Acta zoologica cracoviensia, 59(2) 2016
Kraków, 30 December, 2016
ISSN 2299-6060, e-ISSN 2300-0163
doi:10.3409/azc.59_2.153
ISEA PAS
© Institute of Systematics and Evolution of Animals, PAS

Investigation of the fauna in the Szmaragdowa/Szeptunów Cave in Poland: an example of short time colonization process

Jarosław KUR, Jerzy Michał RADWAŃSKI and Monika MIODUCHOWSKA

Received: 15 March 2016. Accepted: 11 November 2016. Available online: 08 December 2016.

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**(2): 153-162.

We provide the first report on the process of cave colonization and taxa inhabiting the Szmaragdowa Cave, discovered and made open only 25 years ago. The cave is located in the Kraków-Częstochowa Upland (southern Poland) – a region where glacial influence has been observed in the past. Faunal composition of the cave is reported and discussed, along with chemical parameters of water bodies. Noteworthy is the absence of aquatic fauna.

Key words: Cave fauna, cave colonization, the Kraków-Częstochowa Upland.

✉ Jarosław KUR, Institute of Nature Conservation, Polish Academy of Science, Mickiewicza 33, 31-120 Kraków, Poland.
E-mail: jarek.kur@gmail.com
Jerzy Michał RADWAŃSKI, Institute of Systematics and Evolution of Animals, Polish Academy of Science, Sławkowska 17, 31-016 Kraków, Poland.
Monika MIODUCHOWSKA, Department of Genetics, Faculty of Biology, University of Gdańsk, Wita Stwosza 59, 80-308 Gdańsk, Poland.

I. INTRODUCTION

A cave is defined as a natural underground or underwater hollow place with an opening, mostly formed in limestone. For cavers, a cave is a natural hole, which can be penetrated by humans. Although this definition is arbitrary, it is a practical one since only those caves that can be penetrated by humans can be directly studied (ROMERO 2009). In Poland, karst topography can be observed mainly in the Kraków-Częstochowa Upland and the Western Tatra Mts., and to a lesser extent in the mountains Pieniny, Świetokrzyskie, and Sudetes (BAJKIEWICZ-GRABOWSKA 2001).

It is believed that the main factor influencing the distribution of individual taxa in the caves and the so-called “windows to the subterranean environment” (wells, mines or shafts) is the occurrence of glaciations in the past (GALASSI et al. 2001, 2002; STOCH 2000, 2003). Considering the degree of adaptation to subterranean environments, the species inhabiting the caves can be classified as troglobionts, troglophiles and trogloxens (or stygo -bionts, -philes and -xens – for aquatic taxa). Stygobionts are closely associated with groundwaters through the whole life cycle, and only occasionally may occur in surface waters. Stygophiles can often be found in springs, karst springs, pit caves or interstitial waters. They reproduce in the subterranean environment and may have developed a varying degree of features considered characteristic of stygobionts (but they are also present in typical surface waters). The stygoxens in turn are organisms occasionally occurring in the subterranean environment, but periodically they may be present there in large numbers (STOCH 1995).

There is little evidence for animal colonization of "newly open" caves. ASHMOLE et al. (1992) described the animal succession in the lava tube caves of the Canary Islands. They found that the first hypogean communities were characterized by pioneering epigean species common in the surrounding areas that were opportunistically taking advantage of the new environment, mostly for feeding or seeking shelter from predators during the day (ROMERO 2012). Caves are similar to other extreme environments and could be invaded by living organisms following the most conspicuous of all of the evolution's characteristics, i.e., opportunism. Currently, we truly know very little about succession in hypogean environments and how/if organisms interact together (ROMERO 2012). GERS (1998) found that the migration of animals and some organic material could be transported through alternative routes to the cave entrance. HOLSINGER (2000) argued that hypogean environments are 'harsh' because they are poor in nutrients, however, the available data do not confirm this statement as a valid generalization (ROMERO 2009). According to ROMERO (2009) and BELLÈS (1991) the animals that colonize caves can find in those habitats food (FERREIRA & MARTINS 1999), reproductive niches (ROGOWITZ et al. 2001; BRIGGLER & PUCKETTE 2003), protection from predators (ROMERO 1985; TABUKI & HANAI 1999), protection against desiccation (JENSEN et al. 2002), and a place for hibernation (RESETARITS 1986; ZHANG 1986). A cave offers various degree of stability for animals: the closer to the entrance the less stable a cave is. As a result, zonation can be observed in caves (ROMERO 2012).

Collembola are the most abundant arthropod and hexapod taxa in cave ecosystems. However, the typical troglomorphic traits of collembolan taxa, observed in species inhabiting southern and eastern European karst cave ecosystems, are often missing in species from central European cave habitats (MARX & WEBER 2015). This discrepancy was explained by insufficient evolutionary time for troglomorphy to evolve since the last glaciation (CHRISTIAN 2002; PIPAN & CULVER 2012). After deglaciation, surface-dwelling species occupied subterranean habitats and were able to establish stable communities in these ecosystems (CHRISTIAN 2002). Also, the migration of surface-dwelling springtail species into "newly built" subterranean habitats should be extremely high, as observed by MARX & WEBER (2015) in caves and mines of Germany.

Over the past 50 years the understanding of the functioning of groundwater ecosystem in Poland has greatly increased. The cave fauna of the Upland was initially investigated by DEMEL (1918) and followed by other authors, including SKALSKI (1973), BARANEK & POWICHROWSKI (1975), SZEPTYCKI (1967) and SANOCKA-WOŁOSZYNOWA (1981). The subterranean water fauna was investigated by DUMNICKA (1977) and SKALSKI (1978, 1981). Thus far, only several stygobionts are known from the Kraków-Częstochowa Upland (DUMNICKA & WOJTAN 1990). This may be a result of sampling methods – pools and siphons were found only in a few caves in this area. Moreover, the caves in the Upland have not been systematically examined (SKALSKI 1981; DUMNICKA & WOJTAN 1990).

A basic chemical investigation of cave water in the Upland was carried out by DUMNICKA & WOJTAN (1990). The industrial and agricultural impact on the physical and chemical properties of groundwater in the Upland was investigated by GALAS (2005). It was observed that the abundance and distribution of aquatic fauna in such water bodies depends on their chemical composition (DUMNICKA 1977; DUMNICKA & WOJTAN 1990; GALAS 2005; KOPERSKI et al. 2011).

Our continuing studies on the cave known as the Szmaragdowa Cave are pioneering investigations. This cave is the latest great speleological discovery made during commercial stone quarrying in the Upland and has been explored since 1990 (RYBAK 1990). Until then, the Szmaragdowa Cave was not known to science and the entrance was closed. We aimed to inspect the occurrence of cave fauna and surface species, which colonized the Szmaragdowa Cave and we associated their distribution with the influence of constantly changing environmental conditions.

II. MATERIAL AND METHODS

This investigation was carried out in the Szmaragdowa Cave, also known as Szeptunów Cave. It is situated in Rudniki village (50°53´ N, 19°12´ E) near Częstochowa on the Kraków-Częstochowa Upland (southern Poland) (Fig. 1). This area mainly consists of a layer of Upper Jurassic limestone up to 400 m thick. More than 1,800 caves and rock shelters have been discovered in this region (GRADZIŃSKI & SZELEREWICZ 2004). The cave has been explored since 1990 (RYBAK 1990). Currently available knowledge states that

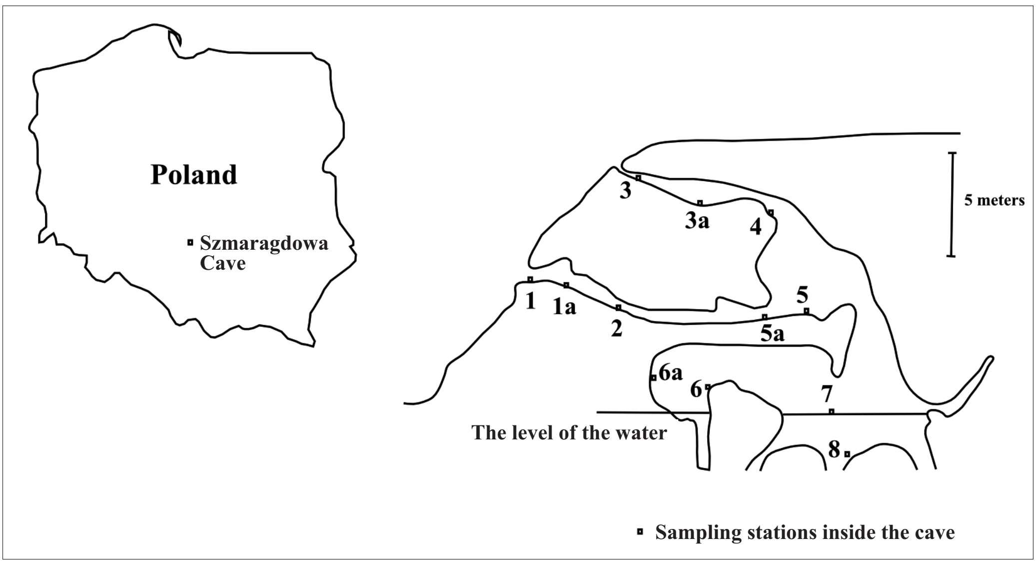

Fig. 1. Map of Poland with the localization of the investigated cave in the Kraków-Częstochowa Upland and horizontal section of the Szmaragdowa Cave with sampling stations.

the cave was totally closed and isolated from the surface environment. After 1990, the cave was permanently open and provides an unlimited access; in the last two years the second exit of the cave was explored. The cave was formed in marly limestone rock with Late Jurassic flints (GRADZIŃSKI & SZELEREWICZ 2004).

The Szmaragdowa Cave is horizontal with narrow passages and leads into a shaft in its farthest section. It has only one main entrance with a small window in the highest shaft. The Szmaragdowa Cave system is 300 m long (Fig. 1). The cave contains a permanent water body with a siphon in its deepest part. The water level of the siphon is situated above the level of local groundwater.

An invertebrate fauna was collected several times from eight sample stations (Fig. 1) using four methods.

Firstly, in December 2005, March 2006 and November 2006, animals were sampled from the surface of the siphon with a plankton net (mesh size 60 µm) and a scraper, and in December 2005 from the bottom with a net (mesh size 0.3 mm). Further bottom samplings were performed in August 2010, June 2014 and May 2015. These procedures were carried out using scuba diving techniques.

Secondly, samples from clay sediments were collected in March and November 2006. Each of them weighed ca. 0.5 kg. Subsequently, arthropods were extracted with the use of Tullgren funnels (HOPKIN 1997) for one week. Part of the fauna was manually separated under a stereomicroscope in a laboratory (at magnifications 60-100x). After the separation and extraction process had been completed, the organisms were identified under an optical microscope with a magnification of 1200-1700x.

Thirdly, baits (CHRISTIANSEN 1970) of cottage cheese with bread were applied at seven different stations in November 2006. These baits were removed after three weeks and again arthropods were extracted using Tullgren funnels for one week.

Fourthly, animals were collected using an exhauster. All fauna specimens obtained were preserved in 96% alcohol or 4% solution of formaldehyde.

Bats were observed in various stations in March and November 2006.

Collected water samples for chemical analysis were stored in plastic bottles. Samples for biochemical oxygen demand (BOD_5) and dissolved oxygen analysis were put into standard laboratory glass containers. Water chemistry analyses were carried out in the laboratory according to the methods described by the AMERICAN PUBLIC HEALTH ASSOCIATION (1992). The temperatures were measured *in situ*.

III. RESULTS

The specimens collected in the cave belong to different groups of animals (Table 1). The trogloxens were represented by: *Cylisticus convexus* (DE GEER, 1778) – Crustacea, *Tomocerus vulgaris* (TULLBERG, 1871), *Folsomia candida* (WILLEM, 1902) – Collembola, *Blaniulus guttulatus* (FABRICIUS, 1798) – Myriapoda, *Scoliopteryx libatrix* (LINNAEUS, 1758), *Triphosa dubitata* (LINNAEUS, 1758) – Insecta, and Mammalia: *Plecotus auritus* (LINNAEUS, 1758), *Myotis myotis* (BORKHAUSEN, 1797), *Myotis daubentonii* (KUHL, 1817). The following troglophiles were observed: *Meta menardi* (LATREILLE, 1804) –

Table 1

List of taxa sampled at particular sampling stations with sampling methods

Taxa and sampling methods	Sampling stations											
	1	1a	2	3	3a	4	5	5a	6	6a	7	8
Isopoda												
Cylisticus convexus (de Geer, 1778) (CL)					+							
Collembola												
Tomocerus vulgaris (Tullberg, 1871) (E)	+											
Heteromurus nitidus (Templeton, 1835) (SS)											+	
Folsomia candida (Willem, 1902) (SS)											+	
Deuterophorura cebennaria (Gisin, 1956) (SS) (CC) (S)							+		+		+	
Arrhopalites sp. (S)					+							
Myriapoda												
Blaniulus guttulatus (Fabricius, 1798) (SS) (CC)					+						+	
Symphyla sp. (CC) (SS) (CC)											+	
Arachnida												
Meta menardi (Latreille, 1804) (O)		+	+	+				+				
Acari sp. (O) (CC)	+		+	+	+	+		+				
Insecta												
Scoliopteryx libatrix (Linnaeus, 1758) (O)	+		+	+		+	+					
Triphosa dubitata (Linnaeus, 1758) (O)	+		+	+				+				
Oligochaeta												
Enchytreus sp. (CL)										+		
Chiroptera												
Myotis myotis (Borkhausen, 1797) (O)							+					
Myotis daubentonii (Kuhl, 1817) (O)					+							
Plecotus auritus (Linnaeus, 1758) (O)			+									

(SS) – Samples from the surface of the water body
(CL) – samples from clay sediments
(CC) – cottage cheese method
(E) – samples collected with the use of exhaustor
(O) – observation
(S) – sampled near the excrement of mammals or from mud.

Arachnida, *Heteromurus nitidus* (Templeton, 1835), *Deuterophorura cebennaria* (Gisin, 1956) – Collembola (Martynova 1969; Pomorski 1998). Additionally, some of trogloxenic fauna (Symphyla and Acari) recovered in the samples and Diptera (mainly Culicidae) found on walls were not identified to the species level. Typical aquatic taxa were not found but terrestrial species were observed on the surface of the water body (Fig. 2).

Table 2 presents a comparison of chemical parameters of water from the Szmaragdowa Cave, a similar Mąciwody Cave, and springs from northern part of the Upland. Good oxygen saturation and somewhat elevated nitrate levels were recorded, as well as increased concentration of chlorides. The average temperature in the Szmaragdowa Cave was about 9°C during the winter season, the average temperature was about 11°C.

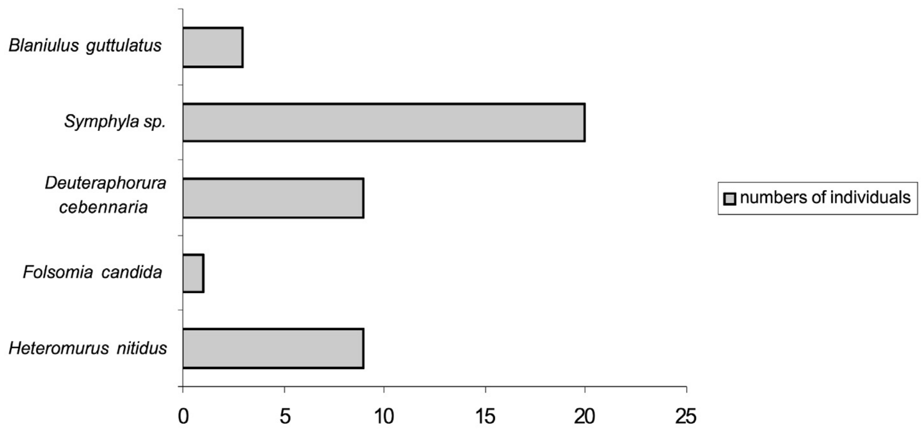

Fig. 2. Number of individuals found during sampling from the surface of the water body (station no. 7).

Table 2

Chemical parameters of water from the investigated cave, the average from springs of the Northern part of the Upland (GALAS 2005) and the maximum value from the Mąciwody Cave in the Upland (DUMNICKA & WOJTAN 1990) (* recalculated from N-NO_3)

Variable	Units	Szmaragdowa Cave	Average of parameters of springs waters of North Upland	Mąciwody Cave (maximum)
pH		7.6	7.9	7.4
Conductivity	µS	528	355.2	427.5
Oxygen dissolved	O_2 mg dm^{-3}	8.16	10.4	10.4
Oxygen saturation	O_2 %	73.1	78	92.9
Calcium	Ca mg dm^{-3}	68.7	25.3	96.5
Magnesium	Mg mg dm^{-3}	21	13	34
Sulphate	SO_4 mg dm^{-3}	52.3	14.2	57.1
Ammonia	N-NH_4 mg dm^{-3}	0.23	0.3	0.22
Nitrate	NO_3^- mg dm^{-3}	26.9	6.6	38.2*
Phosphate	PO_4 mg dm^{-3}	0.1	0.4	0.15
Chloride	Cl^- mg dm^{-3}	24.3	3.34	19.5

IV. DISCUSSION

The Szmaragdowa Cave was opened in 1990. It might appear that nothing in the ecological balance of this cave would change in the short time that has passed since its discovery. However, despite the fact that one would expect to find many troglo- and stygoxenic and troglo- and stygophilic species in this cave – as in other caves in Upland (SZEPTYCKI 1967; SKALSKI 1973; SANOCKA-WOŁOSZYNOWA 1981; DUMNICKA & WOJTAN 1990; DUMNICKA 2005) – it turns out that the number of terrestrial species is low whereas aquatic fauna have not been observed there. The overall terrestrial invertebrate fauna in this cave is generally similar to the fauna of other caves in the Upland. Butterflies (*Scoliopteryx libatrix* and *Triphosa dubitata*), a spider (*Meta menardi*) and three taxa of springtails (*Heteromurus nitidus*, *Arrhopalites* sp. and *Tomocerus vulgaris*) are very common in this region (KOWALSKI 1955; SZEPTYCKI 1967). *Deuterophorura cebennaria* has been observed in caves in other regions, e.g., Sudetes (POMORSKI 1998) and in an old non-ferrous metal mine in Tarnowskie Góry (KŁYS 2004), but before our study it has never been recorded in the caves of the Kraków-Częstochowa Upland. According to earlier studies (CHRISTIANSEN 1970), some of those species could have been introduced by humans. The same situation probably occurs in the Szmaragdowa Cave, e.g., *Folsomia candida*, a cosmopolitan species often associated with the environment cultivated by man, such as greenhouses, flowers pots, etc. (POTAPOV 2001).

Collembola, as well as other invertebrates (except singular enchytraeids) were not observed in clay sediment samples, but were present in the samples from mouldy detritus, which accumulated in some places. This observation may lead to the conclusion that the amount of organic matter in clay sediments is not sufficient for detritivorous species, and animals migrate in search of suitable food. Migration would explain the fact that Collembola occurred in bait three weeks after it was set. A comparison between the Szmaragdowa Cave and a larger cave, e.g., Karst Moulis in the Pyrenees, shows that the biodiversity of Collembola in the former is greater (compare CHRISTIANSEN 1970).

Various taxa of aquatic fauna and some stygobiontic species were found during the previous studies carried out in the caves in the Kraków-Częstochowa Upland (SKALSKI 1978; DUMNICKA & WOJTAN 1990; DUMNICKA 2005; KUR 2006; DUMNICKA 2014), but despite many attempts, aquatic fauna has never been found in the Szmaragdowa Cave up to 2015. This absence of aquatic invertebrates such as Copepoda, Ostracoda, Amphipoda or Oligochaeta in the cave under investigation was not caused by water pollution. Groundwater with only a limited human influence – such as tested by GALAS (2005) – contained low amounts of nitrates and chlorides and in the Szmaragdowa Cave the value of this last parameter was slightly augmented only. The remaining chemical parameters were not significantly different from the values obtained in other caves and springs (Table 2) and were typical for waters in limestone areas. Water chemistry is not necessarily a limiting factor for aquatic fauna. In the polluted caves, such as the Smocza Jama Cave and Kryspinowska Cave in the Upland, water fauna was present in large quantities, and one stygobiontic species was found (DUMNICKA & WOJTAN 1990). The lack of aquatic fauna is probably caused by the location of the studied water body above the groundwater table. The migration of invertebrates to this perched water body would be impossible due to the presence of non-permeable sediments (clay) in the substratum.

Some fauna groups that do not usually occur on the surface of water bodies have been found at the Szmaragdowa Cave (example: Fig. 2). Probably, the reason for their occurrence inside the cave is migration through cracks formed during the exploitation of the quarry. In this case, the water surface would be a natural trap for these animals.

In turn, the relatively high temperature of the cave water is a result of the mean air temperature for this region and its effect on stagnant water (CHEŁMICKI 2001).

Additionally, some remarks on the fauna of bats in the cave. Many studies on bats were carried out in the Upland and 15 species of bats were recorded by POSTAWA & ZYGMUNT (2000). Among the bat species known from this area, only three were observed in the Szmaragdowa Cave: *Plecotus auritus, Myotis myotis,* and *Myotis daubentonii*. Before our investigation, POSTAWA reported the presence of bats in this cave (pers. comm.).

Judging from low accumulation of organic matter and scarce fauna the Szmaragdowa Cave was not accessible before the quarry exploitation and could not be colonized by animals by entering the cave. Terrestrial animals could migrate from epigean environments into the cave via the cracks or fissures formed during the quarry works (e.g., CROUAU-ROY et al. 1992).

In summary, according to BELLÈS (1991), many modern discoveries of cave-restricted animals in lava tubes and European artificial environments have led us to reconsider classic interpretation of cave colonization processes, which in the past were mainly based on the direct influence of glaciation. This author confirmed that organisms can colonize caves (in a short time) for several reasons, including survival, opportunism, convenience. All of these colonization types can be used to explain faunal findings in the Szmaragdowa Cave. Our results are also consistent with the research of MARX & WEBER (2015) on caves and artificial environments in Germany.

Acknowledgements. The research were supported by a grant from The National Center of Science in Poland (Nr ID 46387 N N304 326236). We would like to thank Prof. Elżbieta DUMNICKA for unstinting support.

REFERENCES

AMERICAN PUBLIC HEALTH ASSOCIATION. 1992. Standard Methods for the Examination of Water and Wastewater. 18th edition, APHA, Washington, D.C.: 2-28.

ASHMOLE N.P., OROMI A., ASHOME M.J. & MARTIN J.L. 1992. Primary faunal succession in volcanic terrain: lava and cave studies on the Canary Islands. *Biological Journal of the Linnean Society*, **46**: 207-234.

BAJKIEWICZ-GRABOWSKA E. 2001. Zasoby wodne, gospodarka wodna. Elektroniczny atlas środowiska Polski [Water resources, water management. Electronic Atlas of Polish Environment]. Centrum Informacji o Środowisku, UNEP/GRID Warszawa. (In Polish).

BRIGGER J.T., PUCKETTE W.L. 2003. Observations on reproductive biology and brooding behavior of the Ozark zigzag salamander, *Plethodon angusticlavius*. *The Southwestern Naturalist*, **48**: 96-100.

BELLÈS X. 1991. Survival, opportunism and convenience in the processes of cave colonization by terrestrial faunas. *Oecologia Aquatica*, **10**: 325-335.

BARANEK W., POWICHROWSKI L. 1975. Jaskinie Doliny Wodącej i ich fauna [Caves in Valley Wodąca and their fauna]. *Chrońmy Przyrodę Ojczystą*, **5**: 64-71. (In Polish).

CHEŁMICKI W. 2001. Springs of the Kraków-Wieluń and Miechów Uplands. Changes between 1973 and 2000. Kraków, Jagiellonian University, 127 pp. (In Polish, with English summary).

CHRISTIAN E. 2002. Distribution patterns of cavernicolous Collembola in Austria. *Pedobiologia*, **46**: 261-266.

CHRISTIANSEN K. 1970. Invertebrate populations in the Moulis Cave. *Annales de Spéléologie*, **25**(2): 244-273.

CROUAU-ROY B., CROUAU Y., FERRE C. 1992. Dynamic and temporal structure of the troglobitic beetle *Speonomus hydrophilus* (Coleoptera: Bathysciinae). *Ecography*, **15**: 12-18.

DEMEL K. 1918. Fauna jaskiń Ojcowskich [The fauna of the caves in Ojców]. *Sprawozdanie z Posiedzenia Towarzystwa Nauk, Warszawskiego Wydziału Matematyczno-przyrodniczego*, **11**: 623-659. (In Polish).

DUMNICKA E. 1977. Annual changes of oligochaete fauna in cave of the Kraków-Częstochowa Upland. *Proc. 7th ISC, Sheffield*: 163-165.

DUMNICKA E. 2005. Stygofauna associated with springfauna in southern Poland. *Subterranean Biology*, **3**: 29-36.

DUMNICKA E. 2014. Stygobitic oligochaetes (Annelida, Clitellata) in Poland with remarks on their distribution in Central Europe. *Subterranean Biology*, **14**: 15-24.

DUMNICKA E., WOJTAN K. 1990. Differences between cave water ecological systems in the Kraków-Częstochowa Upland. *Stygologia*, **5**(4): 241-247.

FERREIRA R.L., MARTINS R.P. 1999. Trophic structure and natural history of bat guano invertebrate communities, with special reference to Brazilian caves. *Tropical Zoology*, **12**: 231-252.

GALAS J. 2005. Human impact on physical and chemical properties of springs from Kraków-Częstochowa Upland (Southern Poland). *Polish Journal of Ecology*, **53**(3): 329-341.

GALASSI D., DE LAURENTIIS P., PETITTA M., MARINELLI G., FIASCA B. 2001. Influenza dei fattori storici ed ecologici sulla biodiversita animale: la copepodofauna (Crustacea: Copepoda) delle sorgenti di Presciano (Fiume Tirino, L'Aquila, Abruzzo). [In:] B. CICOLANI (a cura di) (eds). Monitoraggio Biologico del Gran Sasso, **2**: 160-182.

GALASSI D., MARMONIER P., DOLE-OLIVIER M.J., RUNDLE S. 2002. Microcrustacea. [In:] S.D. RUNDLE, A.L. ROBERTSON, J.M. SCHMID-ARAYA (eds). Freshwater Meiofauna: Biology and Ecology, Backhuys Publishers, Leiden, Pp: 135-175.

GERS C. 1998. Diversity of energy fluxs and interactions between arthropod communities: from soil to cave. *Acta Oecologica*, **19**: 205-213.

GRADZIŃSKI M., SZELEREWICZ M. 2004. Jaskinie Wyżyny Krakowsko-Wieluńskiej – liczba i rozmieszczenie [Caves in the Kraków-Wieluń Upland – number and distribution]. [In:] J. PARTYKA (eds). The diversification and transformation of natural and cultural environment of the Kraków-Częstochowa Upland, Volume 1: Nature. Ojców. Pp. 69-82. (In Polish).

HOLSINGER J.R. 2000. Ecological derivation, colonization, and speciation. [In:] D.C. WILKENS, D.C. CULVER, W.F. HUMPHRIES (eds). Subterranean Ecosystems, Ecosystems of the World 30, Elsevier, Pp. 399-415.

HOPKIN S.P. 1997. Biology of the Springtails (Insecta: Collembola). Oxford, UK: Oxford University Press, 330 pp.

JENSEN J.B., CAMP C.D., MARSHALL J.L. 2002. Ecology and life history of the pigeon salamander. *Southeastern Naturalist*, **1**: 3-16.

KŁYS G. 2004. Przyroda Podziemi Tarnogórskich [Underground nature of Tarnowskie Góry]. Oddział Katowicki: Polskie Towarzystwo Geograficzne, 109 pp. (In Polish).

KOPERSKI P., DUMNICKA E., GALAS J. 2011. A biotic parameters determining fauna composition in karstic springs. *Polish Journal of Ecology*, **59**: 153-163.

KOWALSKI K. 1955. Fauna jaskiń [Cave fauna]. *Kosmos*, **3**(14): 387-404. (In Polish).

KUR J. 2006. Distribution of small crustaceans in an old inundated Fort in Krakow (Poland): 18th International Symposium of Biospeleology Cluj-Napoca, Romania, p. 44-45.

MARTYNOVA E. 1969. Springtails of the family Tomoceridae (Collembola) from the fauna of the USSR. *Entomological Review*, **43**: 299-314. (In Russian).

MARX M.T., WEBER D. 2015. Cave Collembola from Southwestern Germany. *Soil Organisms*, **87**(3): 221-228.

PIPAN T., CULVER D. C. 2012. Convergence and divergence in the subterranean realm: A reassessment. *Biological Journal of the Linnean Society*, **107**: 1-14.

POMORSKI R.J. 1998. Onychiurinae of Poland (Collembola: Onychiuridae). *Genus* (*Supplement*), 1-201.

POSTAWA T., ZYGMUNT J. 2000. Zmiany liczebności nietoperzy (Chiroptera) w jaskiniach Wyżyny Częstochowskiej w latach 1975-1999 [Changes in the number of bats (Chiroptera) in the caves of Częstochowa Upland in the years 1975-1999]. *Studia Chiropterologica*, **1**: 83-114. (In Polish).

POTAPOV M.B. 2001. Synopses on Palaearctic Collembola: Isotomidae. *Abhandlungen und Berichte des Naturkundemuseums Görlitz*, **73**(2): 1-603.

RESETARITS S.J.Jr. 1986. Ecology of cave use by the frog, *Rana palustris*. *American Midland Naturalist*, **116**: 256-266.

ROGOWITZ G.L., CANDELARIA C.L., DENIZARD L.E., MELENDEZ L.J. 2001. Seasonal reproduction of a neotropical frog, the cave coqui (*Eleutherodactylus cooki*). *Copeia*, **2**: 542-547.

ROMERO A. 1985. Cave colonization by fish: role of bat predation. *American Midland Naturalist*, **113**:7-12.

ROMERO A. 2009. Cave Biology: Life in Darkness. Cambridge: Cambridge University Press, 291 pp.

ROMERO A. 2012. Caves as biological spaces. *An Interdisciplinary Arts and Sciences Journal, Polymath*, **2**(3): 1-15.

RYBAK J. 1990. Jaskinia Szeptunów [Szeptunów Cave]. *Eksplorancik,* Kraków, **2**(16). (In Polish).

SANOCKA-WOŁOSZYNOWA E. 1981. The investigation of Spiders (Aranei, Opiliones, Pseudoscorpionida) on Kraków-Częstochowa Upland. *Acta Universitatis Wratislaviensis*, **11**: 1-92.

SKALSKI A. 1973. Materiały do znajomości bezkręgowców jaskiń Wyżyny Krakowsko-Częstochowskiej [Materials to the knowledge of invertebrates in the caves of the Kraków-Częstochowa Upland]. III Rocznik Muzeum Okręgowego w Częstochowie. *Przyroda*, 161-200. (In Polish).

SKALSKI A. 1978. Studniczek tatrzański *Niphargus tatrensis* WRZEŚNIOWSKI, 1888 (Amphipoda) na Wyżynie Krakowsko-Częstochowskiej [*Niphargus tatrensis* WRZEŚNIOWSKI, 1888 (Amphipoda) in the Kraków-Częstochowa Upland]. *Przegląd Zoologiczny*, pp. 22-40. (In Polish).

SKALSKI A. 1981. Charakterystyka fauny podziemnej Wyżyny Krakowsko-Częstochowskiej [Characteristics of the underground fauna of the Kraków-Częstochowa Upland]. V Rocznik Muzeum Okręgowego w Częstochowie. *Przyroda*, **2**: 51-59. (In Polish).

SZEPTYCKI A. 1967. Fauna of the springtails (*Collembola*) of the Ojców National Park in Poland. *Acta zoologica cracoviensia*, **12**(10): 219-280.

STOCH F. 1995. The ecological and historical determinants of crustacean diversity in groundwaters, or: why are there so many spacies? *International Journal of Subterranean Biology*, **22**: 139-160.

STOCH F. 2000. Indagini sulla fauna acquatica delle grotte del Trentino (Italia settentrionale). *Studi Trentini di Scienze Naturali, Acta Biologica*, **74**: 117-132.

STOCH F. 2003. Indagini ecologiche e faunistiche sulla meiofauna (Acari e Crostacei) di alcune sorgenti del Parco Naturale delle Prealpi Giulie (Italia nord-orientale). *Gortania, Atti Museo Friulano di Storia Naturale di Udine*, **25**: 239-25.

TABUKI R., HANAI T. 1999. A new sigillid ostracod from submarine caves of the Ryukyu Islands, Japan. *Palaeontology*, **42**: 569-593.

ZHANG C. 1986. On the ecological adaptation and geographical distribution of the barbine fish *Varicorhinus* (*Scaphestes*) *macrolepis*. *Acta Zoologica Sinica*, **32**: 266-272.