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Cave dwelling springtails (Collembola) of Hungary: a review

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Abstract

A historical review of Hungarian cave springtail studies is given. All literature concerning this field is compiled and the species are listed along with their localities. In spite of the relatively low number of caves investigated regarding their Collembola fauna, 67 species have been reported from Hungarian caves until now. Eleven taxa are endemic to the cave or karst system where they were described from, which indicates highly promising perspectives for further biospeleological research in Hungary. The listed species are discussed in relation to the collembolan fauna of neighbouring countries and an attempt is made to discern zoogeographical patterns within the country.

Keywords: Biospeleology, troglobiont, faunistics, endemism, subterranean

1. Introduction

Cave fauna is generally highly specific and especially interesting for faunistics, biogeography and evolutionary biology (Romero 2009). Thus, Hungarian biospeleological research started as early as the middle of the 18th century (Frivaldszky 1865). In spite of this, caves in this country are far from being thoroughly investigated regarding their Collembola fauna, even though Hungary is relatively poor in caves due to its geographical situation compared with surrounding countries. Nevertheless, work in this field almost completely ceased in Hungary towards the end of the 1960's, while biospeleological studies on springtails continued in neighbouring countries (see for example Kováč 2000, Novak 2005 and Kováč & Papáč 2010 for Slovakia, Gruia 2003 for Romania, Vargovich 2005 for the Ukraine, Lukić & Deharveng 2008 and Lukić et al. 2010 for Croatia, Christian & Spötl 2010 for Austria). Even though there is little material available on Hungarian caves, an overview of the data on cave Collembola has never been given in a comprehensive article. A critical review of the data is required since a large amount of the information is scattered in articles published in different journals and because of changes in caves' names makes it very difficult to locate several localities exactly. Thus, a survey on past activities is presented here, including an inventory – according to our present knowledge – of cave-dwelling springtails in Hungary, along with a discussion regarding their geographical distribution and taxonomy as a basis for future research.

1.1. History

The first collembolan collections in Hungarian caves were carried out by Elemér Bokor, Endre Dudich and Antal Gebhardt during the 1920’s and 1930’s. Dudich, the founder of the world’s fourth biospeleological laboratory, worked mainly in the cave Baradla (Aggtelek Karst, NE Hungary, see Fig. 1). Gebhardt investigated the fauna of two caves situated in the Mecsek Mts. (S Hungary), while Bokor collected in several caves throughout the country. Their specimens were identified by the renowned Polish collembologist Jan Wacław Stach, who first reported 14 species (Stach 1929) and subsequently 12 more (Stach 1934, 1945, 1947, 1949, 1951, 1954, 1956) (Tab. 1). Four of his species from Dudich’s and Bokor’s material were new to science, three of them being still valid [*Pygmarrhopalites aggtelekiensis* (Stach, 1929), *Pseudosinella aggtelekiensis* (Stach, 1930), *Hymenaphorura pseudosibirica* (Stach, 1954)], while *Onychiurus subterraneus* Stach, 1929 (from Hajnóczy, Csókás and Anna Caves) was synonymized later by Stach (1934) himself [*Deuteraphorura inermis* (Tullberg, 1869) in the present paper]. Stach’s records were repeated and his further data published in Bokor’s (1924, 1925), Dudich’s (1930, 1932a, 1932b) and Gebhardt’s (1933, 1934, 1937, 1963) comprehensive works (Tab. 1).

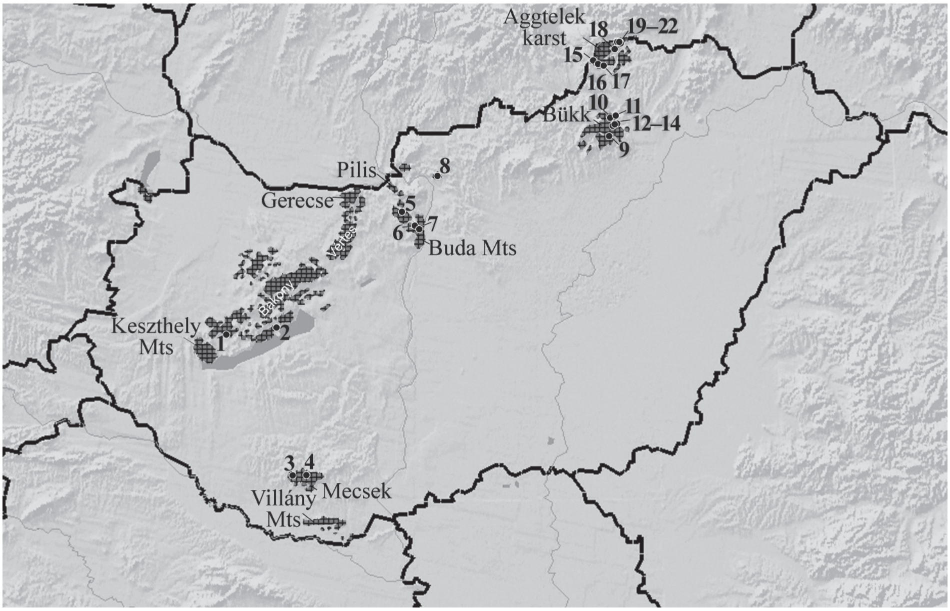

Fig. 1 Karstic regions of Hungary and their caves with Collembola data. Karstic regions marked with checkered pattern. **1**: Tapolca Lake Cave, **2**: Lóczy Cave, **3**: Abaliget Cave, **4**: Mánfai-kőlyuk Cave, **5**: Solymári-ördöglyuk Cave, **6**: Bátori Cave, **7**: Ferenc-hegyi Cave, **8**: Násznép Cave, **9**: Hajnóczy Cave, **10**: Szamentu Cave, **11**: Csókási Cave, **12**: Anna Cave, **13**: Szent István Cave, **14**: Szeleta Cave, **15**: Baradla Cave, **16**: Béke Cave, **17**: Szabadság Cave, **18**: Meteor Cave, **19**: Hideg-lyuk Shaft Cave, **20**: Kifli Shaft Cave, **21**: Őz Shaft Cave, **22**: Vecsembükk Shaft Cave.

Tab. 1 Hungarian caves with data on inhabiting Collembola taxa and the corresponding list of references, with alternative names of caves and the number of reported taxa. More systematically investigated caves in bold. Literature only discussing earlier data from that specific cave given in brackets.

Cave	No. in Figs 1–3 and Tab. 2	Hungarian name and synonyms used in literature	Literature	Taxa
Tapolca Lake Cave	1	Tapolcai Tavasbarlang, Tavasbarlang, Teichhöhle von Tapolca, Tapolcai barlang,	Stach 1929, 1947, (Gebhardt 1934, 1963), (Geyer & Mann 1940), Loksa 1960a, Paclt 1960	8
Lóczy Cave	2	Lóczy-barlang	Loksa 1960b	7
Abaliget Cave	3	Abaligeti-barlang	Bokor 1924, (1925), Stach 1929, 1934, 1945, 1949, 1954, 1956, Gebhardt 1933, 1934, (1963), Paclt 1960	11
Mánfai-kőlyuk Cave	4	Mánfai-kőlyuk, Mánfai-barlang, Mánfaer Höhle	Gebhardt 1933, 1937, 1963, Stach 1934, 1945, 1949, 1954, 1956, (Loksa 1962)	9
Solymári-ördöglyuk Cave	5	Solymári Ördöglyuk, Sólymár Cave, Teufelsloch-Höhle, Solymári Ördöglyuk	Stach 1929, (1934, 1954), (Gebhardt 1934, 1963)	2
Bátori Cave	6	Bátori-barlang, Hárshe-gyi barlang	Stach 1929, (Gebhardt 1934, 1963)	2
Ferenc-hegyi Cave	7	Ferenc-hegyi-barlang	Szent-Ivány 1941	1
Násznép Cave	8	Násznép-barlang	Loksa 1959b, (Bajomi 1977)	7
Hajnóczy Cave	9	Hajnóczy-barlang, Odor barlang	Stach 1929	1
Szamentu Cave	10	Szamentu-barlang	Loksa 1969	1
Csókási Cave	11	Csókási-barlang, Csókás-barlang	Stach 1929	1
Anna Cave	12	Anna-barlang, Forrás-barlang, Hámor-barlang	Stach 1929, Loksa 1962, (Bajomi 1977)	13
Szent István Cave	13	Szent István-barlang, István-barlang	Loksa 1962, (Bajomi 1977)	11
Szeleta Cave	14	Szeleta-barlang	Loksa 1962	11
Baradla Cave	15	Baradla-barlang, Aggteleki csepkőbarlang, Aggteleki barlang, Tropfsteinhöhle ‘Baradla’, Aggteleker Höhle	Stach 1929, 1934, 1945, 1949, 1951, 1954, 1956, Dudich 1930, (1932a), 1932b, (Gebhardt 1934, 1963), (Bajomi 1977), Traser 1999	26
Béke Cave	16	Béke-barlang	Kovács 1953, (1954)	4
Szabadság Cave	17	Szabadság-barlang, Égerszöger Grotte, Freiheitshöhle	Loksa 1959a, 1961, (Bajomi 1977)	14
Meteor Cave	18	Meteor-barlang	Bajomi 1969a, (1969b, 1977), Loksa 1969	9
Hideg-lyuk Shaft Cave	19	Hideg-lyuk, Hideglik-Schachthöhle	Loksa 1967, (Bajomi 1968, 1977)	1
Kifli Shaft Cave	20	Kifli-zsomboly, Kifli-Schachthöhle	Loksa 1967, (Bajomi 1968, 1977)	2
Őz Shaft Cave	21	Őz-zsomboly, Őz-Schachthöhle	Loksa 1967, (Bajomi 1968, 1977)	3
Vecsembükk Shaft Cave	22	Vecsembükki-zsomboly	Traser 1999	2

After Stach, Imre Loksa worked intensely on the fauna of Hungarian caves. In the material collected mostly by himself and by Dániel Bajomi in 13 caves, he identified 47 taxa (Loksa 1959a, 1959b, 1960a, 1960b, 1961, 1962, 1967, 1969, Bajomi 1968, 1969a, 1969b, 1977), 12 of them being new to science [marked with an **X** in Tab. 2 except for *Mesogastrura anthrohungarica* Loksa, 1959 from Násznép Cave, which is a junior synonym of *Mesogastrura ojcoviensis* (Stach, 1919) (Nosek 1962)]. Beside Loksa's work, Jiří Paclt published records of seven species from two caves (Paclt 1960). József Szent-Ivány and István Kovács made further contributions with sporadic data (Szent-Ivány 1941, Kovács 1953, 1954), but some further papers only discuss earlier occurrences (e.g. Geyer & Mann 1940, Dudich 1962, Bajomi 1977).

In spite of the promising intensity of the early Hungarian biospeleological investigations, work in this field almost completely ceased towards the end of the 1960's in this country. Thus, hardly any contributions referring to Hungarian caves' springtail fauna can be found after Loksa, except for a few data published by György Traser (1999).

2. Materials and methods

The present inventory is based on literature records critically reviewed regarding taxonomy, nomenclature and ecological characterisations of the species. Literature information was also critically reviewed regarding the caves' geographical locations, excluding cavities mentioned from historical Hungary (e.g. by Frivaldszky 1865), but situated out of the country's present territory. The location of each cave is mapped on Fig. 1. Further publications exist (e.g. Dudich 1962, Dányi & Traser 2007), but as they are of rather popular style and only repeat earlier data, they have been excluded in the present review. Taxa's synonym names used in the literature can be found in Dányi & Traser (2008).

The terms 'troglobiont' and 'eutroglophile' are based on the definitions given by Sket (2008). According to this, eutroglophiles are essentially epigean species which are able to establish more or less permanent subterranean populations, whereas troglobionts are strongly bound to hypogean habitats and 'normally' do not appear in epigean habitats (irrespective of the reasons for their absence in epigean habitats or their morphological appearance).

To decide whether organisms are troglobionts or eutroglophiles, one can regard either the whole species (all known populations) or refer to certain populations (see Dudich 1931). For the presented overview, only Central European populations were taken into account – in line with the idea of Kováč (2000) of 'regional troglobionts' – which results in disregarding some species´ distant epigean populations. Therefore, some species [*Pygmarrhopalites bifidus* (Stach, 1945), *Pygmarrhopalites pygmaeus* (Wankel, 1860) and *Mesogastrura ojcoviensis*] are listed here as troglobionts, as only troglobiotic populations are known for these species in Central Europe. In calculating percentages of endemic, troglobiont and eutroglophile species, only taxa at species level were included, taxa identified only at a generic level were disregarded.

For the comparison of the caves' collembolan fauna, we used a hierarchical cluster-analysis with an information theory method (minimum pooled entropy in each new cluster) implemented in the SYNTAX 2000 software package (Podani 2001). Only eutroglophile and troglobiotic taxa were included in the analysis, since incidentally occurring epigeic species show more the relation to the surface fauna and might therefore confound the subterranean patterns.

Tab. 2 Occurrences of Collembola taxa in Hungarian caves. Caves coded in the headline according to Fig. 1 and Tab. 1. Records marked with '+', type localities with 'x' in bold. Eutroglophile species marked with '*', troglobiont species underlined.

species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Poduromorpha																						
Hypogastruridae																						
Ceratophysella armata (Nicolet, 1842)			+												+							
Ceratophysella bengtssoni (Ågren, 1904)*													+									
<u>*Ceratophysella cavicola* (Börner, 1901)</u>				+								+						+				
Ceratophysella sigillata (Uzel, 1891)															+							
Ceratophysella succinea (Gisin, 1949)															+							
Hypogastrura purpurescens (Lubbock, 1867)													+	+	+							
Hypogastrura vernalis (Carl, 1901)	+																					
<u>*Mesogastrura ojcoviensis* (Stach, 1919)</u>								+														
Willemia anophthalma Börner, 1901													+									
Willemia scandinavica Stach, 1949															+							
Odontellidae																						
Superodontella lamellifera (Axelson, 1903)																	+					
Onychiuridae																						
<u>*Deharvengiurus microchaetosus* (Loksa, 1959)</u>								**x**														
Deuteraphorura inermis (Tullberg, 1869)*			+						+		+	+	+	+		+	+					
<u>*Hymenaphorura pseudosibirica* (Stach, 1954)</u>															**x**							
Hymenaphorura sibirica (Tullberg, 1877)*				+																		
Kalaphorura burmeisteri (Lubbock, 1873)*								+														
Onychiurus rectospinatus Stach, 1922*																	+					
<u>*Orthonychiurus schoenviszkyi* (Loksa, 1967)</u>																		+		**x**		
Protaphorura armata (Tullberg, 1869)*			+	+	+								+	+	+	+	+					
<u>*Protaphorura kadici* (Loksa, 1967)</u>																					**x**	
Protaphorura tricampata (Gisin, 1956)																		+				

Tab. 2 Occurrences of Collembola taxa in Hungarian caves. (Continued previos page.)

species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Poduromorpha																						
Neanuridae																						
Friesea mirabilis (Tullberg, 1871)	+																					
Endonura dudichi (Loksa, 1967)*																					**x**	
Neanura muscorum (Templeton, 1835)												+			+							
Thaumanura carolii (Stach, 1920)															+							
Tullbergiidae																						
Mesaphorura krausbaueri Börner, 1901														+			+					
Mesaphorura macrochaeta Rusek, 1976															+							
Entomobryomorpha																						
Entomobryidae																						
Coecobrya tenebricosa Folsom, 1902	+																					
Heteromurus nitidus (Templeton, 1835)*	+	+	+	+	+	+	+	+				+	+	+	+		+					
Lepidocyrtus curvicollis (Bourlet, 1839)	+	+	+									+		+	+							
Lepidocyrtus cyaneus Tullberg, 1871				+																		
Lepidocyrtus lanuginosus (Gmelin, 1788)			+														+					
Orchesella flavescens (Bourlet, 1839)				+																		
Orchesella multifasciata (Scherbakov, 1898)			+																			
Pseudosinella aggtelekiensis (Stach, 1930)															**x**	+	+					
Pseudosinella alba (Packard, 1873)*		+										+	+	+								
Pseudosinella argentea Loksa, 1960		**x**																				
Pseudosinella zygophora (Schille, 1908)															+							
Isotomidae																						
Desoria tigrina Nicolet, 1842																						+
Folsomia antricola Loksa, 1959																	**x**	+				
Folsomia candida Willem, 1902*	+	+										+	+		+							
Folsomia fimetaria (Linnaeus, 1758)															+	+						
Folsomia penicula Bagnall, 1939																		+				+
Folsomia quadrioculata (Tullberg, 1871)														+								

species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Isotomiella minor (Schäffer, 1896)																		+				
Parisotoma notabilis (Schäffer, 1896)												+	+	+	+			+				
Proisotoma sp.																	+					
Tetracanthella cf. *wahlgreni* Axelson, 1907															+							
Vertagopus cinereus (Nicolet, 1841)															+							
Oncopoduridae																						
Oncopodura crassicornis Shoebotham, 1911*													+					+				
Oncopodura egerszoegensis Loksa, 1961																	**x**					
Tomoceridae																						
Pogonognathellus flavescens (Tullberg, 1871)			+	+		+																
Tomocerus minor (Lubbock, 1862)				+								+			+							
Tomocerus vulgaris (Tullberg, 1871)								+						+	+							
Neelipleona																						
Neelidae																						
Megalothorax minimus Willem, 1900*												+					+					
Neelides minutus (Folsom, 1901)*	+	+						+														
Neelus murinus Folsom, 1896			+																			
Symphypleona																						
Arrhopalitidae																						
Arrhopalites caecus (Tullberg, 1871)*														+	+							
Arrhopalites loczyi Loksa, 1960		**x**																				
Pygmarrhopalites aggtelekiensis (Stach, 1929)															**x**							
Pygmarrhopalites bifidus (Stach, 1945)												+	+				+					
Pygmarrhopalites buekkensis (Loksa, 1969)										**x**												
Pygmarrhopalites hungaricus (Loksa, 1967)																			+	+	**x**	
Pygmarrhopalites intermedius (Loksa, 1969)																		**x**				
Pygmarrhopalites pygmaeus (Wankel, 1860)	+		+	+				+							+		+					
Pygmarrhopalites terricola (Gisin, 1958)															+							
Sminthuridae																						
Sminthurus sp.												+										

3. Results

3.1. Present inventory

According to a recent inventory (Anonymus 2010), 327 Hungarian caves with more than 100-meters horizontal or more than 25-meters vertical length are known, from which the collembolan fauna of only 22 has been examined up till now (Tab. 1, Fig. 1). Furthermore, the intensity of these investigations has been relatively low and only ten caves were sampled more or less systematically. From the remaining ones only sporadic data for a few species is available (Tab. 1). In spite of this, rather numerous (67) cave-inhabiting Collembola taxa are known from the country (Tab. 2). Of these 17 (26.2%) can be considered to be troglobionts and another 14 (21.5%) eutroglophiles (Tab. 2).

Due to the high degree of isolation, caves tend to have endemic taxa (Culver et al. 2006). Also in Hungary 11 of the troglobiotic species (16.9% of all recorded species from caves) are endemic to a certain cave (8 species) or karst system (3 species).

Several karst regions have been less investigated in the country, such as the Villány, Keszthely, Bakony, Gerecse, Vértes and Pilis Mts., where any kind of subterranean Collembola data is still lacking.

3.2. Taxonomic situation

Some of the species described from Hungarian caves have been revised taxonomically just recently [e.g. *Endonura dudichi* (Loksa, 1967) by Smolis 2008], but many of them are still lacking modern redescriptions:

Pseud. aggtelekiensis was considered to be a 'species dubiae' by Gisin (1960: 251). A revision of many important characters of *Folsomia antricola* Loksa, 1959 is needed (Potapov 2001). The cheatotaxy of *Pygmarrhopalites aggtelekiensis* should be described in detail (e.g. that of abd. VI, dens) (Bretfeld 1999). The absence of eyes should be confirmed in *Arrhopalites loczyi* Loksa, 1960 (a strange state questioned by Bretfeld 1999: 87). *Oncopodura egerszoegensis* Loksa, 1961 requires a redescription (Janssens & De Bruy 2010). *Pseudosinella argentea* Loksa, 1961 nec Folsom was omitted from their key on the genus by Simón-Benito & Moreno (2006), because of the lack of information on the species' chaetotaxy. Along with its detailed redescription, this species should also be renamed, since it is a junior primary homonym of *Pseudosinella argentea* Folsom, 1902.

3.3. Zoogeography – Cluster analysis

The results of the cluster analysis show a different picture, depending on whether only troglobiotic species are included (Fig. 3) or both eutroglophile and troglobiotic taxa (Fig. 2). Apparent in both analyses is the close relation between the Mánfai and Abaligeti caves (1 and 2), the shaft caves and Meteor cave of the Aggtelek Karst region (19–21) as well as their separation from the other Aggtelek caves seems to be supported.

4. Discussion

Examining species richness data, Culver et al. (2006) found unique biodiversity patterns in terrestrial cave invertebrates. This pattern outlines a very narrow latitudinal band in the temperate regions (ca. 42–46º N in Europe and 33–35º N in North America) that has the highest biodiversity of terrestrial cave fauna ('mid-latitude biodiversity ridge'). Although Hungary lies outside of this band, the number of troglobiotic and eutroglophilic taxa are remarkable, especially if the low ratio of exploration in the country is taken into consideration. In contrast to the very low number of caves investigated in Hungary to date (namely 22), for Romania Gruia (2003) summarized Collembola data from 343 caves (with 111 taxa). The number of species known to occur in Hungarian caves might also be considered to be very low, compared with the 58 taxa found in two caves in Slovakia (Kováč et al. 2005).

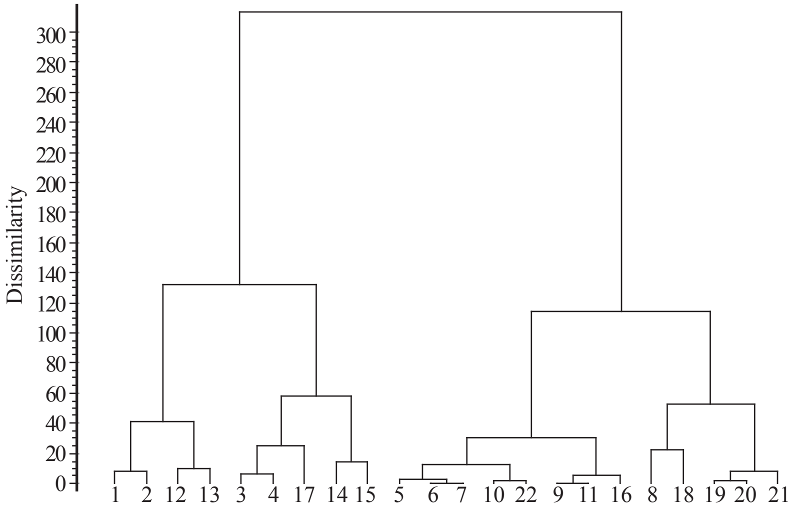

Fig. 2 Cluster analysis for Hungarian caves based on their troglobiotic and eutroglophile Collembola species. (For location and name of the caves, see Fig. 1 and Tab. 1 respectively).

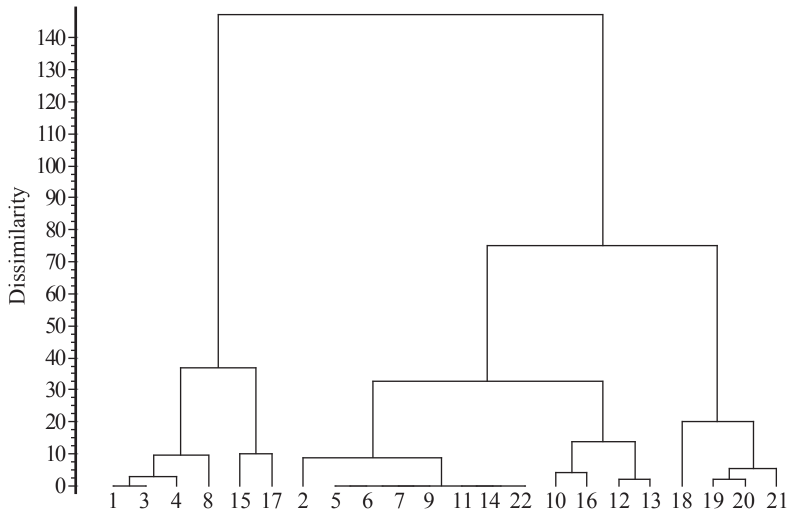

Fig. 3 Cluster analysis for Hungarian caves based on their troglobiotic Collembola species. (For location and name of the caves, see Fig. 1 and Tab. 1 respectively).

4.1. Zoogeography

A small part of the troglobiont springtail species known from Hungarian caves have a wide distribution, such as *Ceratophysella cavicola* (Börner, 1901), *Pygmarrhopalites bifidus*, *Pygm. pygmaeus* and *Mesogastrura ojcoviensis,* which all occur in most parts of Europe (Kováč 2000).

Several species might be considered to be endemic to a smaller area of the Western Carpathians: *Pygm. aggtelekiensis* was reported from the Slovak Paradise (Kováč 2000) about 40 km northwards from the Aggtelek Karst. *Pygmarrhopalites buekkensis* (Loksa, 1969) was also found in the Slovakian part of the Aggtelek Karst (Slovak Karst) by Kováč (2000). A further Western Carpathian endemic is *Endonura dudichi*, an eutroglophile species described from the Őz Shaft Cave.

Some species are restricted to one certain karst region: *Pygmarrhopalites intermedius* (Loksa, 1969), *Pseudosinella aggtelekiensis* and *Orthonychiurus schoenviszkyi* (Loksa, 1967) are known only from the Aggtelek Karst, each of them having been reported from the Slovakian part of the region as well (Barciová et al. 2010, Papáč et al. 2007).

Several other troglobiont species are only known to occur in the cave from which they were described: *A. loczyi*, *Deharvengiurus microchaetosus* (Loksa, 1959), *F. antricola, H. pseudosibirica*, *O. egerszoegensis*, *Protaphorura kadici* (Loksa, 1967), *P. argentea*, *Pygmarrhopalites hungaricus* (Loksa, 1967).

The comparison of the studied caves based on their collembolan fauna can only be preliminary, as abundant data is not yet available. Therefore also the relations obtained by cluster analysis should be handled with care. Most similarities are due to the presence of some widely occurring species. Whether such species are recorded in a certain cave or not is – at the present state of knowledge – a matter of chance in most cases and therefore confounds the obtained picture. This is also the reason for why we obtain a very much different picture if we conduct the analysis with only troglobiotic species (Fig. 3).

If we try to put the known cave Collembola from Hungary into a Central European context, we can see that the Hungarian karstic regions are relatively isolated. Only the Aggtelek Karst and the Bükk Mts. show connections in a northern direction as they are closely related to the Slovakian cave fauna. The two countries share several troglobiont species endemic to the Western Carpathians or to the Aggtelek Karst, one part of which (the 'Slovak Karst') stretches across the border to Slovakia. In Romania, the Eastern and Southern Carpathians as well as the Transylvanian Mountains seem to be inhabited by a rather different cave fauna with their own endemic springtails (Gruia 2003). There are only three troglobiotic species (*M. ojcoviensis*, *P. pygmaeus*, *P. bifidus*) occurring in general in these regions as well as in Hungarian caves, but all of them have a relatively wide distribution area.

To the west, the situation is similar to that of the Austrian Alps (Christian 2002), where also only three widely distributed troglobiotic species are common (*C. cavicola*, *M. ojcoviensis*, *P. pygmaeus*). To the south the fauna of the nearest caves (in the Croatian Papuk Mts.) is still unexplored and other potential habitats lie much further south.

4.2. Evolutionary point of view

From an evolutionary point of view, eutroglophile species' subterranean populations are of special interest, since these have the highest potential to develop into separate troglobiotic taxa. As an interesting example, *Heteromurus nitidus* (Templeton, 1835) can be mentioned. Specimens from subterranean populations show higher levels of morphological adaptation to the subterranean environment (troglomorphy), i.e. a reduced number of ocelli (Paclt 1960).

On the other hand, there are several troglobiotic species co-occurring in one region with closely related eutroglophile taxa. Here, common ancestors might be hypothesized, for example for *F. antricola* and *Folsomia candida* Willem, 1902. The latter has eutroglophile populations in other karstic systems of the region. The situation might be similar with the troglobiotic *H. pseudosibirica* and its closest relative, *Hymenaphorura sibirica* (Tullberg, 1877). *A. loczy* is morphologically very close to *Arrhopalites caecus* (Tullberg, 1871), while *Pygmarrhopalites aggtelekiensis*, *P. buekkensis*, *P. hungaricus* and *P. intermedius* (and also *Pygmarrhopalites slovacicus* (Nosek, 1975) occurring in the Slovakian part of the Western Carpathians) might have common ancestors, which they possibly also share with the troglobiotic *P. pygmaeus* and/or *P. bifidus*. During warm periods in the Pleistocene and Holocene, populations preferring cold habitats, as in periglacial areas, might have retreated to colder subterranean habitats. As these refugia are (more) isolated, this might have served as a basis for subsequent diversification in the genus, similar to the group of *Micraphorura* Bagnall, 1949 species on the northeastern spur of the Alps (Christian 2002). Different levels of troglomorphy existing in these species might indicate colonisation in different periods (*P. bifidus*, *P. pygmaeus* and *P. slovacicus* partially depigmented; *P. hungaricus* and *P. intermedius* completely depigmented; *P. aggtelekiensis* and *P. buekkensis* depigmented and having elongated extremities). In the case of the remaining troglobiotic species our knowledge is too scarce to evaluate their relations and to make any hypothesis on their origin, since they are still waiting for a modern redescription.

The high proportion of endemism indicates promising perspectives for further biospeleological research in Hungary. Intensive collecting especially in the less investigated karst regions is highly needed. Collecting activity should also be carried out in the known caves for obtaining new specimens from the endemic species' type localities to carry out their modern redescription. This is of special need in case of Loksa's species, since their type material could not be located at the Eötvös Loránd University, Budapest, where they had been deposited (J. Farkas pers. com.).

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