

From the dark to the light: A new genus and species of stygobiont hydrobiid (Caenogastropoda, Truncatelloidea) from southern Greece

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Abstract

A new stygobiont hydrobiid genus and species is described from the Stymphalia karst basin (Peloponnese, Greece). *Cyllena hermes* **gen. et sp. nov.** is distinguished from other valvatiform or valvatiform–planorboid stygobiont hydrobiids by a unique combination of shell and anatomical characters, supporting the establishment of a new monotypic genus. It is currently known from a single karstic spring connected to the subterranean hydrological network of the Stymphalia polje, indicating a highly localized distribution. Following a precautionary approach, and in accordance with IUCN criteria, the species is here considered to qualify as Vulnerable (VU D2). The discovery of the new genus contributes to the documentation of subterranean aquatic gastropod diversity in Greece and emphasizes the need for further targeted exploration of karst ecosystems in the region.

Keywords

Endemism, Hydrobiidae, IUCN, Peloponnese, karst aquifer

Introduction

Europe encompasses 11 of the 26 globally recognized hotspots of subterranean biodiversity (Năpăruș-Aljančić et al. 2026) and represents a major center of research in subterranean biology (Deharveng et al. 2019; Koch et al. 2024). Subterranean freshwater fauna in Europe constitutes a substantial component of global subterranean biodiversity, as species richness is markedly higher than on other continents (Gibert and Culver 2005; Moldovan 2018). In particular, stygobionts (i.e. obligately subterranean aquatic species) account for up to 8% of the total freshwater fauna in Europe (Sket 2018).

Mollusca form the second most diverse taxonomic group of stygobionts after Crustacea, with the highest global diversity occurring within Gastropoda (Prié 2019). Among gastropods, Hydrobiidae is by far the most species-rich family, with more than 350 described subterranean species (Marmonier et al. 2023), followed by Moitessieriidae (Prié 2019), whose representatives exhibit an almost exclusively stygobiont lifestyle (Wilke 2019). The Balkan Peninsula (including the non-Dinaric regions of Slovenia and Croatia), together with parts of South France and Spain, is recognized as a major hotspot of stygobiont gastropod diversity with more than 400 described species (e.g. Sket et al. 2004; Ferreira et al. 2007; Prié 2019; Grego 2020, 2022; Raković et al. 2020; Dmitrović et al. 2023; Prié et al. 2024; López-Soriano and Quiñonero-Salgado 2025).

Located at the southern margin of this hotspot, Greece is characterized by extensive karst development, as carbonate rocks underlie a large proportion of the country and constitute the principal geological substrate for speleogenesis, thereby providing extensive habitats for subterranean fauna. These formations cover approximately 41% of the country's surface (Chen et al. 2017) and include more than 10,000 known caves (Beron 2016). Within this geological framework, Greece hosts an exceptionally rich and highly endemic subterranean fauna, comprising more than 981 species assigned to 493 genera. Nearly half of these species are endemic to Greece, while obligate subterranean species (both troglobionts and stygobionts) account for 19.5% of the subterranean fauna; most of these species exhibit pronounced steno-endemism (Paragamian and Paragkamian 2026).

The first stygobiont gastropod species from Greece was recognized as *Paludinella* (*Bythiospeum*) *blanci* Westerlund, 1886 (accepted name: *Paladilhiopsis blanci* (Westerlund, 1886)), from Cephalonia Island (Schütt 1970, 1980). To date, the documented stygobiont gastropod fauna of Greece remains comparatively limited. One hydrobiid species, *Fissuria raehlei* (Schütt, 1980), is known from wells on the Ionian Islands of Cephalonia and Zakynthos (Schütt 1980; Bodon et al. 2001). Two sympatric moitessieriid species, *Clameia brooki* Boeters & E. Gittenberger, 1990 and *Iglica kirea* (Boeters, 1991), have been recorded from Euboea (Boeters and Gittenberger 1990; Boeters 1991). One hydrobiid, *Agrafia wiktoriae* Szarowska & Falniowski, 2011, is found in a well on Mt Agrafa, Evrytania (Szarowska and Falniowski 2011). In addition, one hydrobiid and one moitessieriid species, *Daphniola magdalenae* Falniowski, 2015 and *Iglica hellenica* Falniowski & Sarbu, 2015, respectively, were collected from Melissotrypa Cave in Thessaly (Falniowski and Sarbu 2015). The descriptions of these taxa were based on shell morphology and soft-body anatomy, and the phylogenetic af-

finities of *A. wiktory*, *D. magdalenae* and *I. hellenica* were investigated using molecular data. In contrast, several additional Greek moitessieriid species—namely *Paladilhiopsis janinensis* Schütt, 1962, *Paladilhiopsis thessalica* (Schütt, 1970), *I. maasseni* Schütt, 1980; *I. sidarensis* Schütt, 1980; *P. neaaugustensis* P. L. Reischütz, 1988; *I. alpheus* A. Reischütz & P. L. Reischütz, 2004 and *I. wofischeri* A. Reischütz & P. L. Reischütz, 2004; *Paladilhiopsis saeureli* A. Reischütz & P. L. Reischütz, 2020—as well as the recently described stygobiont hydrobiid *Daphniola wohlschlageri* A. Reischütz & P. L. Reischütz, 2024, were described exclusively on the basis of shell morphology (Schütt 1962, 1980; Reischütz 1988; Reischütz and Reischütz 2004, 2020, 2024). Consequently, the taxonomic validity and systematic placement of these taxa remain unresolved.

A new stygobiont hydrobiid gastropod has been recorded in Korinthia, Peloponnese, Greece, near the Lake Stymphalia (Figs 1, 2).

The Stymphalia basin is a closed karst polje covering approximately 216 km², developed at elevations of 600–800 m and surrounded by the mountain massifs of Kyllini (Cyllene or Ziria), Oligyrtos, and Mavrovouni (Fig. 1). The geological framework is dominated by the carbonate formations of the Tripolis Unit (Upper Triassic–Eocene), tectonically overlying the metamorphosed Zarouchla Unit, while the Pindos Unit occurs as an allochthonous thrust sheet (Doutsos and Koukouvelas 2000; Xypolias and Chatzaras 2010). Karstification is structurally controlled by Alpine fault systems and limestone discontinuities, giving rise to a well-developed underground drainage network characterized by conduit-dominated flow (Morfis and Zojer 1986; Röckel 1987; Nanou and Zagana 2018).

At the lowest part of the basin lies Lake Stymphalia, a shallow and eutrophic lake with pronounced seasonal fluctuations in water level and surface area. The hydrological system is recharged by karst springs, surface runoff, and underground water transfer, whereas drainage occurs through natural swallow holes—most notably Gidomandra and the estavelle-type Forsta sinkhole—as well as through artificial channels associated with the Hadrian aqueduct (Heymann et al. 2013; Walsh et al. 2017; Seguin et al. 2020). Tracer tests have demonstrated that the Stymphalia karst system is hydraulically connected to an extensive regional karst network discharging toward the Argolic Plain and the Argolic Gulf (Dimitroulas and Leontiadis 1971; Leontiadis and Dimitroulas 1972, 1973; Morfis and Zojer 1986). This regional connectivity is further supported by hydrogeological evidence indicating groundwater discharge toward the Argolic Plain (Koskeridou et al. 2022).

Material and methods

A total of seven specimens (six mature and one immature) were obtained from the sampling locality. The specimens were collected by hand from stones, gravel, fallen leaves, caddisflies cases and dead logs. Immediately after collection, they were placed into vials filled with water from the collection site and were transported alive to the lab. Digital images of the examined specimens were taken prior to fixation using a camera (Canon EOS 1000D) attached to a stereomicroscope (Stemi 2000-C, Zeiss, Germany).

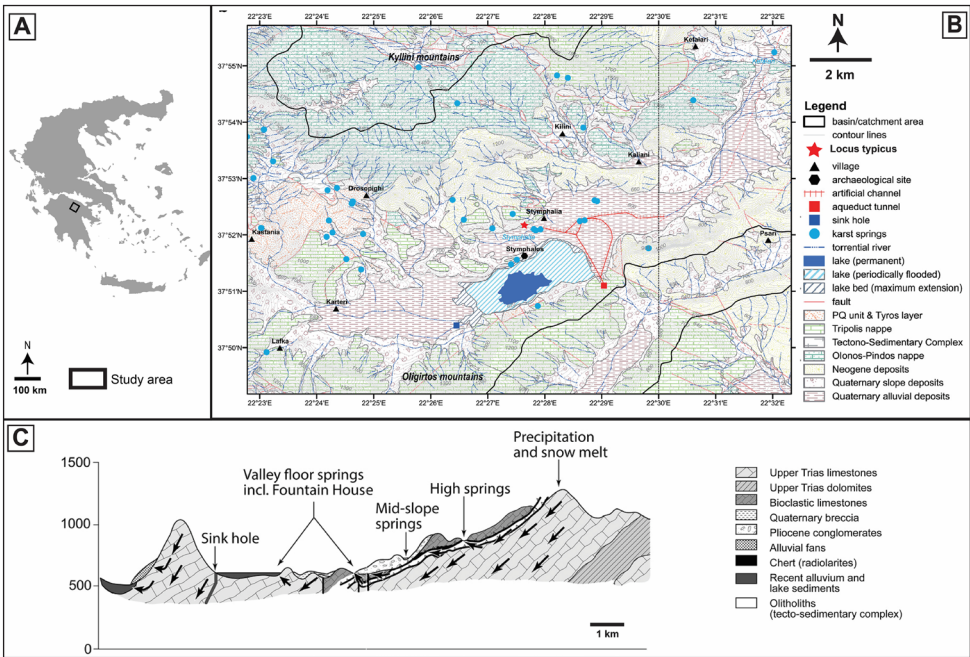


Figure 1. Study area in the Peloponnese, Greece. **A** location map of Greece with the study area (black square) **B** stymphalia basin overview with geology, topography, drainage pattern, and estimated catchment boundary; red star marks the locus typicus (modified after Heymann et al. 2013) **C** hydrogeological cross-section of the Stymphalos polje showing groundwater flow in the Ziria block (after Walsh et al. 2017).



Figure 2. Type locality of *Cyllena hermes* gen. et sp. nov., Korinthia, Peloponnese, Greece. Karstic spring waters emerging from Mt Kyllini and forming a stream flowing toward Lake Stymphalia.

The immature specimen was used for the examination of the shell and protoconch with scanning electron microscopy (SEM; JEOL JSM-90, operating at 25 kV) after being dried and sputter-coated with gold–palladium.

General and diagnostic shell characters were examined, and four shell measurements (shell height and width, aperture height and width) were taken from mature specimens, preserved in 70% (v/v) ethanol solution, using the micrometer of the Stemi 2000-C stereomicroscope (Fig. 3). Four ratios were generated from the raw data (SH/SW, AH/AW, SH/AH and SW/AW).

Four mature specimens preserved in ethanol 70% were dissected under the stereomicroscope using very fine pins and pointed watchmaker's forceps. Prior to dissection, the shell of each specimen was removed by crashing. The soft body features were documented using the digital camera as described above.

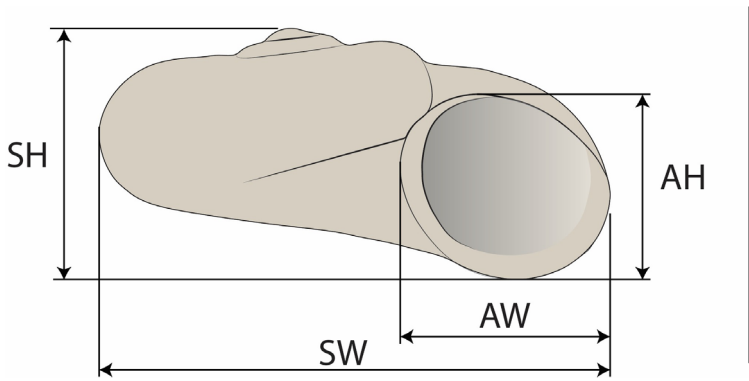


Figure 3. *Cyllena hermes* gen. et sp. nov. Measurements obtained in the shells of six mature specimens. Abbreviations defined in Materials and Methods. Scale bar: 1 mm.

Abbreviations

Shell characters:

AH	aperture height;	Min	minimum;
AW	aperture width;	n	number of specimens;
CV*	$(1+1/4n)*SD/x$ coefficient of variation corrected for sample size (Sokal and Rohlf 1995);	SD	standard deviation;
		SH	shell height;
		SW	shell width;
Max	maximum;	x	mean.

Anatomical characters:

bc	bursa copulatrix;	f penial	fold(s);
bd	bursal duct;	h	head;

op	operculum;	pg	pallial glands;
ovl	oviduct loop;	pp	apical penial papilla;
p	penis;	r	rectum;
pd	penial duct;	rs2	proximal seminal receptacle.

Results

Systematic description

Class Gastropoda Cuvier, 1795

Subclass Caenogastropoda Cox in Moore, 1960

Order Littorinimorpha Golikov & Starobogatov, 1975

Superfamily Truncatelloidea J.E. Gray, 1840

Family Hydrobiidae W. Stimpson, 1865

***Cyllena* Radea & Protopapas, 2026, gen. nov.**

<https://zoobank.org/09FB5396-C50A-4F27-B25D-4A7F23A8E298>

Type species. *Cyllena hermes* sp. nov. by original designation.

Diagnosis. Shell minute, valvatiform to planorboid; umbilicus wide, with earlier whorls visible; soft body unpigmented; eyes absent; bursa copulatrix pyriform; a single seminal receptacle [proximal, rs2 (Radoman 1973)] large and irregular in shape; penis large, dorso-ventrally flattened, distally blunt with papilla and proximally folded, bearing a single, elongate, blunt, medial lobe.

Differential diagnosis. *Cyllena* gen. nov. is distinguished from other stygobiont valvatiform and valvatiform–planorboid genera that possess a bursa copulatrix and a single seminal receptacle (*Arganiella* Fo. Giusti & Pezzoli, 1980; *Hadziella* Kuščer, 1932; *Hauffenia* Pollonera, 1898; *Heraultiella* Bodon, Manganelli & Fo. Giusti, 2002; *Kerkia* Radoman, 1978; *Zaumia* Radoman, 1983). This separation is based primarily on the configuration of the female genital tract and the distinctive morphology of the penis.

Cyllena gen. nov. further differs from genera with unknown female genitalia (*Alagoniella* Quiñonero-Salgado, López-Soriano, Raven & Sánchez, 2025; *Alfahariella* Quiñonero-Salgado, López-Soriano, Raven, Glöer & Prieto, 2024; *Berkanella* Taybi, Glöer & Mabrouki, 2024; *Maroccoarganiella* Ghamizi & Falniowski, 2024; *Onubiella* Martín Álvarez, Quiñonero-Salgado, López-Soriano, Raven & Glöer, 2024; *Robustiella* Quiñonero-Salgado, López-Soriano & García-Meseguer, 2025; *Salaeniella* Boeters, Quiñonero-Salgado & Ruiz-Cobo, 2019; *Siuraniella* Quiñonero-Salgado, López-Soriano, Raven, Pascual, García, Solé & Sánchez, 2025; and *Vilertia* López-Soriano, Quiñonero-Salgado, Suárez, Rolán & Glöer, 2022) in the shape and lobation of the penis.

Finally, the new genus differs from *Dalmatella* Velkovrh, 1970 and *Navalis* Quiñonero-Salgado & Rolán, 2017 in having a nearly smooth teleoconch lacking ornamentation.

In addition, *Cyllena* gen. nov. is distinguished from other stygobiont valvatiform and valvatiform–planorboid genera by several supplementary characters, including the absence of an operculum with a peg (*Bracenic*a Radoman, 1973; *Hauffenia*), a differently shaped rectum (*Arganiella*; *Corbellaria* Callot-Girardi & Boeters, 2012; *Fissuria* Boeters, 1981; *Hadziella*; *Hauffenia*; *Heraultiella*; *Kerkia*; *Pezzolia* Bodon & Giusti, 1986; *Salaeniella*; *Sardohoratia* Manganelli, Bodon, Cianfanelli, Talenti & Fo. Giusti, 1998), and the sculpture of the protoconch (*Fissuria* and *Pezzolia*).

Type-locality. Greece, Peloponnese: (37°52.06'N, 22°27.65'E), karstic spring situated at ca 610 m elevation a.s.l. on the foothills of Mt Kyllini, 11 January 2026, D. Protopapas leg.

Etymology. The generic name derives from the Greek mythology: *Cyllena* (Κυλλήνη in Greek) was a nymph of Mt Kyllini, Korinthia, Peloponnese, and the nurturer of the god Hermes. Gender feminine.

***Cyllena hermes* Radea & Protopapas, 2026, sp. nov.**

<https://zoobank.org/F32A3E2E-1A96-412B-A731-7D9A8DCF4DD4>

Figs 4–8

Type material. Holotype. Ethanol-fixed specimen, deposited in the National Museum of Natural History Goulandris (GNHM), accession number 51-01-045021. **Paratypes** (from the same lot). One ethanol-fixed specimen deposited in the National Museum of Natural History Goulandris (GNHM), accession number 51-01-045022. Four mature ethanol-fixed specimens dissected for anatomical study and one immature specimen coated for SEM in the personal collection of C. Radea deposited in the Section of Ecology and Systematics, Department of Biology, National and Kapodistrian University of Athens.

Diagnosis. As for genus.

Description. Shell (Figs 4A–E, G–R, 5). Valvatiform to planorboid, minute (maximum height 0.76 mm, maximum width 1.46 mm) (Table 1) with up to 2.25 whorls, thin-walled, colourless, glossy, transparent when fresh; spire depressed, blunt; periostracum pale corneous; aperture roundish to slightly ovate, slightly prosocline adhering to the last whorl; peristome continuous, thickened and reflected at columellar margin, the outer margin simple; umbilicus open and extremely wide, revealing the inner (earlier) whorls; teleoconch smooth, bearing fine growth lines with the last portion of the dilated body whorl descending near aperture at an angle of approximately 30°; protoconch of approximately one whorl, slightly elevated, with a broad nucleus; microsculpture of the embryonic shell consisting of shallow, circular to oval pits with concave sides; growth lines visible after the first embryonic whorl, while the pits gradually fade; protoconch–teleoconch transition indistinct.

Operculum (Fig. 4F). Circular, paucispiral, thin, corneous, orange-colored; inner face weakly convex, without any peg; nucleus central.

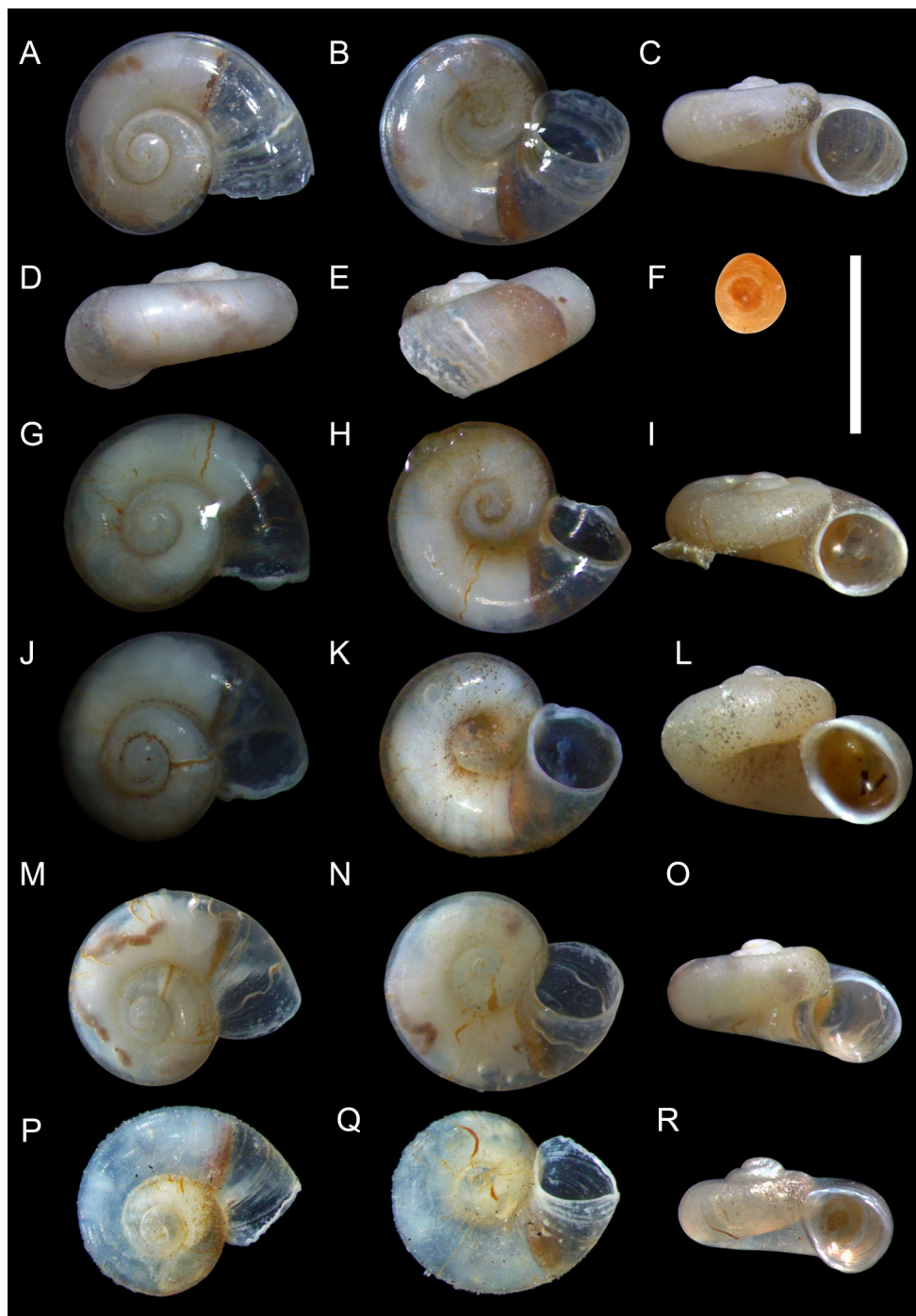


Figure 4. *Cyllena hermes* gen. et sp. nov. Shell views of collected specimens. **A, G, J, M, P** dorsal views **B, H, K, N, Q** ventral views **C–E, I, L, O, R** lateral views **F** operculum **A–E** holotype. Scale bar: 1 mm.

Head (Figs 6E, 8A–J). White-creamy coloured, without dark pigments; eye spots absent; snout about as wide as long, non-tapered, with strong distal lobation; tentacles (in live specimens) parallel-sided and approximately ten times longer than wide.

Ctenidium–Osphradium. Absent.

Radula. Unknown

Table 1. *Cyllena hermes* gen. et sp. nov. Shell morphometry. Measurements in mm; abbreviations defined in Materials and methods.

N=6	SH	SW	AH	AW	SH/SW	AH/AW	SH/AH	SW/AW
Min	0.61	1.31	0.47	0.53	0.43	0.81	1.11	2.34
Max	0.76	1.46	0.55	0.6	0.54	1.02	1.55	2.66
x	0.68	1.40	0.52	0.56	0.48	0.92	1.32	2.51
SD	0.06	0.05	0.03	0.03	0.05	0.08	0.15	0.13
CV*	0.09	0.04	0.06	0.05	0.11	0.09	0.12	0.05

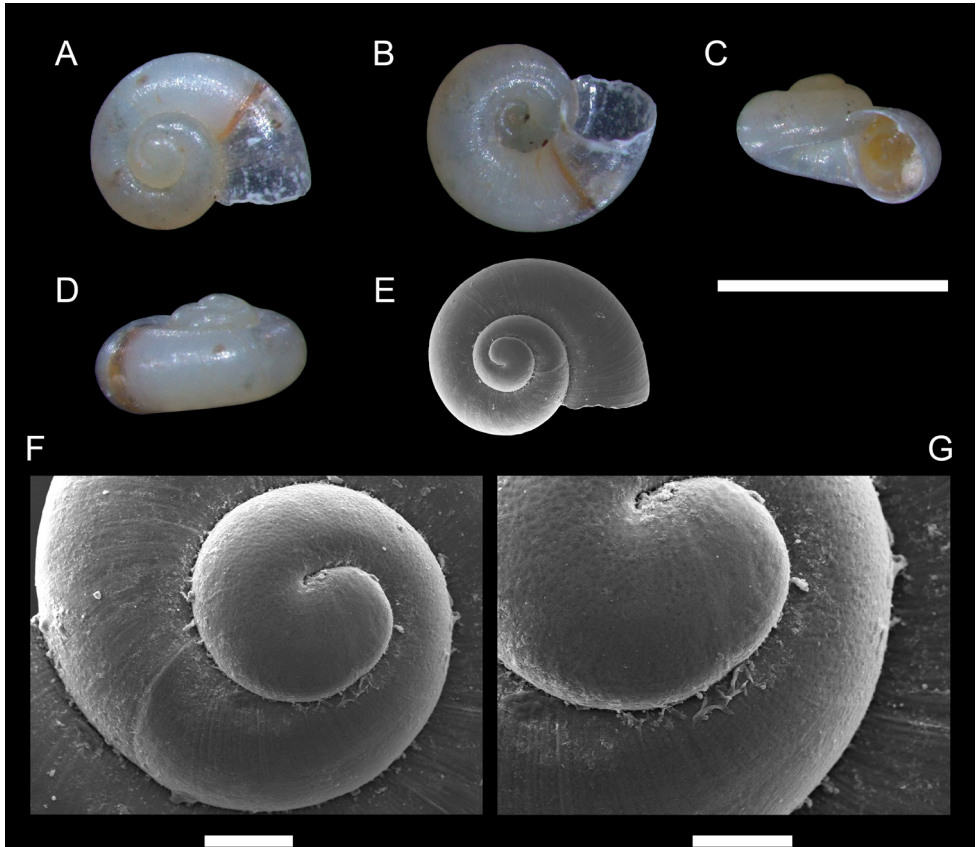


Figure 5. *Cyllena hermes* gen. et sp. nov. Views from a single immature specimen. **A** dorsal view **B** ventral view **C, D** lateral view **E–G** scanning electron micrographs of shell and protoconch respectively. Scale bars: 1 mm (**A–E**); 100 μm (**F**); 50 μm (**G**).

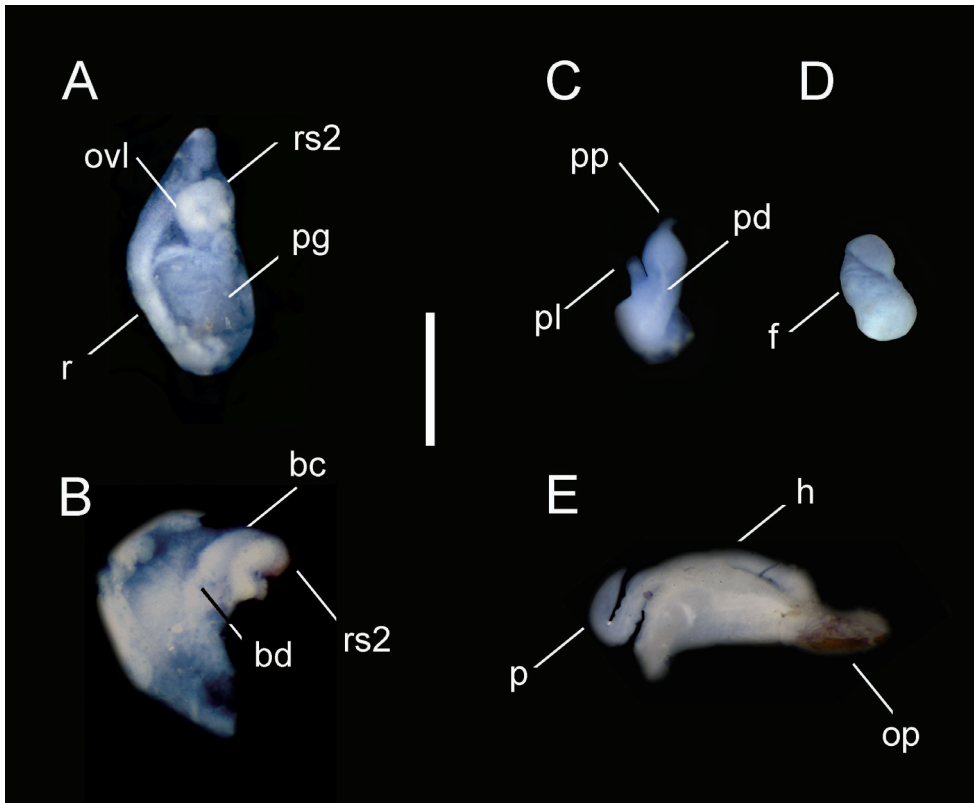


Figure 6. *Cyllena hermes* gen. et sp. nov. Reproductive system. **A, B** anterior female reproductive system **C, D** dorsal and ventral view of penis, respectively **E** Penis in situ, lateral view, right side. Abbreviations defined in Materials and Methods. Scale bars: 0.5 mm (**A, B**); 0.25 mm (**C–E**).

Rectum. Rectum forming a U-shaped bend, wider in females than in males. Faecal pellets ellipsoidal, light orange-colored.

Anterior female reproductive system (Figs 6A, B, 7A). Albumen and capsule glands very small; bursa copulatrix pyriform with bursal duct thick and short (bursal duct length less than 50% of bursa length); coiled oviduct unpigmented, thick, with irregular external surface, forming a single, open, circular loop, fully protruding from posterior end of albumen gland; a single seminal receptacle (proximal, rs2) large and irregular in shape.

Penis (Figs 6C–E, 7B). Large relative to head size, elongate, dorso-ventrally flattened, with a proximal portion bearing distinct folds and a distal portion with blunt apex; a single elongate and blunt lobe at middle-length on the left side; penial duct weakly undulating at base and straight distally, near-centrally positioned, opening in an apical papilla.

Etymology. The specific name, used in apposition, is derived from Greek mythology. Hermes (Ἑρμῆς in Greek) was one of the twelve Olympian gods, the messenger of the other Olympian deities, and was born in a cave on Mt Kyllini.

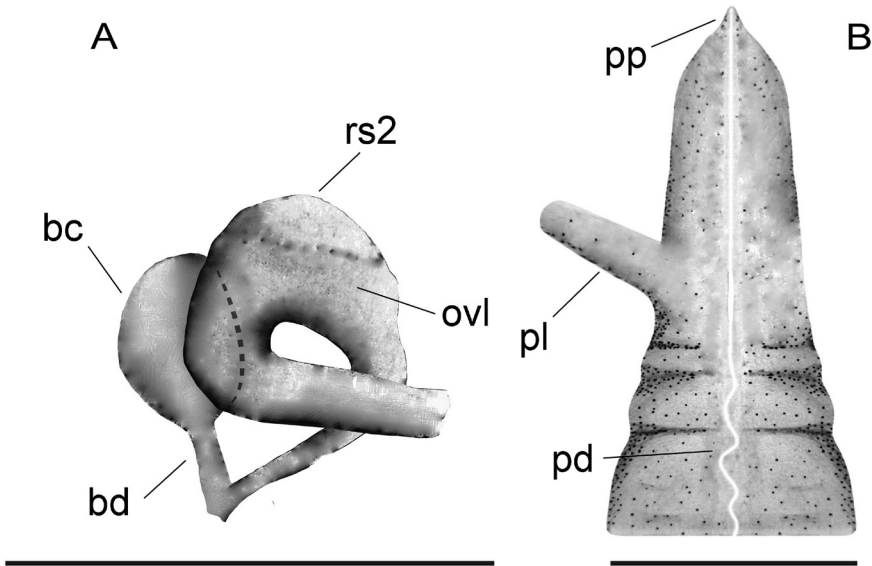


Figure 7. *Cyllena hermes* gen. et sp. nov. Part of female reproductive system **A** part of female reproductive system **B** dorsal view of penis. Abbreviations defined in Materials and Methods. Scale bars: 0.5 mm (**A**); 0.2 mm (**B**).

Distribution and habitat. So far, the distribution of *Cyllena hermes* gen. et sp. nov. is restricted to the type locality. The area is characterized by carbonate bedrock, and owing to karstification of the limestone, groundwater emerges through karstic springs, forming a small stream flowing towards Lake Stymphalia (Figs 1, 2). In several sections, the stream bed is partially covered by *Helosciadium nodiflorum* (L.) W.D.J. Koch. The surrounding landscape is dominated by herbaceous vegetation, while the riparian zone along the stream is sparsely lined by *Platanus* sp. The streambed substrate consists of sand and predominantly angular to subangular clasts, ranging from gravel to boulder size, mainly of limestone origin and derived from the adjacent mountainous massif.

Associated freshwater gastropod species. *Radomaniola* sp., *Bythinella* sp., *Isimerope semele* Radea & Parmakelis, 2013 and *Daphniola longipenia* Grego & Fahnio-wski, 2021 were also recorded in the type locality.

Remarks. Two female and two male specimens were dissected. One female bears a pseudopenis on the right side of the head.

In one male, the distal penial portion is somewhat dilated (Fig. 6C).

Individuals of the species were observed performing circular movements while feeding inside the transport container during transfer from the sampling site to the laboratory (Fig. 8A–J).

Specimens of *Cyllena hermes* gen. et sp. nov., *Radomaniola* sp., *Bythinella* sp., *I. semele* and *D. longipenia* were observed incorporated into larval cases of caddisflies (Insecta, Trichoptera) (Fig. 8K). The new locality record of the last two endemic hydrobiids extends their currently documented distribution in the Peloponnese.

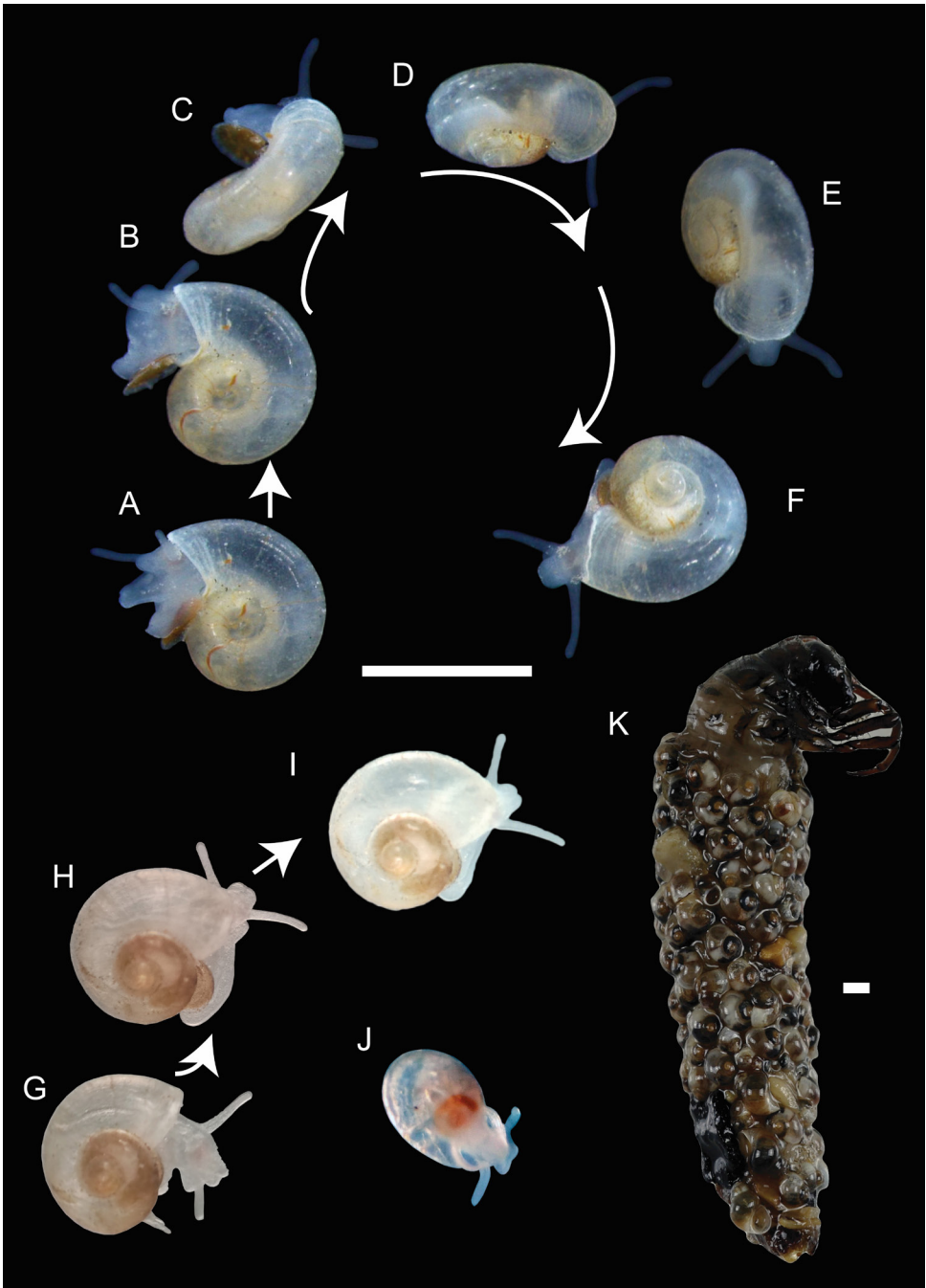


Figure 8. Live specimens of *Cyllena hermes* gen. et sp. nov. **A–F** live mature specimen, shown from the moment of emergence from the shell to active locomotion while foraging **G–I** another mature specimen; White arrows indicate the direction of movement **J** immature specimen floating at the water surface while feeding **K** caddisfly case (Insecta, Trichoptera) constructed from gastropod shells, including shells of *Cyllena hermes* gen. et sp. nov. Scale bars: 1 mm.

Discussion

The highly complex relief and dynamic geological history of the Peloponnese—typical of this predominantly mountainous region—have created conditions conducive to invertebrate diversification and the evolution of endemic taxa (Sfenthourakis and Legakis 2001; Radea et al. 2013, 2016; Allegrucci et al. 2021; Bolanakis et al. 2026).

To date, nine locally endemic hydrobiid species bearing valvatiform or valvati-form–planorboid shells have been described from the area (Table 2, the legend provides additional information for *D. exigua*). These species are assigned to six genera, four of which are endemic to the Peloponnese and five to Greece (Reischütz and Reischütz 2004; Falniowski and Szarowska 2011; Radea et al. 2013, 2016; Hofman et al. 2021; Glöer and Manolas 2024). Among them, only *Daphniola wohlschlageri* and, possibly, *Islamia edlingeri*, have been reported from subterranean freshwater habitats (Reischütz and Reischütz 2004, 2024).

Following the diagnostic framework proposed by Bodon et al. (2001), which emphasizes the combined morphology of male and female genitalia in the delimitation of valvatiform and valvatiform–planorboid hydrobiid genera, *Cyllena hermes* gen. et sp. nov. differs from all other known stygobiont valvatiform or valvatiform–planorboid hydrobiids by a unique combination of shell and anatomical characters (Table 3), thereby precluding its assignment to any previously described genus within Hydrobiidae. Accordingly, the erection of a new monotypic genus is justified.

Despite extensive sampling throughout Korinthia, *Cyllena hermes* gen. et sp. nov. is currently known from a single locality. This restricted distribution is consistent with patterns observed by Hofman et al. (2022), who documented high levels of endemism among species of the stygobiont valvatiform–planorboid hydrobiid genus

Table 2. Valvatiform and valvatiform–planorboid hydrobiid species recorded from the Peloponnese. Habitat, endemism and conservation status according to the IUCN Red List of Threatened Species. Abbreviations: E_p = endemic to Peloponnese; E_G = endemic to Greece; NE = Not Evaluated; EN = Endangered; CR = Critically Endangered; VU = Vulnerable. Conservation status based on present study (*) and published assessments. (**) *Daphniola exigua* is listed here, as it has been reported from Peloponnese under the synonym *Valvata (Cincinna) hellenica* Westerlund, 1898, whose type locality is Vytina, Arkadia, MolluscaBase 2026).

Species	Type locality	Subterranean freshwaters	Genus-level endemism	IUCN Red List category
<i>Cyllena hermes</i> gen. et sp. nov.	Korinthia	+	E _p	VU*
<i>Daphniola exigua</i> (A. Schmidt, 1856)**	Arkadia	-	E _G	EN
<i>Daphniola hadei</i> (E. Gittenberger, 1982)	Laconia	-	E _G	EN
<i>Daphniola longipenia</i> Grego & Falniowski, 2021	Arkadia	-	E _G	EN
<i>Daphniola wohlschlageri</i> A. Reischütz & P. L. Reischütz, 2024	Korinthia	+	E _G	NE
<i>Isimerope semele</i> Radea & Parmakelis, 2013	Argolida	-	E _p	VU
<i>Islamia edlingeri</i> (Reischütz & Reischütz, 2004)	Arkadia	+	-	CR
<i>Islamia pyrgosensis</i> Glöer & Manolas, 2024	Ileia	-	-	NE
<i>Lampetitia panagiotae</i> Glöer & Manolas, 2024	Ileia	-	E _p	NE
<i>Myrtoessa hyas</i> Radea, 2016	Arkadia	-	E _p	VU
<i>Phaethusa johannae</i> Glöer & Manolas, 2024	Ileia	-	E _p	NE

Table 3. *Cyllena* gen. nov. compared with other stygobiont valvatiform and valvatiform–planorboid genera distributed in the Balkan Peninsula and the Mediterranean Basin. Twenty-three morphological and anatomical characters and character-state scores for 24 genera are given.

Genera	Distribution	Sh	Pr	To	Bw	Ap	Per	Op	Opn	U	Ct	R	Ovl	Bc	Pbc	Lbd	Rs	Ps	Pde	Pps	Pdp	Pdo	Pl	Pip	
<i>Alagoniella</i>	Spain	2	2	0	0	1	0	-	-	1	-	-	-	-	-	-	-	3	0	-	-	-	0	0	
<i>Alfaharziella</i>	Spain	2	2	0	0	0	-	-	-	1	-	-	-	-	-	-	-	0	1	-	-	-	1	2	
<i>Argentiella</i>	Italy	1	2	0	1	1	0	0	0	1	0	(S)	1	1	1	1	2	2	A1, B1	1	0	0	0	0	
<i>Berkaniella</i>	Morocco	1	-	0	0,1	1	0	-	0	1	-	-	-	-	-	-	-	0	1	-	-	-	-	1	2
<i>Bracnecia</i>	Montenegro	1	-	0	-	1	0	0	2	1	-	-	1	2,3	1	1	3	0	1	-	-	-	0	1	2
<i>Corbellaria</i>	Spain	1	-	0	0,1	1	1	1	0	1	0	(SS)	1	1	1	1	3	0	1	A0, B0	1	0	1	2	
Cyllena gen. nov.	Greece	1	0	0	1	1	0	0	1	0	0	(U)	1	3	0	0	2	0	3	A0, B0	0	0	1	2	
<i>Dalmatiella</i>	Croatia	2	-	1	1	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Fissiria</i>	Greece, Italy, France	2	2	0	1	1	0	0	0	1	0	(S)	1	1	1	2	3	0	2	A1, B1	1	0	3	1+3	
<i>Hadziella</i>	Slovenia, Spain, Croatia, Italy	0	1	1	1	1	1	1	1	1	0	(Z)	0	1	1	1	1	0	1	A1, B1	1	0	0	0	
<i>Hauffenia</i>	Italy, Slovenia, Croatia	0, 1, 2	2	0	1	1	0	2	1	0,1	(S)	1	4	0	0	2	2	2	0	A1, B1	0	0	0,1	0,4	
<i>Hemuliella</i>	France	0	2	0	1	1	0	0	0	1	0	(U) or (V)	1	2	1	2	1	1	1	A1, B1	1	0	0	0	
<i>Hornatia*</i>	Croatia, North Macedonia	2	2	0	1	1	0	0	0	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Kerkia</i>	Slovenia, Croatia, Bosnia & Herzegovina, Montenegro	1, 2	0, 2	0	1	1	0	0	0,3	1	0	(S)	1	2	1	2	1	0,2,4	2	A1, B1	1	0	0,1	3	
<i>Maroccoraganiella</i>	Morocco	1	-	0	0	-	-	-	-	1	-	-	-	-	-	-	-	0	2	-	-	-	0	0	
<i>Navalis</i>	Spain	2	2	1	-	-	-	-	-	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Onubiella</i>	Spain	1	0	0	0	-	1	-	-	1	-	-	-	-	-	-	-	0	0	-	-	-	0	0	
<i>Pezzolia</i>	Italy	2	2	0	1	1	0	0	0	1	1	(S)	1	4,5	1	0	3	3	2	A1, B1	1	0	0	0	
<i>Robustiella</i>	Spain	3	2	0	0	-	0	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Saleniella</i>	Spain	2	-	0	0	-	1	0	-	1	-	(S)	-	-	-	-	-	0	1	-	-	-	1	3	
<i>Sardobonatia</i>	Italy	2	0	0	0,1	1	0	0	0	1	1	(S)	1	1	1	1	3	0	1	A1, B1	0	0	0	0	
<i>Siunniella</i>	Spain	2	2	0	0	1	0	-	-	1	-	-	-	-	-	-	-	0	2	-	-	-	0	0	
<i>Vilertia</i>	Spain	2	0	0	0	-	1	-	-	1	-	-	-	-	-	-	-	2	0	-	-	-	1	4	
<i>Zaunmia</i>	North Macedonia	2/4	-	0	1	1	0	0	0	1	-	-	1	1	1	2	2	0	2	-	-	-	0	0	

Character states and symbols: **Sh**, shell shape: planorboid (0), valvatiform-planorboid (1), valvatiform (2), valvatiform-neritiform (3), trochiform (4); **Pr**, protoconch sculpture: pits (0), spirals (1), other (2); **To**, ornaments of telococonch: absence of keel(s) (0), presence of keel(s) (1); **Bw**, inclination of the last part of body whorl relative to coil axis: non-descending (0), descending (1); **Ap**, aperture inclination: ortholine (0), prosoline (1); **Per**, peristome: simple (0), reflected (1); **Op**, operculum coiling: paucispiral (0), multispiral (1); **Opn**, nucleus area of operculum: simple (0), thickened (1), knob/peg-bearing (2), low crest-like thickening (3); **U**, umbilicus: narrow (0), wide (1); **Ct**, ctenidium: absent (0), present (1); **R**, rectum: Z-like (2), U-like (3), S-like (4); **Ovl**, oviduct loop: absence of loop (0), single loop (1); **Bc**, shape of bursa copularis: triangular (0), ovoid (1), globular (2), pyriform (3), elongate or cylindrical (4); **Pbc**, position of bursa copularis relative to coiled oviduct: completely covered by the coiled oviduct (0), partially or not covered by the coiled oviduct (1); **Lbd**, length of bursal duct: less than 50% of bursal length (0), 50%-100% of bursal length (1), longer than bursa (2); **Rs**, seminal receptacles: absent (0), distal seminal receptacle s1 (1), proximal seminal receptacle s2 (2), distal and proximal seminal receptacle (3); **Ps**, gross penis shape: gradually tapering (0), broadly triangular (1), rectangular (2), strap-like (3), other (4); **Pde**, shape of distal end of penis: blunt (0), tapered (1), subapically expanded and tapered near apex (2), blunt with papilla (3); **Pps**, shape of distal (A) and proximal (B) portion of penial duct: straight to weakly undulating (1); **Pdp**, penial duct position: near center (0), near outer edge (1); **Pdo**, penial duct opening: apical (0), subapical (1); **Pl**, penial lobe (s): absent (0), one lobe (1), two lobes (2), more than two lobes (3); **Pip**, penial lobe(s) position: absent (0), basal lobe (1), medial lobe (2), lobe at 2/3 of penis length (3), apical lobe (4); *Stygobiont species; - no data. Based on Hershler and Ponder (1998), Manganielli et al. (1998), Bodon et al. (2001), Callot-Girardi and Boeters (2012), Faltynowski and Sarbu (2015), Radea et al. (2016), Quintero-Salgado and Rolán (2017), Faltynowski et al. (2021), Hofman et al. (2021), López-Soriano et al. (2022), Chamiz et al. (2024), Martín Álvarez et al. (2024), Quintero-Salgado et al. (2024, 2025).

Kerkia, many of which exhibit extremely narrow geographic ranges. Although interstitial habitats may facilitate dispersal of stygobiont fauna (Falniowski et al. 2021), dispersal appears particularly limited in taxa with low-spired, wide-umbilicate shells. Consequently, such species appears to display pronounced endemism and much more restricted distributions than turbospiral taxa (Falniowski 2022).

Subterranean freshwater habitats and their specialized fauna are increasingly threatened by multiple interacting anthropogenic stressors, including groundwater overextraction, contamination, and climate change. These pressures alter hydrological regimes, degrade habitat quality, and drive shifts in community structure, often resulting in biodiversity loss and reduced ecosystem functioning. Additionally, disruptions in groundwater–surface water connectivity may further disadvantage specialized stygobiotic taxa, favoring opportunistic surface species (Koch et al. 2024 and references therein). The Stymphalia basin hosts several karstic springs, including that of the type locality. However, it is currently facing serious threats due to repeated events of prolonged drought and water abstraction for supply to neighboring areas, resulting in a dramatic shrinkage of Lake Stymphalia in recent years (Nanou and Zagana 2018).

Owing to its apparently restricted distribution, *Cyllena hermes* gen. et sp. nov. was assessed for extinction risk using the IUCN Red List Categories and Criteria. The species is currently known from a single stream emerging from a karstic system, with both its extent of occurrence (EOO) and area of occupancy (AOO) estimated at 4 km².

Although additional populations may exist but remain undetected, the available data indicate a very limited known range. Following a precautionary approach, and in accordance with IUCN guidelines, species with such restricted distributions and occurring at a single location may be susceptible to potential threats. These include reduction of groundwater availability or alterations of flow regimes, whether due to water abstraction for drinking water or irrigation, or to climate-driven drought, which could potentially affect the entire population. On this basis, *Cyllena hermes* gen. et sp. nov. is here considered to qualify as Vulnerable (VU) under Criterion D2.

Of approximately 10,000 caves recorded in Greece (Beron 2016), faunistic data are available for only 550; yet Greece remains a global hotspot of subterranean biodiversity. For terrestrial gastropods alone, 30 genera and 68 species have been documented, including 33 Greek endemics and 14 obligate troglobionts (Karakasi et al. 2024). In contrast, knowledge of aquatic subterranean (stygobiont) gastropods remains highly fragmentary. To date, the only fully described stygobiont assemblage originates from Melissotrypa Cave, one of the few subterranean ecosystems worldwide sustained by chemoautotrophic sulfur-oxidizing bacteria. It hosts an aquatic fauna of 16 species, including one hydrobiid and one moitessieriid gastropod, half of which are endemic and new to science (Popa et al. 2019).

The Stymphalia subterranean karst aquifer constitutes a highly sensitive, heterogeneous, and dynamic hydrogeological system (Nanou and Zagana 2018), comparable to other Mediterranean karst aquifers that support diverse and highly specialized stygobiont fauna, which occur sporadically in springs (Manenti et al. 2024). *Cyllena hermes*

gen. et sp. nov. is currently known only from this system, consistent with its status as a stygobiont species with a localized distribution within the Stymphalia karst aquifer.

Overall, these findings highlight the still incomplete knowledge of stygobiont gastropods in Greece and underline the importance of further targeted exploration of subterranean habitats.

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