RICH AND DIVERSE SUBTERRANEAN INVERTEBRATE COMMUNITIES INHABITING MELISSOTRYPA CAVE IN CENTRAL GREECE

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Abstract. Located in central Greece, Melissotrypa Cave is a hypogenic cave that contains a sulfidic lake. Biological investigations in this cave led to the discovery of several endemic troglobitic invertebrates, some of which occur in high densities of up to 200 specimens per square meter. The subterranean aquatic community appears to rely on a rich autochthonous food-base provided by chemoautotrophic sulfur-oxidizing microorganisms that form microbial biofilms floating on the surface of the sulfidic lake. Several terrestrial species inhabiting the upper sections of the cave rely on allochthonous food brought in from the surface such as vegetal detritus falling into the cave's entrance shaft, and bat guano. Melissotrypa Cave allows the comparative study of chemoautotrophically and photoautotrophically based subterranean communities thriving within the same cave.

Key words: sulfidic cave, subterranean invertebrates, chemoautotrophy, Melissotrypa Cave, Greece.

1. INTRODUCTION

Subterranean ecosystems share the following characteristics: absence of light, buffered fluctuations of climatic conditions, and limited availability of food (CULVER & PIPAN, 2009). In general, allochthonous, photosynthetically-produced food enters the subterranean environment as particulate or dissolved organic matter that serves as substrate for microbial growth, or can serve as food for subterranean detritivores (HUTCHINS *et al.*, 2016). Autochthonous primary production by chemolithoautotrophic bacteria may also contribute to the food budget of subterranean ecosystems but its significance is usually negligible (HUTCHINS *et al.*, 2016). However, rich and diverse subterranean ecosystems have been discovered in several caves with documented high chemolithoautotrophic production (POR, 2007).

The first chemoautotrophically based groundwater ecosystems was discovered in Movile Cave (Romania) in 1986 (SARBU, 2000). Stable isotope studies have shown that the input of allochthonous photosynthetically produced food is insignificant for

this system (SARBU *et al.*, 1996). The trophic basis for the underground community is produced by sulfur- and methane-oxidizing and nitrifying bacteria that oxidize the reduced compounds present in the groundwater using oxygen from the cave atmosphere as electron acceptor (HUTCHINS *et al.*, 2016). A few additional chemoautotrophically based underground ecosystems have been studied, most notably in the Frasassi cave system, Italy (SARBU *et al*., 2000) and in Ayyalon Cave and Tabgha Spring in Israel (POR *et al*., 2007).

The discovery in 2010 of a rich population of niphargid amphipods in a sulfidic lake located in Melissotrypa Cave in central Greece drew our attention to the study of its subterranean ecosystem. We present the subterranean invertebrate community discovered in this cave.

Melissotrypa Cave (39°52'40"N, 22°02'57"E, UTM 34N, WGS 84) is a hypogenic cave developed in marble and is located close to Elassona, in central Greece, at the altitude of 299 m (VAXEVANOPOULOS, 2006). The cave contains a 5 m deep sulfidic lake and two non-sulfidic lakes located in the southern- and eastern maze areas (Fig. 1). Temperatures of 16° to 19°C have been measured in the air and in the lakes.

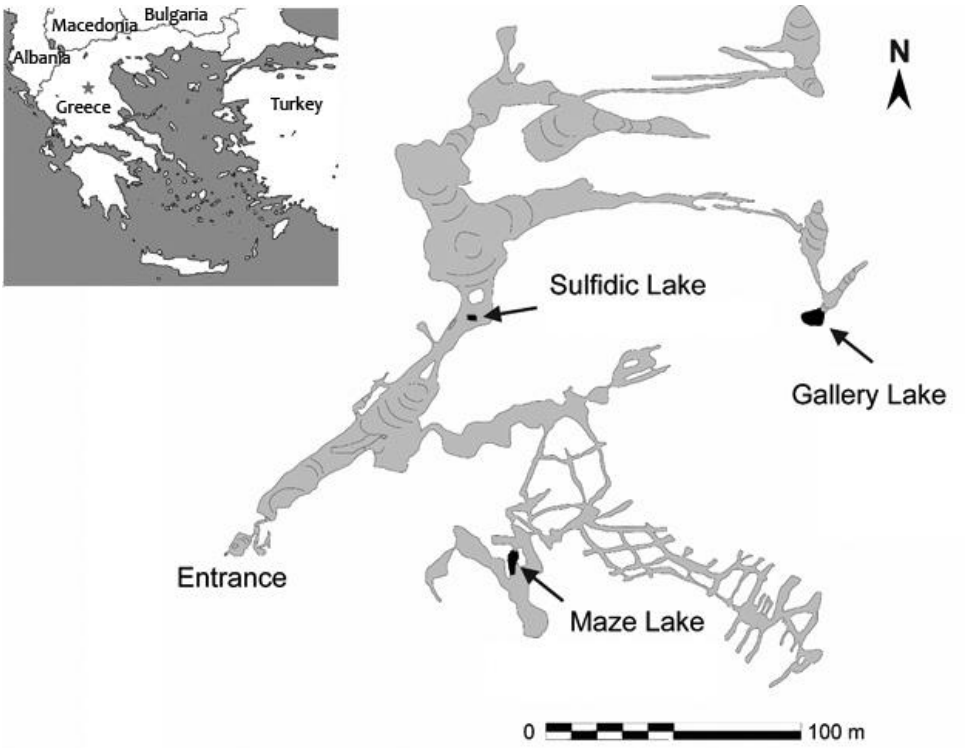

Fig. 1. Map (plan) of Melissotrypa Cave (modified after Vaxevanopoulos, 2006).
The location of the cave in the Greek Mainland is marked with a star.

2. MATERIAL AND METHODS

The first systematic observations and sampling of the community of aquatic cave adapted invertebrates was performed in September 2012 when the Sulfidic Lake and the Gallery Lake were visited. Subsequent research expeditions (2013 – 2018) led to the detailed survey of the aquatic as well as the terrestrial fauna inhabiting the cave (Fig. 1). The aquatic fauna was sampled using tweezers, large pipettes and planktonic nets. For the terrestrial fauna, we used direct sampling with tweezers. All the aquatic and terrestrial specimens were transferred and preserved in 96% ethyl alcohol.

3. RESULTS AND DISCUSSIONS

To date, 30 species of invertebrates were identified: 16 aquatic species (Table 1) and 14 terrestrial species (Table 2).

3.1. AQUATIC FAUNA

The aquatic fauna of Melissotrypa Cave is represented by 16 species of stygobionts which thrive in the three underground lakes (Fig. 1). Seven species are common in both sulfidic and non-sulfidic waters, three species are only present in the Sulfidic Lake, while six other species are only present in the two non-sulfidic lakes (Table 1). The high diversity of aquatic invertebrates in the Sulfidic Lake is presumed to be the consequence of a rich food base produced *in-situ* by chemoautotrophic sulfur-oxidizing microorganisms (J.-F. Flot, pers. comm.).

Dendrocoelidae (Det. G. A. Stocchino)

Flatworms are represented by a relatively dense population (10-15 specimens × m^{-2}) of *Dendrocoelum* sp. (Tricladidae) that only inhabits the Sulfidic Lake (G.A. Stocchino, pers. comm.). Being predatory, they feed presumably on the abundant populations of ciliate protozoans and on cyclopoid copepods, but they may also consume the floating microbial biofilms that develop on the lake surface. They swim under the water surface or crawl on the limestone cave walls in shallower water. Similar *Dendrocoelum* species have been described from chemoautotrophically-based ecosystems in Movile Cave in Romania: *Dendrocoelum obstinatum* Stocchino & Sluys, 2017 (STOCCHINO *et al*., 2017a), and in the Frasassi Caves in Italy: *Dendrocoelum leporii* Stocchino & Sluys, 2017 (STOCCHINO *et al*., 2017b). The species in Melissotrypa Cave may become the subject of yet another new species description.

Annelida (Det. P. Martin)

Two species of oligochaetes (Clitellata) have been found so far in Melissotrypa Cave (P. Martin, pers. comm.). Specimens of *Haplotaxis* sp. nov. and *Delaya* sp.

nov. have been collected both in the Sulfidic Lake as well as in the Gallery Lake. Both species are new for science, endemic to this cave and currently under description. Preliminary molecular analyses suggest a sister relationship of *Haplotaxis* sp. nov. with an undescribed species from Sweden, belonging to a clade which groups the European species. *Delaya* sp. nov. resembles and is a sister species to *Delaya bureschi* (Michaelsen, 1925) known from the Balkan Peninsula (Macedonia, Bulgaria, Slovenia) and Banat (SW Romania).

Gastropoda (Det. A. Falniowski)

Two new and endemic species of aquatic gastropods (Truncatelloidea, Caenogastropoda) were described from Melissotrypa Cave (FALNIOWSKI & SARBU, 2015). Both the turriform *Iglica hellenica* Falniowski & Sarbu, 2015 (Moitessieriidae) and the valvatiform-tronchiform *Daphniolla magdalenae* Falniowski & Sarbu, 2015 (Hydrobiidae) were first collected in the Sulfidic Lake, but later they were observed in larger numbers crawling on rocks and sediments in the non-sulfidic Gallery Lake. Both species are only known from the type locality.

Ostracoda (Det. S. Iepure)

Relatively rich populations of ostracods belonging to the genus *Mixtacandona* Klie, 1938 are present in the Sulfidic Lake and in the Gallery Lake. The specimens of *Mixtacandona* found in Melissotrypa Cave show close morphological similarities with *Mixtacandona idrisi* Mazzini & Rossetti, 2017, the most southern species reported to date, and described from a cave near Palermo in Sicily (MAZZINI *et al*., 2017). *Mixtacandona* is one of the most diverse genera of ostracods represented by 20 species, all stygobites (MEISCH, 2000). One fossil species of this genus has been reported from the Holocene filling sediments succession in a cave in Umbria (Central Italy) (MAZZINI *et al*., 2017) and other fossil species assigned to four distinct morphotypes of *Mixtacandona* from the species-groups *riongessa* and *laisi-chappuisi* have also been found in Holocene fluvial-cave sediments in the Frasassi Cave System (Marche, Italy) indicating small scale speciation within the genus in the near past (IEPURE *et al*., 2012, PETERSON *et al*., 2013). *Mixtacandona* species are distributed in the Palearctic region and show a high diversification in the Mediterranean area.

Copepoda (Det. D. M. P. Galassi)

Several specimens of the ciclopoid copepod *Tropocyclops prasinus* (Fischer, 1860) and one juvenile specimen of *Acanthocyclops* sp. were found in the Sulfidic Lake. The non-sulfidic Gallery Lake is inhabited by two harpacticoid species: *Pseudectinosoma reductum* Galassi & De Laurentiis, 1997 and Parastenocarididae gen. sp. and one cyclopoid *Diacyclops maggii* Pesce & Galassi, 1987 (D.M.P. Galassi, pers. comm.). Presumably, *T. prasinus* has a higher tolerance for the toxicity of H_2S in the water and this may explain the differences between the distribution of the copepod populations in the two observed lakes.

Isopoda (Det. S. Prevorcnik)

A new and endemic species of cirolanid isopod *Turcolana lepturoides* Prevorčnik, Konec & Sket, 2016 was described initially from the non-sulfidic Maze Lake (PREVORCNIK *et al*., 2016). Recent field studies have also reported a dense population (5 specimens × m^{-2}) of this isopod crawling on the walls in the Sulfidic Lake, at depths ranging between 10 and 25 cm, but is has not been observed in shallower water. In August 2017 and July 2018, multiple specimens of *T. lepturoides* were observed walking on the sediments and on the limestone walls in the non-sulfidic Gallery Lake. *Turcolana* is a genus containing mainly species living in fresh and groundwater environments around the eastern Mediterranean. *T. lepturoides* is the first species described from caves in Europe, as all the other species of this genus are from the Middle East.

Amphipoda (Det. C. Fiser)

The amphipods are the best represented aquatic invertebrate group in Melissotrypa Cave. Of the four species found in the cave so far, *Niphargus gammariformis* Fiser in Borko *et al*., 2019 was encountered in all of the lakes, either sulfidic or non-sulfidic. It occurs in very high densities of up to 200 specimens × m^{-2} in the Sulfidic Lake where it feeds on the rich microbiota covering the water surface and the cave walls (BORKO *et al*., 2019). In addition, a dense population of *Niphargus lindbergi* S. Karaman, 1956 was found in the Gallery Lake (10 specimens × m^{-2}), while *Niphargus jovanovici* S. Karaman, 1931 was collected so far only from the Maze Lake. Tiny and fragile amphipod specimens belonging to the genus *Bogidiella* (Bogidiellidae family) were collected from the Gallery Lake. All individuals of *Bogidiella* were damaged and a bogidiellid specialist (R. Vonk, the Netherlands) could not identify them beyond the genus level (BORKO *et al*., 2019).

3.2. TERRESTRIAL FAUNA

The terrestrial fauna of Melissotrypa Cave is the least studied so far and is represented by 14 invertebrate species (Table 2): one Isopoda, three Araneae, one Opiliones, one Pseudoscorpiones, one Chilopoda, one Diplopoda, three Collembola and three Coleoptera. More field work is needed for a thorough survey of the terrestrial fauna in this cave. The cave entrance consists of a 14 m deep shaft that acts as a trap for surface fauna. Goat skeletons, rodents, snakes, frogs etc., as well as beetles, diplopods, centipedes, terrestrial isopods, and various other species of invertebrates roam the pile of detritus located at the base of the vertical entrance shaft.

Isopoda (Det. G. Gentile)

A rich population of the trichoniscid isopods belonging to the genus *Androniscus* (Verhoef, 1908) inhabits the upper sections of Melissotrypa Cave and feeds on the deposits of guano and vegetal debris originating from the surface. Isolated specimens can rarely be found roaming in the vicinity of the Sulfidic Lake where they appear

to feed on microbial biofilms consisting of sulfur-oxidizing microorganisms. The most common species of this genus is *A. dentiger*, which is frequently found in caves in the southern part of its European distribution range.

Araneae (Det. A. Nae)

Three species of spiders have been identified (A. Nae, pers. comm.). These are the trogloxene *Microctenonyx subitaneus* (O. Pickard-Cambridge, 1875), *Megalepthyphantes collinus* (L. Koch, 1872) and the troglophile *Histopona thaleri* Gasparo, 2005. *H. thaleri*, endemic species for Greece (MAMMOLA *et al*., 2018), was described by GASPARO, 2005, from Megalo Spilio Cave, altitude 1000 m, Mount Serekas, Monastiraki. The type locality is situated almost 150 km SW of the Melissotrypa Cave. *Histopona laeta* (Kulczynski, 1897), a closely related species, lives in the Carpathian Mountains (Apuseni Mountains, Romania) and in the northern part of the Balkan Peninsula (WEISS & RUSDEA, 1998).

Opiliones (Det. R. Plăiașu)

Several specimens of *Mediostoma stussineri* (Simon, 1885), including juveniles from different developmental stages as well as a female with eggs, were collected from the cave floor. Previous reports on the occurrence of *M. stussineri* both in caves and in epigean habitats warrant its troglophylic assignment. This is the largest species within the genus *Mediostoma*, which includes 12 species (SCHÖNHOFER, 2013). The species has a European distribution and lives at low altitudes in caves as well as in a range of moist surface habitats such as deciduous forests, olive plantations and river valley (MITOV, 2002; MITOV, 2004; MITOV, 2012).

Pseudoscorpiones (Det. R. Dimitrijević & M. Harvey)

One specimen of *Lasiochernes graecus* Beier, 1963, belonging to the Chernetidae family, was recently collected in the upper dry section of the cave. This species has previously been recorded from caves in Greece and from an unspecified locality in Albania. The original description suggests it is a troglophile, although it might even be fully troglobitic.

Chilopoda (Det. Șt. Baba)

We mention here the second record (locality) for the endemic troglophile species *Cryptops dianae* Matic & Stravropoulos, 1990. Previously, it was known only from the type locality, represented also by an underground environment, the Drakotrypa Cave, situated on the island of Thassos in the Gulf of Kavala (northern Aegean Sea), 8 km from the Greek Mainland (STAVROPOULOS & MATIC, 1990).

Diplopoda (Det. A. Giurginca)

The diverse and likely paraphyletic genus *Typhloiulus* Latzel, 1884, comprises blind, depigmented millipedes, known mostly from caves and endogean habitats. The vast majority of the species live in underground habitats on the Balkan Peninsula

(ANTIĆ *et al*., 2018), but the genus is known also from the Apennine Peninsula, the Alps, and the Carpathians. Up to now, the genus consisted of 37 species, including four hydrophilous cave-dwellers (a very rare lifestyle among millipedes) from the Carpatho-Balkan Arc, the Dinarides, and northeastern Italy (ANTIĆ *et al*., 2017; VAGALINSKI *et al*., 2015). *Typhloiulus gellianae* Makarov & Rada, 2006 (Fig. 2) was described from the Jama u Kukljici Pit, Island of Ugljan, Croatia, by Makarov and Rada in 2006 and was considered an endemic and relict species (MAKAROV *et al*., 2006). It is distinguished, among all, by the shape of the velum: wide, triangular, ending in a simple spine, characteristics that are obvious in the population inhabiting Melissotrypa Cave (see Fig. 2). We have to point out that this is the first time when the species was found outside of its type locality. Its presence in this cave means that its distribution cannot be considered as "restricted to the cave-system on an island in Middle Dalmatia" (MAKAROV *et al*., 2006), but as endemic for the Balkan Peninsula, if further findings endorse it.

Collembola (Det. I. Popa)

Two troglophile species of Collembola, *Ceratophysella denticulata* (Bagnall, 1941) and *Deuteraphorura scotaria* (Gisin, 1954), and one troglobiont, *Pseudacherontides spelaeus* (Ionesco, 1922) (Fig. 3), were identified. Of them, the most interesting one is the guanophilous *P. spelaeus*. This blind and depigmented species is characteristic for fresh guano deposits, where it sometimes forms populations of thousands of individuals. It prefers guano with a pH of 6.5-7.5. In Romania, it was also found in M.S.S. in the Motru Mare area, at depths of 0.3-0.7 m (GRUIA & ILIE, 2000-2001, NITZU *et al*., 2010). *P. spelaeus* is known only from Romania, Bulgaria and Spain. Greece is the least colembologically surveyed country in the whole of Europe (RAMEL *et al*., 2008). For this reason, we believe this could be the first record of *P. spelaeus* for Greece. Another guanophilous species, *C. denticulata*, was collected near guano piles in the intermediary zone of the cave. It has affinities for mold-covered guano (constant species in the guano synusia) and can be found also on rotten bat corpses. Outside of caves it was found in endogeous, lapidicolous and lithoclasicolous wet zones, including river and lake shores (GRUIA & ILIE, 2000-2001). *D. scotaria*, with a Palaearctic distribution, is a saprophagous species that can be found in the vestibular and intermediary zone of the caves (GRUIA, 2000).

Coleoptera (Det. E. Nitzu)

The terrestrial species of Coleoptera are represented by the trogloxene *Falagrioma thoracica* (Stephens, 1832), *Catops nigricans* (Spence, 1815) and the subtroglophile *Aglenus brunneus* (Gyllenhal, 1813). *F. thoracica* is widespread in Europe, but relatively rare in all its distributional range (FREUDE *et al*., 1974). *C. nigricans*, a saprophagous-necrophagous species with a European distribution, was recorded from caves in Romania by NITZU, 2013. *A. brunneus*, coprophagous (guano deposits) and fungivorous species (DAJOZ, 1977), was recorded in Romania from Limanu Cave, Southern Dobrogea (leg. and det. by E. Nitzu).

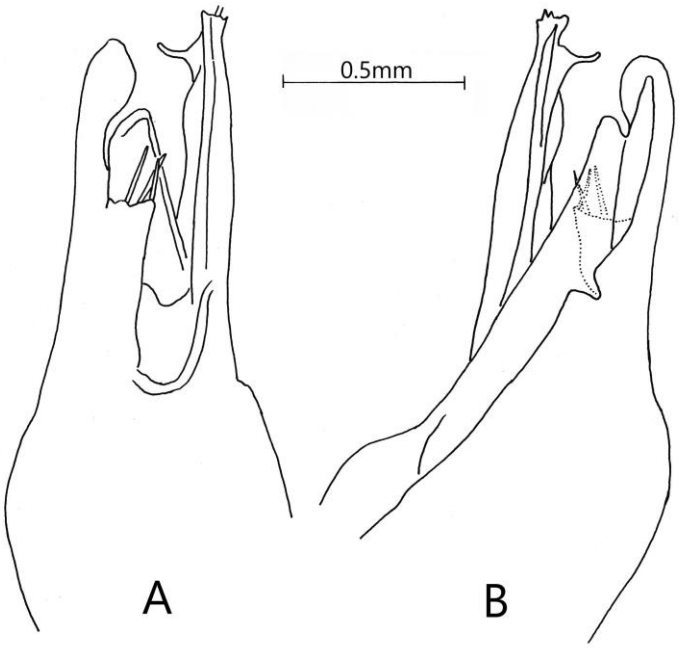

Fig. 2. *Typhloiulus gellianae*, gonopods: A. mesal view; B. lateral view.

Fig. 3. *Pseudacherontides spelaeus*.
Dorsolateral habitus, body length 1.56 mm (photo by E. Nitzu).

Table 1

List of aquatic species from the Melissotrypa Cave

Species	Sulfidic Lake	Non-sulfidic lakes
Phylum Platyhelminthes		
Subphylum Turbellaria		
Ord. Seriata		
Fam. Dendrocoelidae		
Dendrocoelum sp.*	Present	Absent
Phylum Annelida		
Cls. Oligochaeta		
Ord. Haplotaxida		
Fam. Haplotaxidae		
Haplotaxis sp.*	Present	Present
Delaya sp.*	Present	Present
Phylum Mollusca		
Cls. Gastropoda		
Ord. Littorinimorpha		
Fam. Moitessieriidae		
*Iglica hellenica**	Present	Present
Fam. Hydrobiidae		
*Daphniolla magdalenae**	Present	Present
Subphylum Crustacea		
Cls. Ostracoda		
Ord. Podocopida		
Fam. Cyprididae		
Mixtacandona sp.	Present	Present
Cls. Maxillopoda		
Subcls. Copepoda		
Ord. Cyclopoida		
Fam. Cyclopidae		
Tropocyclops prasinus	Present	Absent
Acantocyclops sp.	Present	Absent
Diacyclops magii	Absent	Present
Ord. Harpacticoida		
Fam. Ectinosomatidae		
Pseudectinosoma reductum	Absent	Present
Fam. Parastenocarididae g. sp.	Absent	Present
Cls. Malacostraca		
Ord. Isopoda		
Fam. Cirolanidae		
*Turcolana lepturoides**	Present	Present

Table 1 (continued)

Ord. Amphipoda		
Fam. Bogidiellidae g. sp.	Absent	Present
Fam. Niphargidae		
Niphargus gammariformis	Present	Present
Niphargus lindbergi	Absent	Present
Niphargus jovanovici	Absent	Present

*the species marked with asterisk are endemic for the Melissotrypa Cave; noteworthy is the fact that they all occur in sulfidic waters.

Table 2

List of terrestrial species from the Melissotrypa Cave

Systematic Classification	Species
Cls. Malacostraca **Ord. Isopoda** Fam. Trichoniscidae	*Androniscus* sp.
Cls. Arachnida **Ord. Araneae** Fam. Linyphiidae	*Microctenonyx subitaneus* *Megalepthyphantes collinus*
Fam. Agelenidae	*Histopona thaleri*
Ord. Opiliones Fam. Nemastomatidae	*Mediostoma stussineri*
Ord. Pseudoscorpiones Fam. Chernetidae	*Lasiochernes graecus*
Cls. Chilopoda **Ord. Scolopendromorpha** Fam. Cryptopidae	*Cryptops dianae*
Cls. Diplopoda **Ord. Julida** Fam. Julidae	*Typhloiulus gellianae*
Cls. Collembola **Ord. Poduromorpha** Fam. Hypogastruridae	*Ceratophysella denticulata* *Pseudacherontides spelaeus*
Fam. Onychiuridae	*Deuteraphorura scotaria*
Cls. Insecta **Ord. Coleoptera** Fam. Staphylinidae	*Falagrioma thoracica*
Fam. Leiodidae	*Catops nigricans*
Fam. Salpingidae	*Aglenus brunneus*

4. CONCLUSIONS

Melissotrypa Cave is one of the very few caves in the world, where the subterranean community relies on autochthonous food produced chemoautotrophically by sulfur-oxidizing bacteria. The rich and diverse aquatic community inhabiting the Sulfidic Lake and the two non-sulfidic lakes comprises 16 species, eight of which (50%) are new for science and endemic to this cave. The unusually high densities of aquatic fauna observed in the Sulfidic Lake are the consequence of the presence of sulfur-oxidizing chemoautotrophic microorganisms in this lake. These microorganisms form microbial biofilms that float on the water surface and cover the limestone walls in and around the lake. The complex food web from the Sulfidic Lake consists of a large variety of microorganisms, both prokaryotic (bacteria and Archaea) and eukaryotic (Protozoa), worms, snails, and crustacean species that create various niches in this peculiar cave ecosystem. Melissotrypa Cave offers a unique opportunity: within the same cave one can compare the less common case of a chemoautotrophically based cave community relying on autochthonous food production by sulfur oxidizing bacteria, with the more commonly encountered photoautotrophically based cave community relying on allochthonous food production by surface green plants. Stable isotope studies that are being conducted currently will provide a better understanding of the food web structure in Melissotrypa Cave. Among the terrestrial species inhabiting Melissotrypa Cave, only *Cryptops dianae* and *Histopona thaleri* are endemic for Greece. This may be explained by the large cave entrance that acts as a trap for copious amounts of surface detritus as well as for surface terrestrial species.

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