of Olsztyn (Poland). In: Indykiewicz, P., Jerzak, L., Böhner, J., Kavanagh, B. (Eds.), Urban Fauna. Studies of Animal Biology, Ecology and Conservation in European Cities. University of Technology and Life Sciences, Bydgoszcz, pp. 51–63.
Cichocka, M., Pakulnicka, J., 2006. Wodopójki (Hydrachnidia, Acari) Parku narodowego "Bory Tucholskie". In: Banaszak, J., Tobolski, K. (Eds.), Park Narodowy Bory Tucholskie u progu nowej dekady. Kazimierz Wielki University, Bydgoszcz, pp. 269–276.
Cohen, K.M.P.L., Gibbard, H., Weerts, J.T., 2014. North Sea paleographical reconstructions for the last 1 Ma. Neth. J. Geosci. 93, 7–29. https://doi.org/10.1017/njg.2014.12.

Ciężkowski, W., Buczyński, S., Rzonca, B., Marszałek, H., Wąsik, M., Staśko, S., 2009. Groundwater of karst terrains in the Sudetes. In: Stefaniak, K., Tyc, A., Socha, P. (Eds.), Karst of the Częstochowa Upland and of the Eastern Sudetes: Palaeoenvironments and Protection. Studies of the Faculty of Earth Sciences. University of Silesia, No. 56, Sosnowiec–Wrocław, pp. 371–384.

Deharveng, L., Stoch, F., Gibert, J., Bedos, A., Galassi, D., Zagmajster, M., Brancelj, A., Camacho, A., Fiers, F., Martin, P., Giani, N., Magniez, G., Marmonier, P., 2009. Groundwater biodiversity in Europe. Freshw. Biol. 54, 709–726. https://doi.org/10.1111/j.1365–2427.2008.01972.x.

Dole-Olivier, M.-J., Malard, F., Martin, D., Leféburе, T., Gibert, J., 2009. Relationships between environmental variables and groundwater biodiversity at the regional scale. Freshw. Biol. 54, 797–813. https://doi.org/10.1111/j.1365-2427.2009.02184.x.

Dumnicka, E., 2014. Stygobitic oligochaetes (Annelida, Clitellata) in Poland with remarks on their distribution in Central Europe. Subterr. Biol. 14, 15–24. https://doi.org/10.3897/subtbiol.14.7700.

Dumnicka, E., Biesiadka, E., Namiotko, T., 2016. Zoobenthos (selected groups). In: Krzyściak–Kosińska, R., Wilk–Woźniak, E. (Eds.), The Aquatic Ecosystems of Białowieża National Park. Białowieża National Park, Białowieża, pp. 213–231.

Dumnicka, E., Galas, J., 2017. An overview of stygobiontic invertebrates of Poland based on published data. Subterr. Biol. 23, 1–18. https://doi.org/10.3897/subtbiol.23.11877.

Dumnicka, E., Galas, J., Krodkiewska, M., 2017. Patterns on benthic fauna distribution in wells: the role of anthropogenic impact and geology. Vadose Zone J. 16, 1–9. https://doi.org/10.2136/vzj2016.07.0057.

Dumnicka, E., Konopacka, A., Żurek, R., 2018. Changes in the benthic fauna composition in the Upper Vistula over the last 50 years – the consequences of the water pollution reduction and alien species invasion. Oceanol. Hydrobiol. Stud. 47, 303–312. https://doi.org/10.1515/ohs–2018–0029.

Dumnicka, E., Koszałka, J., 2005. The effect of draught on Oligochaeta communities in small woodland streams. Biologia 60, 143–150.

Ehlers, J., Grube, A., Stephan, H.–J., Wansa, S., 2011. Pleistocene glaciations of North Germany – new results. In: Ehlers, J., Gibbard, P.L., Hughes, P.D. (Eds.), Quaternary Glaciations – Extent and Chronology. Elsevier, Amsterdam, pp. 149–162.

Eme, D., Malard, F., Konecny-Dupre, L., Lef-Ebure, T., Douady, C.J., 2013. Bayesian phylogeographic inferences reveal contrasting colonization dynamics among European groundwater isopods. Mol. Ecol. 22, 5685–5699. https://doi.org/10.1111/mec.12520.

Fila, H., Grabska, I., Kilar, B., Laskoś, K., Pardulla, M., Szymańska, H., Włodarczyk, A., Wojda, A., Zięba, S., 1986. Atlas Zanieczyszczenia Rzek W Polsce – 1983. Instytut Ochrony Środowiska, Wrocław.

Fišer, C., Coleman, C.O., Zagmajster, M., Zwittnig, B., Gerecke, R., Sket, B., 2010. Old museum samples and recent taxonomy: a taxonomic biogeographic and conservation perspective of the *Niphargus tatrensis* species complex (Crustacea: Amphipoda). Org. Divers. Evol. 10, 5–22. https://doi.org/10.1007/s13127–010–0006–2.

Florczyk, H., Wasilewski, M., Jermolińska, K., Blezel, H., Korol, R., Grabska, I., Nalberczyński, A., 1971. Atlas Zanieczyszczenia Rzek W Polsce – 1967. Instytut Gospodarki Wodnej, Warszawa.

Galassi, D.M.P., 2001. Groundwater copepods: diversity patterns over ecological and evolutionary scales. Hydrobiologia 453/454, 227–253.

Gibert, J., Danielopol, D.L., Stanford, J.A., 1994. Groundwater Ecology. Academic Press, Inc., San Diego.

Gibert, J., Culver, D.C., 2009. Assessing and conserving groundwater biodiversity: an introduction. Freshw. Biol. 54, 639–648. https://doi.org/10.1111/j.1365–2427.2009.02202.x.

Gledhill, T., 1982. Water–mites (Hydrachnellae, Limnohalacaridae, Acari) from the interstitial habitat of riverine deposits in Scotland. Pol. Arch. Hydrobiol. 29, 439–451.

Gradziński, M., Hercman, H., Kicińska, D., Barczyk, G., Bella, P., Holubek, P., 2009. Karst in the Tatra Mountains – developments of knowledge in the last thirty years. Prz. Geol. 57, 674–684 (In Polish with English abstract).

Hahn, H.J., Fuchs, A., 2009. Distribution patterns of groundwater communities across aquifer types in south-western Germany. Freshw. Biol. 54, 848–860. https://doi.org/10.1111/j.1365-2427.2008.02132.x.

Hervant, F., Malard, F., 2012. Responses to low oxygen. In: White, W.B., Culver, D.C. (Eds.), Encyclopedia of Caves, second ed. Academic Press, Chennai, pp. 651–658.

Hewitt, G., 2000. The genetic legacy of the Quaternary ice ages. Nature 405, 907–913.

Hobbs III, H.H., 2012. Diversity patterns in the United States. In: White, W.B., Culver, D.C. (Eds.), Encyclopedia of Caves, second ed. Academic Press, Chennai, pp. 251–264.

Holsinger, J.R., 1980. *Stygobromus canadensis*, a new subterranean amphipod crustacean (Crangonyctidae) from Canada, with remarks on Wisconsin refugia. Can. J. Zool. 58, 290–297.

IBM Corp, 2016. IBM SPSS Statistics for Windows. Version 24. IBM Corp. Armonk, NY.

Isarin, R.B., 1997. Permafrost distribution and temperatures in Europe during the younger Dryas. Permafrost Periglac 8, 313–333.

Jania, J., 1993. Glacjologia. Wydawnictwo Naukowe PWN, Warszawa.

Karaman, G.S., Pinkster, S., 1977. Freshwater *Gammarus* species from Europe, North Africa and adjacent regions of Asia (Crustacea–Amphipoda). Part I. *Gammarus pulex*–group and related species. Bijdr. Dierkd. 47, 1–97.

Karpowicz, M., 2016. New data to the knowledge on the Harpacticoida (Crustacea, Copepoda) fauna in Poland. Fragm. Faun. 59, 87–98. https://doi.org/10.3161/00159301FF2016.59.2.087.

Knopik, J., 2011. Preliminary reconstruction of geometry of the ice sheet of the Odra galciation in northern part of the Cracow–Częstochowa Upland. Prz. Geol. 59, 474–478 (In Polish with English abstract).

Kornobis, E., Pálsson, S., Kristjánsson, B.K., Svavarsson, J., 2010. Molecular evidence of the survival of subterranean amphipods (Arthropoda) during Ice Age underneath glaciers in Iceland. Mol. Ecol. 19, 2516–2530. https://doi.org/10.1111/j.1365–294X.2010.04663.x.

Kur, J., Radwański, J.M., Mioduchowska, M., 2016. Investigation of the fauna in the Szmaragdowa/Szeptunów Cave in Poland: an example of short time colonization process. Acta Zool. Cracov. 59, 153–162. https://doi.org/10.3409/azc.59_2.153.

Leruth, R., 1939. La biologie du domaine souterrain et la faune cavernicoles de la Belgique. Mém. Mus. R. Hist. Nat. Belg. 87, 1–506.

Lewandowski, J., 2011. „Glacial Oasis" in the Cracow–Częstochowa Upland – results of studies during the last fifty years. Prz. Geol. 59, 732–738 (in Polish with English abstract).

Lindner, L., 2004. Outline of Pleistocene stratigraphy of the Holy Cross Mts. area in light of new data. In: Sołtysik, R. (Ed.), Quaternary of Poland on the Background of Older Bedrock Structures, Works of the Institute of Geography. Jan Kochanowski University in Kielce 13, pp. 7–31 (in Polish with English abstract).

Lindner, L., Marks, L., 1995. Outline of paleomorphology of the Polish territory during the Scandinavian glaciation. Prz. Geol. 43, 591–599 (in Polish with English summary).

Lindner, L., Marks, L., Nita, M., 2012. Climatostratigraphy of interglacials in Poland: middle and Upper Pleistocene lower boundaries from a polish perspective. Quat. Int. 292, 113–123. https://doi.org/10.1016/j.quaint.2012.11.01.

Mamos, T., Jażdżewski, K., Grabowski, M., 2016. Kryptyczne refugia oraz poglacjalna kolonizacja północnych Karpat na przykładzie *Gammarus balcanicus* (Crustacea Amphipoda). Materiały Konferencyjne XXIII Ogólnopolskie Warsztaty Bentologiczne. Lasy Janowskie 35–36, 19–21.05.2016.

Marks, L., Dzierżek, J., Janiszewski, R., Kaczorowski, J., Lindner, L., Majecka, A., Makos, M., Szymanek, M., Tołoczko–Pasek, A., Woronko, B., 2016. Quaternary stratigraphy and paleogeography of Poland. Acta Geol. Pol. 66, 403–427. https://doi.org/10.1515/agp–2016–0018.

Martin, P., de Broyer, C., Fiers, F., Michel, G., Sablon, R., Wouters, K., 2009. Biodiversity of Belgian groundwater fauna in relation to environmental conditions. Freshw. Biol. 54, 814–829. https://doi.org/10.1111/j.1365–2427.2008.01993.x.

Matolicz, A., Iglikowska, A., Namiotko, T., 2006. Małżoraczki (Ostracoda) źródeł Wyżyny Krakowsko–Częstochowskiej. Materiały XIII Ogólnopolskie Warsztaty Bentologiczne. Ochotnica–Kraków 81, 18–20.05.2006.

McInerney, C.E., Robertson, A.L.M., Knight, L.R.F.D., Arnscheidt, J., Venditti, C., Dooley, J.S.G., Mathers, T., Mattthijs, S., Eriksson, K., Proudlove, G.S., Hänfling, B., 2014. The ancient Britons: groundwater fauna survived extreme climate change over tens of millions of years across NW Europe. Mol. Ecol. 23, 1153–1166. https://doi.org/10.1111/mec.12664.

Meleg, I.N., Zakšek, V., Fišer, C., Kelemen, B.S., Moldovan, O.T., 2013. Can environment predict cryptic diversity? The case of *Niphargus* inhabiting Western Carpathian groundwater. PloS One 8, e76760. https://doi.org/10.1371/journal.pone.0076760.

Mojski, J.E., 2005. Ziemie Polskie W Czwartorzędzie Zarys Morfogenezy. Państwowy Instytut Geologiczny, Warszawa.

Namiotko, T., 1990. Freshwater Ostracoda (Crustacea) of Żuławy Wiślane (Vistula fen country, northern Poland). Acta Zool. Cracov. 33, 459–484.

Pešić, V., Chaniecka, K., 2006. Water mites (Acari: Hydrachnidia) from spring areas of the Gorce National Park in Poland. Lauterbornia 56, 49–59.

Proudlove, G.S., Wood, P.J., Harding, P.T., Horne, D.J., Gledhill, T., Knight, L.R.F.D., 2003. A review of the status and distribution of the subterranean aquatic Crustacea of Britain and Ireland. Cave Karst Sci. 30, 53–74.

Provan, J.K.D., Bennett, 2008. Phylogeographic insights into cryptic glacial refugia. Trends Ecol. Evol. 23, 564–571. https://doi.org/10.1016/j.tree.2008.06.010.

Rewicz, T., Wattier, R., Grabowski, M., Rigaud, T., Bącela–Spychalska, K., 2015. Out of the Black Sea: phylogeography of the invasive killer Shrimp *Dikerogammarus villosus* across Europe. PloS One 10, e0118121. https://doi.org/10.1371/journal.pone.0118121.

Rull, V., 2010. On microrefugia and cryptic refugia. J. Biogeogr. 7, 1623–1627. https://doi.org/10.1111/j.1365–2699.2010.02340.x.

Särkkä, J., Mäkelä, J., 1998. *Troglochaetus beranecki* Delachaux (Polychaeta, Archiannelida) in esker groundwaters of Finland: a new class of limnic animals for northern Europe. Hydrobiologia 379, 17–21.

Skalski, A.W., 1978. *Niphargus tatrensis* Wrześniowski, 1888 (Amphipoda) in the Kraków–Częstochowa Upland. Prz. Zool. 22, 40 (in Polish with English summary).

Skalski, A.W., 1980. *Niphargus leopoliensis* Jaworowski, 1893 (Amphipoda) in Poland. Prz. Zool. 24, 97–101 (in Polish with English summary).

Skalski, A.W., 1981. Underground Amphipoda in Poland, 2. V Rocznik Muzeum Okręgowego w Częstochowie, Przyroda, pp. 61–83 (in Polish with English summary).

Skalski, A.W., 1982. Groundwater fauna of the Małopolska Gap of the Vistula. Pol. Arch. Hydrobiol. 29, 387–404.

Stein, H., Griebler, C.H., Berkhoff, S., Matzke, D., Fuchs, A., Hahn, H.J., 2012. Stygoregions – a promising approach to a bioregional classification of groundwater systems. Sci. Rep. 2, 1–9. https://doi.org/10.1038/srep00673, 673.

Strayer, D.L., May, S.E., Nielsen, P., Wollheim, W., Hausam, S., 1995. An endemic groundwater fauna in unglaciated eastern North America. Can. J. Zool. 73, 502–508.

Stryjecki, R., 2009. Water mites (Acari, Hydrachnidia) of the Bug river valley between Włodawa and Kodeń. Teka Kom. Ochr. Kszt. Środ. Przyr. – OL PAN 6, 335–344.
Stryjecki, R., Pawlęga, K., Ścibior, R., 2012. Habitat distribution of water mites (Acari: Hydrachnidia) in Kozłowiecki landscape Park. Teka Kom. Ochr. Kszt. Środ. Przyr. – OL PAN 9, 224–233.
Sywula, T., 1981. Ostracoda of underground water in Poland. V Rocznik Muzeum Okręgowego w Częstochowie, Przyroda 2, 89–96 (in Polish with English summary).
Thienemann, A., 1950. Verbreitungsgeschichte derSüsswassertierwelt Europas. Versuch einer historischen Tiergeographie der europäischen Binnengewässer. Die Binnengewässer 18.
Tyráček, J., 2011. Continental glaciation of the Moravian gate (Czech Republic). J. Geol. Sci. - Anthropozoic 27, 39–49.
Vandel, A., 1964. Biospéologie. La Biologie des Animaux Cavernicoles. Gauthier–Villars, Paris.
Verovnik, R., Sket, B., Trontelj, P., 2005. The colonization of Europe by the freshwater crustacean *Asellus aquaticus* (Crustacea: Isopoda) proceeded from ancient refugia and was directed by habitat connectivity. Mol. Ecol. 14, 4355–4369. https://doi.org/10.1111/j.1365–294X.2005.02745.x.
White, W.B., Culver, D.C. (Eds.), 2012. Encyclopedia of Caves, second ed. Academic Press, Chennai.
Witek, M., 2010. Der Einfluss der Flussregulierung am Beispiel des Gebirgsflusses der Steine/Ścinawka zwischen Niedersteine und Glatz. Przyroda Sudetów 13, 275–292 (in Polish with German summary).
Witek, M., Latocha, A., 2009. Zabudowa hydrotechniczna Bystrzycy Dusznickiej w warunkach zmian społeczno–gospodarczych w ciągu ostatnich 100 lat. In: Bochenek, W., Kijowska, M. (Eds.), Zintegrowany monitoring środowiska przyrodniczego. Funkcjonowanie środowiska przyrodniczego w okresie przemian gospodarczych w Polsce. Biblioteka Monitoringu Środowiska, Szymbark, pp. 154–171.
Zawal, A., 2006. Materials for knowledge of water mites (Acari: Hydrachnidia) in the neighbourhood of Złocieniec (NW Poland). Zesz. Nauk. Uniw. Szczecińskiego. Acta Biol. 13, 163–168 (In Polish with English summary).
Zawal, A., Sadanowicz, P., 2012. Water mites (Hydrachnidia) of the „Źródlisko Skrzypowe" nature reserve. Parki Nar. Rez. Przyr. 31, 3–10 (in Polish with English abstract).
Zielinski, R., Soroka, M., Wachowiak–Zielinska, M., 1996. Genetic variability in selected Polish population of *Dreissena polymorpha* (Pallas) (Bivalvia: Dreissenidae). J. Appl. Gen. 37, 105–120.
Zieliński, P., Jekatierynczuk-Rudczyk, E., 2010. Dissolved organic matter transformation in the hyporheic zone of a small lowland river. Oceanol. Hydrobiol. Stud. 39, 97–103. https://doi.org/10.2478/v10009-010-0021-9.