

What's crawling in the dark? An annotated list of gastropods in Greek caves

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Abstract

Greece is covered by a high percentage of carbonate rocks, resulting in a significant number of over 10,000 caves within its territory. Their fauna is not well known. Concerning gastropods, 68 terrestrial species have been reported from 70 caves. In this study, we contribute to the knowledge of the snails inhabiting Greek caves. We analyzed the literature and studied all the material deposited in the Natural History Museum of Crete, to create a first comprehensive list of gastropods of Greek caves. The number of caves from which gastropod species were reported increased to 182, while the number of known terrestrial species increased to 113. Fourteen of these species live only in caves, twelve of which are endemic of Greece. However, the fauna of Greek caves is still understudied. With the increasing exploration of Greek caves, the number of the known cave-dwelling gastropod species will increase and new species will be discovered.

Keywords

Biodiversity, cave fauna, gastropoda, Greece, snails

Introduction

Karst terrains and karstic processes are significant components of the physical geography of the Mediterranean basin. A substantial percentage of the land area of Greece is covered by carbonate rocks, where most caves are formed. According to Chen et al. (2017), approximately 41% of the land surface of Greece is characterised by the

presence of carbonate rocks. As a result, Greece, an area of 132,000 km², hosts more than 10,000 known caves (Beron 2016).

Among these caves, several hundred have been studied speleobiologically but faunistic data have been published only for 550. For terrestrial gastropods, 68 species have been reported from 70 caves (Paragamian et al. 2023). These species belong to 30 genera within 15 families, while half of them are Greek endemics (33/68). Fifty-nine of the species have been identified at species level; while 14 have been characterised as troglobionts, 30 as troglaphiles and 15 as troglaxenes.

The classification of species living in subterranean environments has been a subject of debate [for a review, see Sket (2008, 2016) and Trajano and de Carvalho (2017)]. In this study, we refer to the terms of the Schiner-Racovitza's classification system, according to the lifestyle of the species as such: troglobiont, if a species lives exclusively in caves; troglaphile, if it lives and reproduces in surface habitats but is also able to live and reproduce inside caves; troglaxene, if a species has an accidental presence in the cave or is considered an occasional visitor that does not live or reproduce in caves.

In this study, we contribute to the knowledge of the Greek cave gastropod fauna by presenting data from Greek caves based on the collections of the Natural History Museum of Crete (NHMC) and a thorough analysis of the literature.

Materials and methods

The present list is based on samples from caves in the collections of the NHMC and on the published data. The studied material is stored in the collections of the NHMC and consists of 96% ethanol-preserved specimens and dry material (empty shells). Most of the material was part of the collection of Kaloust Paragamian (KP, co-author) who donated his collection to the NHMC in 2018. It includes specimens from 137 caves and potholes (a single shaft, or an entire cave system that is dominantly vertical) that were collected between 1976 and 2019, mainly by KP but also by other Greek speleobiologists and cavers during their excursions (Fig. 1).

The majority of the specimens were identified at species level, following the taxonomy of MolluscaBase (2023). Where necessary, anatomical features of the reproductive system were also used for identification. In a few specimens, the anatomical characteristics were not clear due to preservation in 96% alcohol or the shells were broken. These specimens are reported at a genus level as *Genus* sp. or, if they resemble a specific species, they are reported as *Genus* aff. sp. (having affinity with but not identical to).

Additionally, we analysed the published data on cave-dwelling gastropods of Greece and included in the presented list all records reported as occurring in a cave. We excluded records, where it was unclear whether the species were collected inside or outside the cave (e.g. around the cave entrance).

For each species, we indicate the cave(s) in which it was found, based on the literature and the NHMC samples. The latter are reported as "present study". Note that if no other bibliographic references are given in a record, it is a new record for the Greek cave fauna.

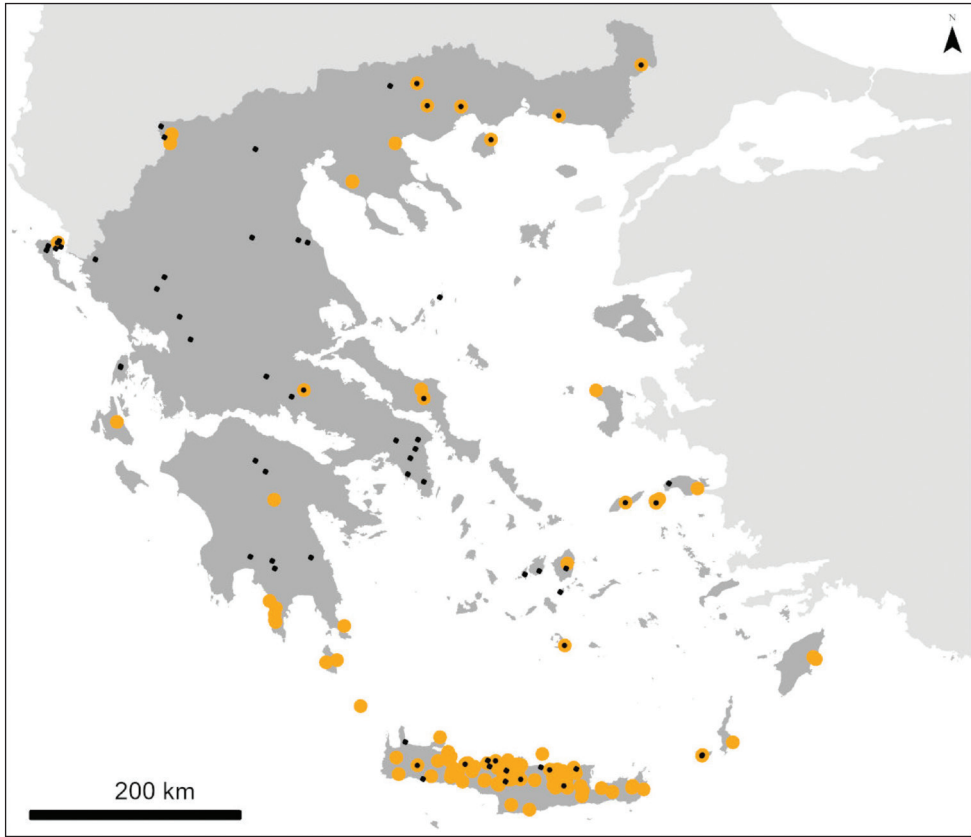


Figure 1. Caves in Greece with records of terrestrial gastropods from the literature (black dots) and from the present study (orange circles).

Sometimes the cave may have more than one name, in which case we follow the cave nomenclature of the Hellenic Institute of Speleological Research (Paragamian and Paragamian 2023), whereas the Greek letter transliteration is based on ELOT 743 standard.

The list is presented in alphabetical order of Order, Family, Genus and Species name. For each species, the cave(s) in which it is recorded, is given. The caves are presented in an alphabetical order of their TRADITIONAL GEOGRAPHIC REGION, Regional Unit and Cave name. However, for all islands, the island name is preferred to the Regional Unit, and they are divided into Aegean (including all islands of the Aegean Sea), Ionian (including all islands of the Ionian Sea) and Crete (including Crete island and its adjacent islets) areas (Fig. 2). The general distribution/endemism (Distribution), is also given for each species. Single-cave endemics, single-island endemics and stenoendemics (species with a few known localities within a very restricted area) are specifically mentioned. Finally, the ecological classification (Classification: Troglobiont, Troglophile, Trogloxene) and the published IUCN Red List category (IUCN 2023) are given for each species. The IUCN Red List categories are: Extinct (EX),

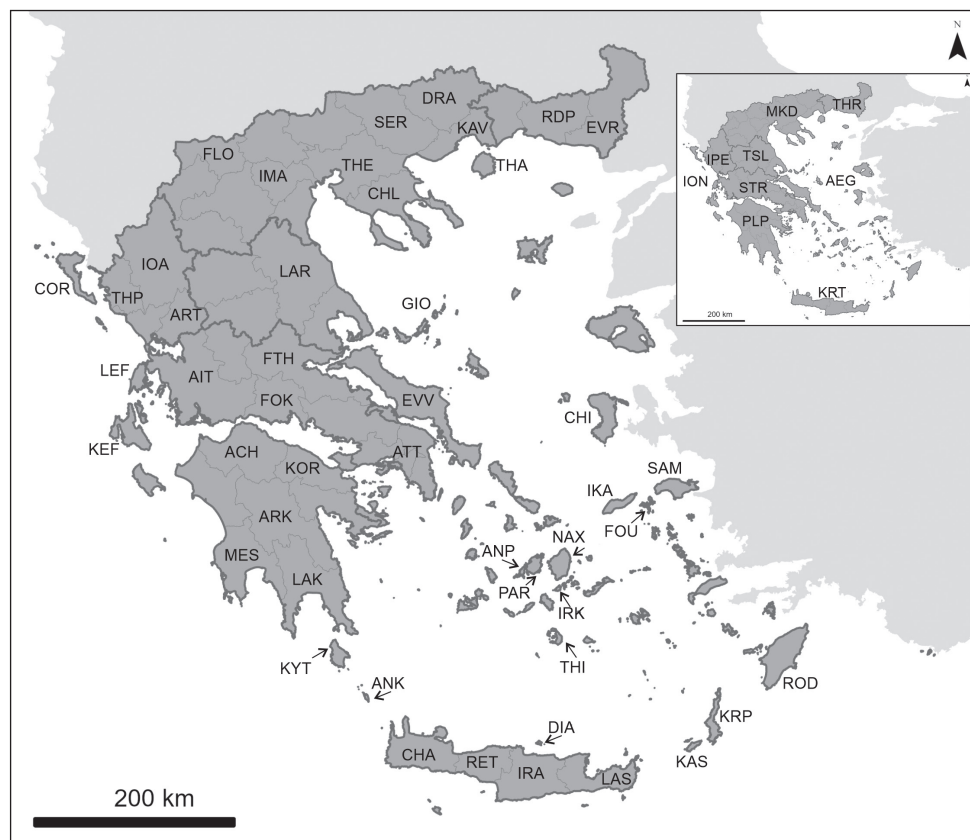


Figure 2. Map showing the Regional Units and Islands of Greece that are mentioned in the text. **Regional Units:** Achaia: **ACH**, Aitoloakarnania: **AIT**, Arkadia: **ARK**, Arta: **ART**, Artiki: **ATT**, Chalkidiki: **CHL**, Chania: **CHA**, Drama: **DRA**, Evros: **EVR**, Florina: **FLO**, Fokida: **FOK**, Fthiotida: **FTH**, Imathia: **IMA**, Ioannina: **IOA**, Irakleio: **IRA**, Kavala: **KAV**, Korinthia: **KOR**, Lakonia: **LAK**, Larisa: **LAR**, Lasithi: **LAS**, Messinia: **MES**, Rethymno: **RET**, Rodopi: **RDP**, Serres: **SER**, Thesprotia: **THP**, Thessaloniki: **THE**, Trikala: **TRI**. **Islands:** Antikythira: **ANK**, Antiparos: **ANP**, Chios: **CHI**, Corfu: **COR**, Dia: **DIA**, Evvoia: **EVV**, Fournoi: **FOU**, Gioura: **GIO**, Ikaria: **IKA**, Irakleia: **IRK**, Karpathos: **KRP**, Kasos: **KAS**, Kefalonia: **KEF**, Kythira: **KYT**, Lefkada: **LEF**, Naxos: **NAX**, Paros: **PAR**, Rodos: **ROD**, Samos: **SAM**, Thira: **THI**, Thasos: **THA**. Inset map showing the Traditional Geographic Regions of Greece. Aegean Islands: **AEG**, Crete: **KRT**, Ionian Islands: **ION**, Ipeiros: **IPE**, Makedonia: **MKD**, Peloponnisos: **PLP**, Sterea Ellada: **STR**, Thessalia: **TSL**, Thraki: **THR**.

Extinct In The Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC) for evaluated species with adequate data, Data Deficient (DD) for evaluated species with inadequate data and Not Evaluated (NE) for not evaluated species. Detailed geographical information on the exact location of each cave is provided in Supplementary Material. The data underpinning the analysis reported in this paper are deposited at GBIF, the Global Biodiversity Information Facility, and are available at <https://doi.org/10.15468/k57z2a>.

Results

List of species in the caves of Greece

Terrestrial species

Phylum Mollusca

Class Gastropoda

Order Architaenioglossa

Family Cochlostomatidae

Genus *Cochlostoma*

Cochlostoma cretense (Maltzan, 1887)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Irakleio:** Lakki Kontari Pothole (present study).

Family Cyclophoridae

Genus *Pholeoteras*

Pholeoteras euthrix Sturany, 1904

Distribution. Western Balkan.

Classification. Troglobiont.

IUCN RedList. LC.

Records in Greek caves. IONIAN: **Corfu:** Grava Tsouka Cave (Gittenberger 1977, 1985, 1986; Bernasconi and Riedel 1994; Štamol et al. 1999; Beron 2016; Paragamian et al. 2023).

Order Stylommatophora

Family Argnidae

Genus *Speleodentorcula*

Speleodentorcula beroni Gittenberger, 1985

Distribution. Greek endemic, Evvoia-Peloponnisos.

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. AEGEAN: **Evvoia:** Skoteini Cave (Gittenberger 1985; Beron 2016; Paragamian et al. 2023; present study).

Notes. The species was until recently known only from its type locality. A new subspecies, *S. beroni maniates* Reischütz, Steiner-Reischütz & Reischütz, 2017, was described from a site 250 kilometres southwest from its type locality by Reischütz et al. (2017). Further research is needed to clarify the taxonomy and distribution of this genus.

Family Azecidae

Genus *Hypnophila*

Hypnophila zacynthia (Roth, 1855)

Distribution. Greek endemic, Ionian Islands–Opposite Greek mainland.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. IONIAN: **Corfu:** Katsouri Cave (Sturany 1904; Gittenberger 1977, 2000; Beron 2016; Paragamian et al. 2023).

Family Chondrinidae

Genus *Granopupa*

Granopupa granum (Draparnaud, 1801)

Distribution. Mediterranean–Macaronesian–Turanian.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Lasithi:** Pelekita Cave (present study).

Genus *Rupestrella*

Rupestrella rhodia (Roth, 1839)

Distribution. Eastern Mediterranean.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: **Rodos:** Koumelou Cave (present study).

Family Clausiliidae

Genus *Albinaria*

Albinaria contaminata (Rossmässler, 1835)

Distribution. Greece–Albania.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: **Kefalonia:** Melissani Cave (present study).

Albinaria corrugata (Bruguère, 1792)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Irakleio:** Agia Paraskevi Cave (Frank 1988; Paragamian et al. 2023; present study), Neraidospilios Cave (Frank 1988; Paragamian et al. 2023).

Albinaria discolor (Pfeiffer, 1846)

Distribution. Greek endemic, Aegean Islands-Stereia Ellada-Peloponnisos.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: **Kythira:** Katofygadi Cave (present study).

Albinaria eburnea (Pfeiffer, 1854)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Chania:** Drakolaki Cave (present study).

Albinaria freytagi (Böttger, 1889)

Distribution. Greek endemic, Aegean Islands.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: **Fournoi:** Votsos Agiou Charalampous Pothole, Megalos Votsos Panagias Pothole, Mikros Votsos Panagias Pothole (present study).

Albinaria grayana (Pfeiffer, 1846)

Distribution. Greek endemic, Aegean Islands-Peloponnisos.

Classification. Troglaxene.

IUCN RedList. NT.

Records in Greek caves. AEGEAN: **Kythira:** Niorou Cave (present study).

Albinaria munda (Rossmässler, 1836)

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: **Samos:** Vrysoulia Cave (present study).

***Albinaria senilis* (Rossmässler, 1836)**

Distribution. Greek endemic, Ionian Islands–Opposite Greek mainland.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: **Kefalonia:** Melissani Cave (present study).

***Albinaria teres* (Olivier, 1801)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Lasithi:** Pelekita Cave (present study).

***Albinaria* sp.**

Records in Greek caves. CRETE: **Irakleio:** Latsida sto Makry Lakki Pothole (present study).

Notes. The specimen could not be identified at species level because only a broken shell was collected, which belongs to a species of the genus *Albinaria*.

Genus *Carinigera****Carinigera buresi* (Wagner, 1928)**

Distribution. Greece–Bulgaria.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. MAKEDONIA: **Kavala:** Agia Eleni Cave; **Serres:** Alistrati Cave (present study).

Genus *Montenegrina****Montenegrina dofleini* (Wagner, 1928)**

Distribution. Western Balkan.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. MAKEDONIA: **Florina:** Panagia Eleousa Cave (Fehér and Szekeres 2016; Paragamian et al. 2023).

***Montenegrina sattmanni* Nordsieck, 1988**

Distribution. Greece–Albania–North Macedonia.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. **MAKEDONIA: Florina:** Kokkali Cave (Fehér and Szekeres 2016; Paragamian et al. 2023).

Genus *Sciocochlea*

Sciocochlea collasi (Sturany, 1904)

Distribution. Greek endemic, Ionian Islands (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. NT.

Records in Greek caves. **IONIAN: Corfu:** Katsouri Cave (Sturany 1904; Wolf 1938; Gittenberger 1977, 1985, 1986, 2000; Beron 2016; Reischütz et al. 2016; Paragamian et al. 2023).

Sciocochlea nordsiecki Subai, 1993

Distribution. Greece-Albania.

Classification. Troglobiont.

IUCN RedList. NT.

Records in Greek caves. **IPEIROS: Thesprotia:** Agios Neilos Cave (Subai 1993; Reischütz et al. 2016; Paragamian et al. 2023).

Notes. All known *Sciocochlea* material has been collected from deposits or debris originating from deep limestone crevices that are known, or thought to be, connected to caves. So far, no live specimens have been found (Reischütz et al. 2016).

Genus *Stigmatica*

Stigmatica stigmatica (Rossmässler, 1836)

Distribution. Balkan-Italy.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. **IONIAN: Kefalonia:** Melissani Cave (present study).

Genus *Tsoukatosia*

Tsoukatosia christinae Reischütz & Reischütz, 2003

Distribution. Greek endemic, Peloponnisos (stenoendemic).

Classification. Troglobiont.

IUCN RedList. LC.

Records in Greek caves. PELOPONNISOS: Messinia: Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Reischütz et al. 2016, 2020; Paragamian et al. 2023).

Notes. No specimen of the genus *Tsoukatosia* has been recorded alive. The type locality of *T. christinae* is the indicated Agioi Anargyroi Cave, but empty shells have been recorded in other sites within coarse gravel. It is not known whether the species lives subterranean or in caves (Reischütz et al. 2020).

Family Enidae

Genus *Napaeopsis*

Napaeopsis ossica (Böttger, 1885)

Distribution. Greek endemic, Makedonia-Thessalia.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. THESSALIA: Larisa: Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Bank and Menkhorst 1992; Paragamian et al. 2023).

Notes. All literature references are based on specimens from the Senckenberg Museum Frankfurt (SMF), but according to Bank and Menkhorst (1992) the specimens of *N. ossica* from this cave do no longer exist. The presence of this species from Kokkinos Vrachos Cave needs confirmation.

Genus *Rhabdoena*

Rhabdoena cosensis (Reeve, 1849)

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: Fournoi: Votsos sta Chalara Pothole (present study).

Genus *Mastus*

Mastus sitiensis Maassen, 1995

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Trogloxene.

IUCN RedList. LC.

Records in Greek caves. CRETE: Lasithi: Chonos Pothole (present study).

Genus *Zebrina****Zebrina detrita* (Müller, 1774)**

Distribution. European.

Classification. Troglaxene.

IUCN RedList. NE.

Records in Greek caves. **MAKEDONIA:** **Florina:** Daoula Pothole; **Serres:** Alistrati Cave (present study). **THESSALIA:** **Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Bank and Menkhorst 1992; Paragamian et al. 2023).

Family Ferussaciidae**Genus *Cecilioides******Cecilioides acicula* (Müller, 1774)**

Distribution. Euro-Mediterranean-Turanian-Macaronesian.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN:** **Antikythira:** Pano Spiliarida Cave; **Rodos:** Karolos Cave, Koumelou Cave (present study).

***Cecilioides michoniana* (Bourguignat, 1864)**

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. **AEGEAN:** **Rodos:** Koumelou Cave (present study).

***Cecilioides tumulorum* (Bourguignat, 1856)**

Distribution. Mediterranean.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN:** **Rodos:** Koumelou Cave. **CRETE:** **Lasithi:** Pelekita Cave, Theriospilios Cave. **PELOPONNISOS:** **Lakonia:** Agios Andreas Cave, Koukouri Cave; **Messinia:** Nerospiliako Cave (present study).

***Cecilioides* sp.**

Records in Greek caves. **IONIAN:** **Corfu:** Kerkyra caves (Gittenberger 1977; Paragamian et al. 2023).

Family Gastrodontidae**Genus *Zonitoides******Zonitoides nitidus* (Müller, 1774)**

Distribution. Holarctic.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. MAKEDONIA: Imathia: Apano Skala Cave (Riedel 1959, 1992; Beron 2016; Paragamian et al. 2023).

Family Helicidae**Genus *Helix******Helix* aff. *lucorum***

Records in Greek caves. THRAKI: Rodopi: Maroneia Cave (present study).

Genus *Cantareus****Cantareus apertus* (Born, 1778)**

Distribution. Mediterranean.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: Irakleio: Arkalospilios Cave (present study).

Family Helicodontidae**Genus *Lindholmiola******Lindholmiola barbata* (Férussac, 1821)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: Chania: Achyrosopilios Cave, Lentaka Trypa Cave (present study); **Rethymno:** Gerani Cave (Subai and Neubert 2014; Paragamian et al. 2023; present study).

***Lindholmiola corcyrensis* (Rossmässler, 1838)**

Distribution. Balkan.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: Kefalonia: Melissani Cave (present study). **IPEIROS: Thesprotia:** Agios Neilos Cave (Subai and Neubert 2014; Paragamian et al. 2023).

Lindholmiola lens (Férussac, 1832)

Distribution. Greece-W Turkey.

Classification. Troglodexene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: Kefalonia: Melissani Cave (present study). **STEREA ELLADA: Fthiotida:** Mavri Troupa Cave (Subai and Neubert 2014; Paragamian et al. 2023). **PELOPONNISOS: Achaia:** Limnon Cave (Subai and Neubert 2014; Paragamian et al. 2023); **Arkadia:** Small caves near Agios Dimitrios (Subai and Neubert 2014; Paragamian et al. 2023); **Lakonia:** Agios Andreas Cave (present study).

Lindholmiola spectabilis Urbański, 1960

Distribution. Greek endemic, Makedonia.

Classification. Troglodexene.

IUCN RedList. LC.

Records in Greek caves. MAKEDONIA: Serres: Alistrati Cave (present study).

Family Hygromiidae

Genus *Metafruticicola*

Metafruticicola nicosiana (Mousson, 1854)

Distribution. Eastern Mediterranean.

Classification. Troglodexene.

IUCN RedList. DD.

Records in Greek caves. CRETE: Chania: Amoutsas Cave (present study).

Metafruticicola noverca (Pfeiffer, 1853)

Distribution. Greek endemic, Aegean Islands and Crete

Classification. Troglodexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: Chania: Lentaka Trypa Cave, Metaxari Cave (present study).

Metafruticicola redtenbacheri (Pfeiffer, 1856)

Distribution. Eastern Mediterranean.

Classification. Troglodexene.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Chios:** Agio Gala Cave; **Fournoi:** Votsos sta Chalara Pothole (present study).

***Metafruticicola sublecta* (Maltzan, 1884)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. **CRETE: Irakleio:** Latsida sto Vathy Lakko I Pothole (present study).

Genus *Monacha*

***Monacha parumcincta* (Menke, 1828)**

Distribution. Balkan-Italy.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. **IONIAN: Kefalonia:** Melissani Cave (present study).

Family Geomitridae

Genus *Xerocrassa*

***Xerocrassa* sp.**

Records in Greek caves. **AEGEAN: Rodos:** Koumelou Cave. **CRETE: Lasithi:** Pelekita Cave (present study).

Genus *Xerolenta*

***Xerolenta obvia* (Menke, 1828)**

Distribution. European.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. **MAKEDONIA: Serres:** Alistrati Cave (present study).

Family Lauriidae

Genus *Lauria*

***Lauria cylindracea* (Da Costa, 1778)**

Distribution. Euro-Mediterranean-Turanian.

Classification. Troglaxene.

IUCN RedList. NE.

Records in Greek caves. **AEGEAN: Fournoi:** Megalos Votsos Panagias Pothole (present study).

Family Limacidae

Genus *Limacus*

Limacus flavus Linnaeus, 1758

Distribution. Euro-Mediterranean.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **THRAKI: Rodopi:** Maroneia Cave (present study).

Genus *Limax*

Limax conemenosi Böttger, 1882

Distribution. Balkan.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Samos:** Panagia Spiliani Cave (present study).

Limax graecus Simroth, 1889

Distribution. Balkan-Italy.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **MAKEDONIA: Chalkidiki:** Nychteridon Cave; **Kavala:** Agia Eleni Cave; **THRAKI: Rodopi:** Maroneia Cave (present study).

Notes. A slug was collected and identified as *Limax* aff. *graecus* in Petralona Cave (Makedonia: Chalkidiki) (present study).

Limax sp.

Records in Greek caves. **CRETE: Irakleio:** Afentis Christos Pothole (present study). **IPEIROS: Arta:** Trypa Rendes Cave (Beron 2016; Paragamian et al. 2023). **STEREA ELLADA: Aitolokarnania:** Gouva II Cave (Bonzano and Calandri 1984; Beron 2016; Paragamian et al. 2023)

Notes. Two species referred as *Limax maximus* var. *carbonaria* and *Limax maximus* var. *submaculata* are reported from **THESSALIA: Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Paragamian et al. 2023). Their taxonomy is not clear and their presence has never been confirmed since their description.

Family Milacidae**Genus *Tandonia******Tandonia cretica* (Simroth, 1884)**

Distribution. Greek endemic, Greece.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. CRETE: **Irakleio:** Chamoto Spiliari Cave, Aspalathospilios Cave; **Lasithi:** Tafos Cave (present study).

***Tandonia totevi* (Wiktor, 1975)**

Distribution. Greece-Bulgaria.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. MAKEDONIA: **Kavala:** Agia Eleni Cave. THRAKI: **Rodopi:** Maroneia Cave (present study).

***Tandonia* sp.**

Records in Greek caves. CRETE: **Chania:** Kourna Cave; **Irakleio:** Latsida sto Vathy Lakko I Pothole, Latsida ston Gkremismeno Cave, Latsida tou Siganou Cave, Trachinolakka Pothole; **Rethymno:** Diplotafki Pothole, Gerani Cave, Profitis Ilias Cave, Sipouli Pothole; **Dia islet:** Petrokotsyfou Pothole (present study).

Family Oleacinidae**Genus *Poiretia******Poiretia compressa* (Mousson, 1859)**

Distribution. Greece-Albania.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: **Corfu:** Anonymous cave at Pantokrator Mt. (Käufel 1930; Paragamian et al. 2023).

Family Orculidae**Genus *Orcula*****? *Orcula* sp.**

Records in Greek caves. AEGEAN: **Thira:** Zoodochou Pigis Cave (Beron 2016; Paragamian et al. 2023).

Notes. This record needs confirmation, since the genus is absent from the Aegean islands. Most likely it is a misidentification.

Genus *Orculella*

Orculella exaggerata (Fuchs & Käufel, 1936)

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Kasos:** Stylokamara Cave (Gittenberger and Hausdorf 2004; Paragamian et al. 2023).

Orculella ignorata Hausdorf, 1996

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Fournoi:** Votsos Agiou Theologou Pothole (present study).

Orculella sp.

Records in Greek caves. **CRETE: Lasithi:** Pelekita Cave (present study).

Notes. Only juveniles collected. Around the cave, *Orculella cretiminuta* Gittenberger & Hausdorf, 2004 is present.

Family Oxychilidae

Genus *Carpathica*

Carpathica cretica (Forcart, 1950)

Distribution. Eastern Mediterranean.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **CRETE: Irakleio:** Agia Paraskevi Cave (present study); **Rethymno:** Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023).

Carpathica insularis Riedel & Mylonas, 1988

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: Fournoi: Megalos Votsos Panagias Pothole (Riedel 1988a, Riedel 1992; Paragamian et al. 2023).

Genus *Daudebardia*

Daudebardia brevipes (Draparnaud, 1805)

Distribution. European.

Classification. Trogloxene.

IUCN RedList. NE.

Records in Greek caves. CRETE: Rethymno: Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023).

Daudebardia rufa (Draparnaud, 1805)

Distribution. European.

Classification. Trogloxene.

IUCN RedList. NE.

Records in Greek caves. AEGEAN: Evvoia: Katavothra Pothole (present study). **STEREA ELLADA: Attiki:** Panos Cave (Riedel 1978; Riedel 1992; Paragamian et al. 2023). **CRETE: Chania:** Tzani Spilios Cave; **Irakleio:** Lakki Kontari Pothole (present study); **Rethymno:** Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023). **PELOPONNISOS: Arkadia:** Kapsia Cave (present study).

Genus *Eopolita*

Eopolita protensa (Férussac, 1832)

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. AEGEAN: Rodos: Koufovouni Pothole, Koumelou Cave (present study). **STEREA ELLADA: Attiki:** Nymfolyptou Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023), Rachi I Cave (Riedel 1959; Paragamian et al. 2023). **CRETE: Chania:** Agia Sofia Cave (present study), Kolympari Cave (Riedel 1968; Beron 2016; Paragamian et al. 2023), Kourna Cave; **Irakleio:** Afentis Christos Pothole, Anonymous cave at Chersonisos, Anonymous Latsida of Geraki Pothole, Chainospilios Cave, Chamoto Spiliari Cave, Fragkadoni Cave, Karvounolakos Pothole, Lakki Kontari Pothole, Meires Trypa Cave, Palmeti Tafkos Pothole; **Lasithi:** Achnistra Cave (present study); **Rethymno:** Idaio Antro Cave (Riedel 1968; Paragamian et al. 2023), Mythia Kampathoura Pothole (present study).

Genus *Mediterranea****Mediterranea amalthaeae* (Riedel & Subai, 1982)**

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. **CRETE: Irakleio:** Faneromeni Cave, Latsida ston Gkremismeno Cave (present study); **Lasithi:** Diktaio Antro Cave (Riedel and Subai 1982; Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023, present study), Gaidourotrypa Cave, Peristeras Pothole, Tou Sfakianou i Trypa Pothole, Latsida Bempona Pothole (present study).

Notes. A remarkable extension of the distribution of *M. amalthaeae* is reported. Until now, the species was known only from its type locality, Diktaio Antro Cave in Dikti Mt. (Lasithi, Crete). It is found in six other caves on the island and is therefore no longer a single-cave endemic but an island endemic.

***Mediterranea depressa* (Sterki, 1880)**

Distribution. Euro-Mediterranean.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **MAKEDONIA: Kavala:** Agia Eleni Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023), Mavri Trypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023).

***Mediterranea hydatina* (Rossmässler, 1838)**

Distribution. European.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Antiparos:** Antiparos Cave (Riedel 1983, 1992, 1996; Beron 2016; Paragamian et al. 2023); **Fournoi:** Votsos Agiou Charalampous Pothole (present study), Megalos Votsos Panagias Pothole (Riedel 1992, 1996; Paragamian et al. 2023; present study); **Ikaria:** Foutra Raos Cave (Martens 1889; Riedel 1983, 1992, 1996; Paragamian et al. 2023; present study); **Kasos:** Ellinokamara Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023); **Paros:** Kalampaki Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023); **Rodos:** Koufovouni Pothole (present study). **CRETE: Chania:** Kolympari Cave (Riedel 1968, 1992; Beron 2016; Paragamian et al. 2023), Tzani Spiliou Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Irakleio:** Afentis Christos Pothole, Latsida ston Gkremismeno Cave. **MAKEDONIA: Florina:** Mikrolimni Cave (present study); **Serres:** Alistrati Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023; present study); **Thessaloniki:** Drakotrypa Cave (present study).

Mediterranea ionica* (Riedel & Subai, 1978)*Distribution.** Balkan-Italy.**Classification.** Troglophile.**IUCN RedList.** LC.

Records in Greek caves. **IONIAN: Corfu:** Anonymous cave at Pantokrator Mt. (Käufel 1930; Riedel 1992, 1996; Paragamian et al. 2023), Katsouri Cave (Riedel 1978, 1992, 1996; Riedel and Subai 1982; Paragamian et al. 2023). **IPEIROS: Ioannina:** Anemotrypa Cave (Riedel 1992, 1996; Paragamian et al. 2023); **Thesprotia:** Agios Neilos Cave (Riedel and Subai 1993; Paragamian et al. 2023).

Mediterranea juliae* (Riedel, 1990)*Distribution.** Greece-Albania.**Classification.** Troglophile.**IUCN RedList.** LC.

Records in Greek caves. **IONIAN: Corfu:** Megali Grava Cave (Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

Notes. Riedel and Subai (1993) reported this species from Agios Neilos Cave (Ipeiros, Thesprotia) but they note that its presence needs to be confirmed by anatomical data.

Mediterranea ? mylonasi* (Riedel, 1983)*Distribution.** Greek endemic, Aegean Islands.**Classification.** Troglophile.**IUCN RedList.** LC.

Records in Greek caves. **AEGEAN: Evvoia:** Skoteini Cave (Riedel 1993, 1996; Beron 2016; Paragamian et al. 2023); **Gioura:** Kyklopa Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Samos:** Panagia Spiliani Cave (present study).

Notes. The taxonomy of the species is uncertain (Riedel 1992).

***Mediterranea* sp.**

Records in Greek caves. **IPEIROS: Ioannina:** Platanousa Cave, (Klemm 1962 as *Oxychilus eudedaleus*; Riedel 1979, 1992 as *Oxychilus* (*Riedelius* ?) sp. (nova?); Beron 2016 as *Oxychilus* (*Riedelius*?) sp. (nova?); Paragamian et al. 2023 as *Oxychilus* sp.).

Genus *Morlina****Morlina glabra* (Rossmässler, 1835)****Distribution.** European.**Classification.** Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Evvoia:** Katavothra Pothole (present study); **Thasos:** Drakotrypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023; present study). **MAKEDONIA: Drama:** Maara Cave; **Florina:** Mikrolimni Cave (present study); **Imathia:** Apano Skala Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023); **Kavala:** Agia Eleni Cave (present study), Mavri Trypa Cave (Riedel 1992; Beron 2016; Paragamian et al. 2023; present study); **Serres:** Pestereta Cave (Riedel 1959; Beron 2016; Paragamian et al. 2023); **Thessaloniki:** Drakotrypa Cave (present study). **THESSALIA: Larisa:** Kokkinos Vrachos Cave (Stussiner and Böttger 1885; Riedel 1992; Beron 2016; Paragamian et al. 2023).

Genus *Oxychilus*

***Oxychilus cyprius* (Pfeiffer, 1847)**

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. **MAKEDONIA: Imathia:** Apano Skala Cave (Riedel 1959, 1983, 1992; Beron 2016; Paragamian et al. 2023).

***Oxychilus seidli* Riedel, 1999**

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Fournoi:** Votsos Agiou Charalampous Pothole, Megalos Votsos Panagias Pothole (present study).

***Oxychilus superfluus* (Pfeiffer, 1849)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **CRETE: Irakleio:** Chainospilios Cave, Latsida sto Vathy Lakko I Pothole (present study); **Rethymno:** Idaio Antro Cave (Riedel 1968; Paragamian et al. 2023).

***Oxychilus* sp.**

Records in Greek caves. **STEREA ELLADA: Fokida:** Zoodochos Pigi Cave (Alexiou et al. 2014), Mayer Cave (Alexiou et al. 2014; Paragamian et al. 2023). **CRETE: Chania:** Agia Sofia Cave (present study), Kolympari Cave as ? *Oxychilus subeffusus* (Riedel

1968, 1992; Beron 2016; Paragamian et al. 2023); **Irakleio**: Stou Bokou ton Poro Pothole; **Rethymno**: Katerianos Tafkos Pothole (present study). **PELOPONNISOS**: **Messinia**: Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Genus *Schistophallus*

Schistophallus minoicus (Riedel, 1968)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **CRETE**: **Irakleio**: Faneromeni Cave, Latsida sto Vathy Lakko I Pothole (present study); **Lasithi**: Diktaio Antro Cave (Riedel 1968, 1996; Maassen and Riedel 1991; Beron 2016; Paragamian et al. 2023, present study), Tou Sfakianou i Trypa Pothole (present study).

Schistophallus samius (Martens, 1889)

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. NE.

Records in Greek caves. **AEGEAN**: **Chios**: Agio Gala Cave (present study), Cave in Chios (Martens 1889); **Fournoi**: Megalos Votsos Panagias Pothole (Riedel 1993, 1996; Paragamian et al. 2023); **Naxos**: Za Cave (Beron 2016; Paragamian et al. 2023); **Samos**: Cave on Kerketeas Mt. (Martens 1889; Riedel 1958, 1972, 1992, 1996; Beron 2016; Paragamian et al. 2023), Panagia Spiliani Cave (present study). **STEREA ELLADA**: **Attiki**: Vredou Cave (Riedel 1972; Beron 2016; Paragamian et al. 2023). **PELOPONNISOS**: **Achaia**: Limnon Cave (Riedel 1986, 1992, 1996; Beron 2016; Paragamian et al. 2023); **Lakonia**: Katafygi Cave (Anavryti) (Riedel 1992, 1996; Paragamian et al. 2023); **Korinthia**: Cave at Saitas Mt. (Arndt and Subai 2012).

Schistophallus spratti (Westerlund, 1892)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **CRETE**: **Chania**: Amoutsas Cave, Arapi Trypa Pothole, Kourna Cave, Lentaka Trypa Cave, Metaxari Cave (present study), Tzani Spilios Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Zoures Cave (present study); **Irakleio**: Kynigotafkos Pothole, Poros Stenou Lagkou Pothole, Stou Bokou ton Poro Pothole (present study); **Rethymno**: Afroimou Cave, Dolonas Cave (present study), Gerani Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023), Kaoudi Tafkos Pothole, Maryle Trypa Cave, Platani Cave, Tafkos Myristis Pothole, Tigania Cave, Voreini Trypa Cave, Skylogkremiti Cave (present study).

Family Pagodulinidae**Genus *Pagodulina******Pagodulina* sp.**

Records in Greek caves. PELOPONNISOS: Messinia: Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Family Pleurodiscidae**Genus *Pleurodiscus******Pleurodiscus balmei* (Potiez & Michaud, 1838)**

Distribution. Eastern Mediterranean.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. AEGEAN: Fournoi: Megalos Votsos Panagias Pothole, Mikros Votsos Panagias Pothole; **Samos:** Panagia Spiliani Cave, Vrysoulia Cave (present study).

***Pleurodiscus sudensis* (Pfeiffer, 1846)**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. CRETE: Irakleio: Chainospilios Cave, Chonos Sarchou Cave, Anonymous Latsida of Geraki Pothole, Chamoto Spiliari Cave, Fraggadoni Cave, Doxa Cave, Arkalospilios Cave, Faneromeni Cave, Karvounolakkos Cave, Karvounolakos Pothole, Lakki Kontari Pothole, Latsida of Moni Kaleri Pothole, Latsida sto Makry Lakki Pothole, Megalos Tafkos Pothole, Moni Kaleri Cave, Palmeti Tafkos Pothole, Peristerotafkos Pothole, Skararolithos Pothole, Stravomyti Cave, Trachinolakka Pothole, Xerakolagoufo Pothole; **Lasithi:** Trapeza Cave; **Rethymno:** Alykes Cave, Gerani Cave, Kamariti Cave, Karafti Tafkos Pothole, Katerianos Tafkos Pothole, Melidoni Cave, Peiraton Cave, Porou Trypa Cave, Skoteinospilios Cave, Stin Koryftis Viglas Pothole, Tafkos sti Gonia Pothole, Tafkos stin Poda Faragka Pothole, Trypiti Cave, Xepatomenos Tafkos Pothole (present study).

Family Pomatiidae**Genus *Pomatias******Pomatias elegans* (Müller, 1774)**

Distribution. Euro-Mediterranean.

Classification. Troglaxene.

IUCN RedList. LC.

Records in Greek caves. **IONIAN: Kefalonia:** Melissani Cave (present study).

Family Pristilomatidae

Genus *Gyalina*

***Gyalina formosa* Riedel & Subai, 1993**

Distribution. Greek endemic, Ipeiros (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. **IPEIROS: Thesprotia:** Agios Neilos Cave (Riedel and Subai 1993).

Notes. The shells were found in rock debris, on limestone rocks in the small cave chapel (Riedel and Subai 1993). In the type locality the species is known from 10 empty shells, including 7 adults, some very fresh. The species may also occur in other subterranean environments other than caves (unpublished data). If this is confirmed, then the species should be considered as a subterranean, troglophilous species.

***Gyalina tsatsae* Gittenberger, 1977**

Distribution. Greek endemic, Ionian Islands (single-island endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. **IONIAN: Corfu:** Anthropograva Cave (Gittenberger 1977; Riedel 1992; Beron 2016; Paragamian et al. 2023), Grava Tsouka Cave (Gittenberger 1977; Riedel 1992; Beron 2016; Paragamian et al. 2023).

Genus *Lindbergia*

***Lindbergia beroni* Riedel, 1984**

Distribution. Greek endemic, Aegean Islands (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. **AEGEAN: Thira:** Zoodochou Pigis Cave (Riedel 1984, 1992, 1996; Beron 1985, 2016; Di Russo and Rampini 2001; Gasparo 2009; Paragamian et al. 2023; present study).

Notes. In the collections of the NHMC there are specimens of *Lindbergia* aff. *beroni* from Kanavari Cave (Aegean: Naxos).

***Lindbergia ? gittenbergeri* Pintér & Riedel, 1983**

Distribution. Greek endemic, Ionian Islands (single-island endemic).

Classification. Troglobiont.

IUCN RedList. CR.

Records in Greek caves. IONIAN: Corfu: Megali Grava Cave (Pintér and Riedel 1983; Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023), Anonymous cave (Riedel 1992; Beron 2016; Paragamian et al. 2023).

Notes. The presence of the genus on the island of Corfu requires confirmation (Riedel 1992).

Lindbergia aff. *karainensis*

Records in Greek caves. AEGEAN: Karpathos: Diaolospilios Cave (present study).

Lindbergia orbicularis (Riedel, 1962)

Distribution. Greek endemic, Crete (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. CRETE: Chania: Agia Roumeli Cave (Riedel 1992, 1996; Paragamian et al. 2023), Metaxari Cave (present study), Tzani Spilios Cave (Riedel 1993, 1996; Beron 2016; Paragamian et al. 2023; present study); **Irakleio:** Agio Pneuma Cave, Anonymous Latsida of Geraki Pothole (present study), Chainospilios Cave (Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Doxa Cave, Karvounolakkos Cave, Lakki Kontari Pothole, Peristerotafkos Pothole, Schistra Cave, Skararolithos Pothole, Stou Bokou ton Poro Pothole, Trachinolakka Pothole, Xerakolagoufo Pothole (present study); **Lasithi:** Achnistres Cave, Peristera Cave (Agios Georgios), Peristera Cave (Vrachasi), Tafos Cave, Xepatomeni Latsida Pothole (present study); **Rethymno:** Chomatotafkos Pothole, Diplotafki Pothole, Erfoi Cave (present study), Gerani Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023), Kakalonia Pothole, Kamariti Cave, Karafti Tafkos Pothole, Katerianos Tafkos Pothole (present study), Melidoni Cave (Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023), Porou Trypa Cave, Tafkos stin Pode Faragka Pothole, Xanthou Cave, Xylouri Tafkos Pothole (present study).

Lindbergia ? *pageti* Riedel, 1968

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. CRETE: Chania: Kolympari Cave (Riedel 1968, 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023).

Notes. Previously, the species was reported with certainty only from the type locality—Kolympari Cave—and was considered to be a troglobiont. Specimens from other locations in Crete and its adjacent islands have been reported in the past but their identification was uncertain and therefore not confirmed by Riedel (1992). The collection

of the NHMC has a lot more material than the material Riedel had the opportunity to study and as a result, Mylonas was able to confirm the presence of the species in other localities on Crete island and Western Paximadi islet. A specimen from Tafos Cave (Crete: Lasithi), most probably belongs to this species, *Lindbergia* aff. *pageti*. Research on the taxonomy of the species is still needed, as there are no anatomical data to confirm the genus.

***Lindbergia pinteri* Riedel, 1981**

Distribution. Greek endemic, Aegean Islands (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. **AEGEAN: Ikaria:** Foutra Raos Cave (Riedel 1981a, 1992, 1996; Beron 2016; Paragamian et al. 2023).

***Lindbergia pseudoillyrica* Riedel, 1960**

Distribution. Greek endemic, Crete and adjacent islets.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **CRETE: Chania:** Tzani Spilios Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023); **Irakleio:** Achnistra Cave, Afentis Christos Pothole (present study), Agia Paraskevi Cave (Riedel 1960, 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023), Chonos Sarchou Cave (Riedel 1960, 1968, 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study), Meires Trypa Cave (present study); **Lasithi:** Agios Stavros Cave (present study), Diktaio Antro Cave (Riedel 1992, 1996; Beron 2016; Paragamian et al. 2023), Theriospilios Cave (present study); **Rethymno:** Peristere Cave (ancient quarry) (Riedel 1968, 1992, 1996; Beron 2016; Paragamian et al. 2023), Prinos Cave (Beron 2016; Paragamian et al. 2023), Sfentoni Trypa Cave (Riedel 1977, 1992, 1996; Beron 2016; Paragamian et al. 2023).

***Lindbergia spiliaenymphis* Riedel, 1959**

Distribution. Greek endemic, Sterea Ellada (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. VU.

Records in Greek caves. **STEREA ELLADA: Attiki:** Keratea Cave (Riedel 1959, 1960, 1968, 1977, 1992, 1996; Pintér and Riedel 1983; Beron 2016; Paragamian et al. 2023).

***Lindbergia stylokamarae* Riedel, 1981**

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. **AEGEAN: Kasos:** Stylokamara Cave (Riedel 1981a, 1992; Beron 2016; Paragamian et al. 2023; present study).

***Lindbergia* sp.**

Records in Greek caves. **AEGEAN: Irakleia:** Agios Ioannis Cave, as *Lindbergia* sp. (nova) aff. *pseudodillyrica* (Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023). **PELOPONNISOS: Messinia:** Agioi Anargyroi Cave (Reischütz and Reischütz 2003; Paragamian et al. 2023).

Genus *Vitrea*

***Vitrea clessini* (Hesse, 1882)**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Kasos:** Ellinokamara Cave (present study).

***Vitrea contracta* (Westerlund, 1871)**

Distribution. Euro-Mediterranean-Turanian-Macaronesian.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Fournoi:** Megalos Votsos Panagias Pothole (Riedel 1992; Paragamian et al. 2023), Votsos Agiou Charalampous Pothole (Riedel 1992). **CRETE: Lasithi:** Diktaio Antro Cave (Riedel 1992; Paragamian et al. 2023); **Rethymno:** Erfoi Cave (present study), Gerani Cave (Riedel 1977, 1992; Beron 2016; Paragamian et al. 2023). **PELOPONNISOS: Lakonia:** Agios Andreas Cave (present study), Kaiadas Cave (Riedel 1992; Paragamian et al. 2023).

***Vitrea klemmi* Pintér, 1972**

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Ikaria:** Foutra Raos Cave (Riedel 1981a, 1981b, 1992; Beron 2016; Paragamian et al. 2023).

***Vitrea neglecta* Damjanov & Pintér, 1969**

Distribution. Greece-Bulgaria-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **MAKEDONIA: Drama:** Maara Cave (Georgiev 2016; Paragamian et al. 2023).

***Vitrea ossaea* Pintér, 1983**

Distribution. Greek endemic, Thessalia (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. DD.

Records in Greek caves. **THESSALIA: Larisa:** Profitis Ilias Cave (Pintér 1983; Riedel 1992; Riedel 1996; Beron 2016; Paragamian et al. 2023).

Notes. This species has also been reported from Peristera islet (Aegean) but the taxonomy of the specimen requires confirmation (Riedel 1992).

***Vitrea riedeli* Damjanov & Pintér, 1969**

Distribution. Greece-Bulgaria-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Fournoi:** Megalos Votsos Panagias Pothole (Riedel 1992; Paragamian et al. 2023; present study).

***Vitrea riedeliana* Paget, 1976**

Distribution. Greece-Turkey.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **AEGEAN: Rodos:** Koufovouni Pothole, Koumelou Cave (present study).

***Vitrea schuetti* Pintér, 1972**

Distribution. Greek endemic, Greece.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. **STEREA ELLADA: Attiki:** Ntavelis Cave (Pintér 1972; Riedel 1992; Beron 2016; Paragamian et al. 2023).

***Vitrea subrimata* (Reinhardt, 1871)**

Distribution. Euro-Mahrebian.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. IPEIROS: Thesprotia: Agios Neilos Cave (Riedel and Subai 1993).

Family Zonitidae

Genus *Allaegopsis*

Allaegopsis jonicus (Käufel, 1930)

Distribution. Greek endemic, Ionian Islands-Opposite Greek mainland.

Classification. Troglonexene.

IUCN RedList. LC.

Records in Greek caves. IONIAN: Lefkada: Egklouvi Cave (Käufel 1930; Riedel 1982, 1992; Beron 2016; Paragamian et al. 2023), Poly Trypes Cave (Käufel 1930; Riedel 1992; Paragamian et al. 2023).

Genus *Balcanodiscus*

Balcanodiscus beroni Riedel, 1995

Distribution. Greek endemic, Makedonia (single-cave endemic).

Classification. Troglobiont.

IUCN RedList. NT.

Records in Greek caves. MAKEDONIA: Drama: Maara Cave (Riedel 1995, 1996; Beron 2016; Paragamian et al. 2023).

Notes. In the studies of Riedel (1995) and Beron (2016), the species is reported from two caves, Maara I and Maara II. These are not two different caves, but part of the same cave system called Maara.

Balcanodiscus cerberus Riedel, 1985

Distribution. Greek endemic, Thraki (stenoendemic).

Classification. Troglophile.

IUCN RedList. NT.

Records in Greek caves. THRAKI: Rodopi: Maroneia Cave (Riedel 1985b, 1988b, 1992, 1996; Reischütz 1986, 1988; Paragamian et al. 2004, 2023; Beron et al. 2004; Eröss et al. 2011; Beron 2016; present study).

Balcanodiscus difficilis Riedel, 1988

Distribution. Greek endemic, Aegean Islands (single-island endemic).

Classification. Troglophile.

IUCN RedList. NT.

Records in Greek caves. AEGEAN: Thasos: Drakotrypa Cave (Riedel 1988b, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

***Balcanodiscus frivaldskyanus* (Rossmässler, 1842)**

Distribution. Eastern Balkan.

Classification. Troglophile.

IUCN RedList. LC.

Records in Greek caves. THRAKI: Evros: Koufovouno Cave (Riedel 1969, 1985b, 1988b, 1992, 1996; Beron et al. 2004; Beron 2016; Paragamian et al. 2023; present study).

***Balcanodiscus* sp.**

Records in Greek caves. MAKEDONIA: Serres: Alistrati Cave (Beron 2016; Paragamian et al. 2023).

Genus *Doraegopsis*

***Doraegopsis subatii* Riedel, 1990**

Distribution. Greek endemic, Sterea Ellada (stenoendemic).

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. STEREA ELLADA: Fthiotida: Mavri Troupa Cave (Bank and Menkhorst 1988; Riedel 1990, 1992, 1996; Beron 2016; Paragamian et al. 2023; present study).

***Doraegopsis* sp.**

Records in Greek caves. PELOPONNISOS: Achaia: Limnon Cave (Riedel 1982, 1986, 1992; Bank and Menkhorst 1988; Beron 2016; Paragamian et al. 2023).

Genus *Zonites*

***Zonites casius* Martens, 1889**

Distribution. Aegean Islands-Opposite Turkish mainland.

Classification. Trogloxene.

IUCN RedList. NT.

Records in Greek caves. AEGEAN: Kasos: Stylokamara Cave (Riedel 1985a).

***Zonites nikariae* Pfeffer, 1930**

Distribution. Greek endemic, Aegean Islands.

Classification. Troglophile.

IUCN RedList. VU.

Records in Greek caves. **AEGEAN: Ikaria:** Foutra Raos Cave (Martens 1889; Riedel 1985a, 1992; Beron 2016; Paragamian et al. 2023).

Among the 113 species, 15 were not identified at the species level, i.e. *Pagodulina* sp., and were therefore excluded from any cave-dwelling category. The remaining 98 species include 14 troglobionts (14%), 39 troglophiles (40%) and 45 (46%) troglonexes (Fig. 3). The percentage of troglobiont gastropods is lower than the total percentage of troglobionts in the cave fauna in Greece (22.2%) (Paragamian et al. 2023). The troglobiont gastropods belong to eight genera, namely *Balcanodiscus* (1 species) (Zonitidae), *Gyalina* (2 species), *Lindbergia* (4 species), *Vitrea* (1 species) (Pristilomatidae), *Mediterranea* (1 species) (Oxychilidae), *Pholeoteras* (1 species) (Cyclophoridae), *Sciocochlea* (2 species), *Tsoukatosia* (1 species) (Clausiliidae) and *Speleodentorcula* (1 species—monotypic genus) (Argnidae). All but two species (*Pholeoteras euthrix* and *Tsoukatosia christinae*) are endemic to Greece and are listed as Threatened or Near Threatened in the IUCN Red List (2023) but none is legally protected. It is interesting to note that five of the endemic species are distributed on the mainland while the remaining eight are found on islands (Fig. 4). In particular, Corfu, an Ionian island, hosts four troglobiont species belonging to four genera, three of which are endemic to the island.

Almost half of the cave-dwelling gastropod species (49%), are endemic to Greece, which is close to the endemism percentage of the entire cave fauna of Greece, which is 45% (Paragamian et al. 2023). Many of these have a very restricted distribution, with twelve species being single-island endemics, and seven being single-cave endemics (Fig. 5).

The island of Crete is the most studied region of Greece, containing 55% of the explored caves. Mainland Greece and most of the Aegean and Ionian islands have not been intensively explored (Fig. 1). The reason for this difference in between regions is mostly a matter of sampling bias rather than the presence or absence of caves.

The maximum number of species reported in a cave—nine species—is recorded in two caves: Gerani Cave in Crete and Megalos Votsos Panagias Pothole in Fournoi. The majority of the caves (101) are reported to host only one species while 60 caves host 2–3 species and the remaining 19 host 4–7 species (Fig. 6).

Discussion and conclusions

In this study, 113 terrestrial gastropod species are reported from 182 Greek caves, thereby doubling the number of known cave-dwelling species and providing first records for 113 caves. The species belong to 49 genera within 23 families. The most species- and genus-rich families are Oxychilidae (19 species, 7 genera), Pristilomatidae (19 species, 3 genera), Clausiliidae (16 species, 6 genera) and Zonitidae (8 species, 4 genera). These, with the exception of Clausiliidae, are the most diverse subterranean families worldwide (Grego 2022) while all of them are among the most species-rich families in Greece with Clausiliidae being the most speciose family in Greece (Vardinoyannis et al. 2018).

Classification of cave-dwelling gastropods of Greece

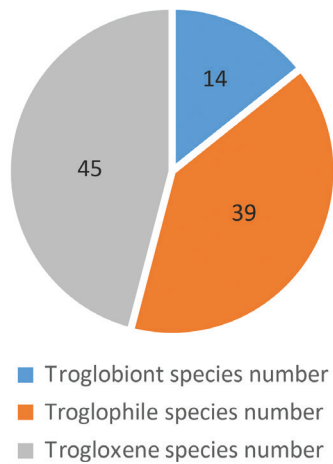


Figure 3. Ecological classification of the cave-dwelling gastropods in Greek caves.

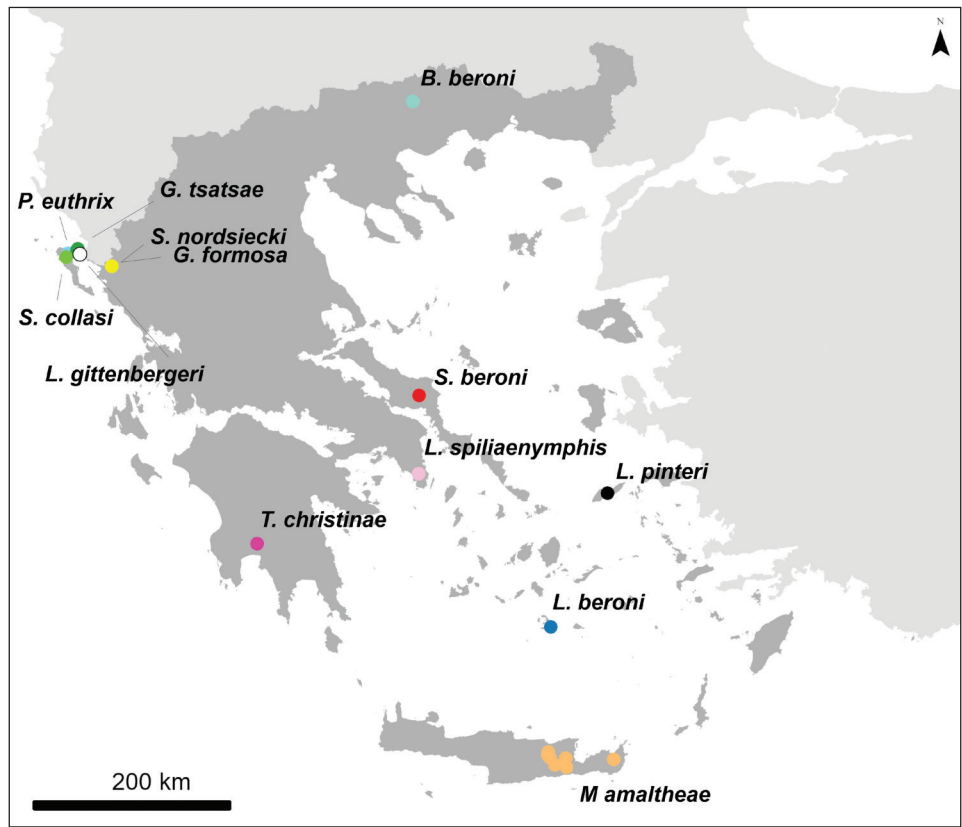


Figure 4. Troglobiont gastropod species of Greece.

Endemism in cave-dwelling gastropods of Greece

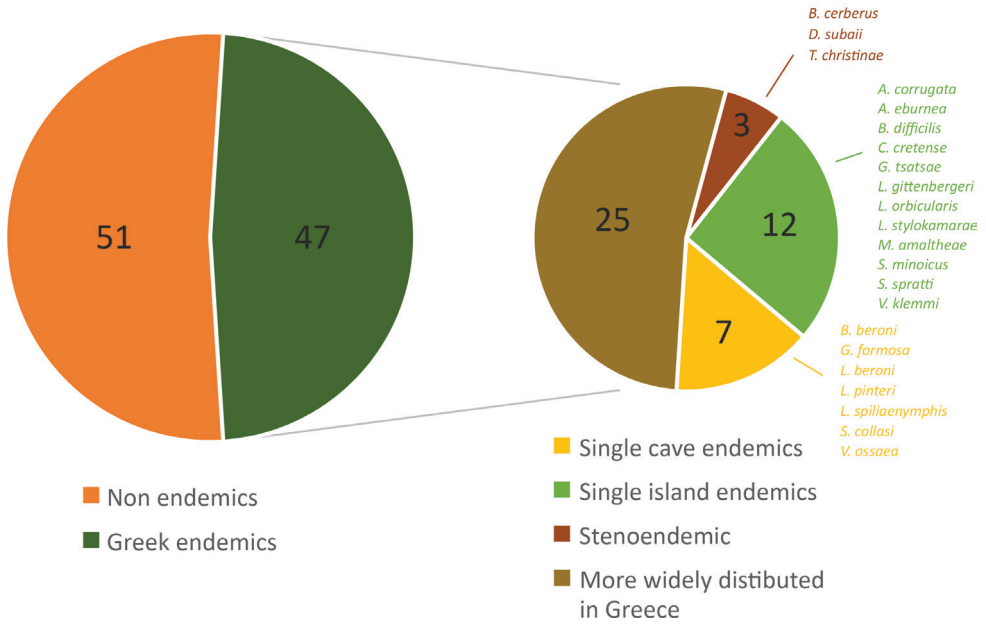


Figure 5. Number of endemic and non-endemic cave-dwelling gastropods in Greek caves.

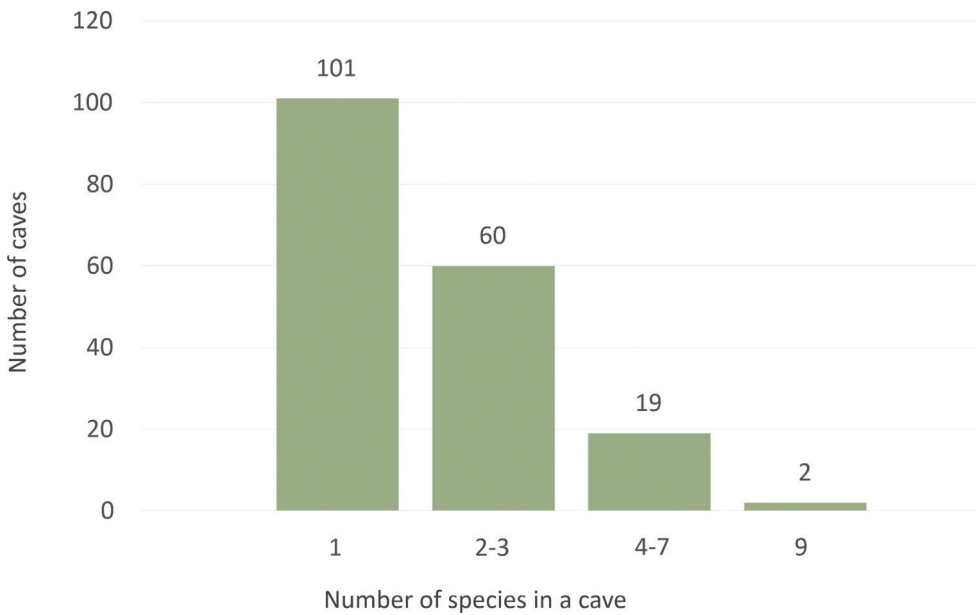


Figure 6. The number of caves in Greece that are reported to host from one to nine cave-dwelling gastropods.

Troglobionts and troglaphiles comprise 14% and 40% of the cave-dwelling gastropod fauna respectively while 46% is characterized as troglaxene. Note that for a high proportion of taxa, the ecological classification cannot be made with certainty, regardless the chosen classification system (Sket 2004). For this reason, the reader should be cautious with these numbers. For example, many species classified as troglaxenes may have a variety of reasons penetrating caves such as seeking for more stable climatic conditions or—for the carnivorous species—searching for food (Weigand 2014). Most of the troglaxenes however, probably have an accidental presence in the caves. Many of these are not active visitors or by chance crawling in the caves but could have been washed into the cave by the rain. This is especially true for the species collected only as empty shells.

To date, more than 322 terrestrial gastropod species have been reported from subterranean habitats around the world, classified into 74 genera within 32 families (Grego 2022). The highest diversity of underground terrestrial gastropods is known from Europe (accounting for 59% of global taxa) and includes the Dinaric region (accounting for 25% of the global taxa) (Grego 2022). According to Sket et al. (2004), 49 species of obligate subterranean terrestrial gastropods have been reported from the Balkans. Thirty-six species are known from the western Balkans (Slovenia, Croatia, Bosnia and Herzegovina, Montenegro, Serbia, and North Macedonia) and 13 species from Greece (including the Aegean islands and Crete). Since then, more species have been described, e.g. at least seven species of the genus *Zospeum* [*Z. bucculentum*, *Z. clathratum*, *Z. manitaense*, *Z. pagodulum*, *Z. robustum* and *Z. simplex* all described by Inäbnit, Jochum & Neubert, 2019 in Inäbnit et al. (2019) and *Z. tholussum* Weigand, 2013 (Weigand 2013)].

It is difficult to compare the fauna of Greece with other countries, mainly the neighboring ones. One reason for this is that caves are generally underexplored (Wynne 2022). Even if a cave has been explored for its fauna, the data sometimes depend on the specialty of the researcher. For example, a bat specialist, will in general focus on bats and not on snails while a malacologist may not focus on or collect arthropods. Another reason is that the data is not easily accessible and there are not lists for every region and/or country. Finally, it is difficult to define the exact number of troglobiontic taxa of terrestrial gastropods, due to different definitions of the term “troglobiont”, to inadequate knowledge of the morphology and biology of the taxa, and undefined taxonomic status (Gottstein 2002). Focusing on the Balkans, aggregated data are available for Bulgaria and Croatia. Although the latter is not a direct neighbour of Greece, it is worth mentioning because the karst areas in Croatia, are part of the Dinarides and most part of Greece, is an extension of them. The Dinarides, have been defined as a global hotspot for subterranean biodiversity (Gottstein 2002; Grego 2022; Lukić et al. 2023). In Croatia (56,600 km², more than 7,000 registered caves and potholes), although there has been no systematic research on terrestrial cave malacofauna, at least 19 troglobiont molluscan species have been recorded, seven of which are endemic to Croatia and one species common to Greece, *Pholeoteras euthrix* (Gottstein 2002). In total, two genera are common between the two countries (*Pholeoteras* and *Gyrallina*).

On the other hand, Bulgaria (111,000 km², 5,000 caves and potholes) and Greece, two neighbouring countries that share the speleozoogeographic zones of Rhodopes (Georgiev 1977 in: Beron 2001), do not share any troglobiont species. According to Beron (2001), of the 20 terrestrial mollusc species reported from the 250 researched Bulgarian caves, none are considered troglobionts.

Of the 10,000 known caves of Greece, only 558 have been speleobiologically explored, while snails have been recorded in 182. Although speleobiologists have done a lot of work in the recent decades, there are still many more caves to be surveyed. The case of *Mediterranea amaltheae*, which was considered a single-cave endemic and in the present study was found in six more caves on the island of Crete, is evidence that the caves of Greece are undersurveyed. The new generation of speleobiologists in Greece, still have a broad field to explore. We believe that with the increasing exploration of Greek caves, the number of known species inhabiting caves will increase and new species will be discovered.

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Supplementary material I

List of caves and their locality. Caves with an asterisk (*) are artificial caves.

Authors: Danae Karakasi

Data type: xlsx

Explanation note: The table contains all caves mentioned in the text with detailed geographic information.

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