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First record of an alien animal species in a Greek cave: the invasive topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1846) (Actinopterygii, Gobionidae) in the Angitis (Maaras) river cave, northern Greece

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Abstract

The topmouth gudgeon, *Pseudorasbora parva*, is one of Europe's most invasive freshwater fish and an invasive alien species of Union concern under Regulation (EU) No 1143/2014, and has been reported from deep inside the Angitis (Maaras) river cave, Drama, northern Greece. During fieldwork on July 24–26, 2026, the species was observed along the subterranean river up to 6 km from the entrance, and five specimens (one adult 7.5 cm TL and four smaller individuals of 3–5 cm TL) were captured from residual pools 3–6 km inside. This is the first record of the species in a Greek cave, and, to our knowledge, the first record of any alien animal species in a Greek cave. The fish co-occurs with the native barbel *Barbus strumicae*, amphipods of the genera *Niphargus* and *Turcogammarus*, and a deep-cave population of the stone crayfish *Austropotamobius torrentium*, a priority species under the EU Habitats Directive. We discuss the colonisation pathway, parasite risks, and the need to extend invasive alien species surveillance to groundwater ecosystems.

Keywords

Angitis underground river, Biological invasion, groundwater-dependent ecosystems, *Pseudorasbora parva*, Strymon basin, subterranean fauna

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Introduction

Subterranean formations are energy-poor ecosystems that host specialised faunas with small, restricted populations, which makes them highly susceptible to invasion; however, caves remain almost absent from invasive species surveillance. Here, we report the presence of the topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel, 1846) from deep inside the Angitis (Maaras) river cave in northern Greece, the first record of the species in a Greek cave, and, as far as we are aware, the first record of any alien animal species from the caves of Greece.

Pseudorasbora parva is a small gobionid native to East Asia. It was released accidentally with carp fry into fish ponds of the Danube Delta, Romania, in 1961, and has since spread across Europe (Bianco 1988; Rosecchi et al. 1993; Gavriloaie et al. 2014), favoured by early maturity, a protracted breeding season with parental care, a broad diet, and a high tolerance of varied lotic and lentic habitats, including degraded waters (Rosecchi et al. 1993; Ekmekçi and Kırankaya 2006). In Greece, it was first recorded from the Prespa lakes and the Aliakmon River (Bianco 1988) and then from lakes Kerkini and Koroneia and the Axios and Loudias rivers, spreading largely as a contaminant of carp (*Cyprinus carpio*) fry used for stocking (Economidis 1991; Rosecchi et al. 1993; Economidis et al. 2000; Perdikaris et al. 2010). It is now widespread in the transboundary basins of northern Greece, including the Strymon, and has reached the Peloponnese (Koutsikos et al. 2019; Kalogianni et al. 2024).

Methods

Study area

The Angitis spring cave (Maaras) opens at approximately 123 m a.s.l. at the south-western foot of Mount Falakro, some 25 km north-west of Drama (Fig. 1A). It is the resurgence of the Angitis River, the largest tributary of the Strymon, and the longest river cave known in Greece, with more than 10 km of active subterranean river waters interrupted by siphons. The cave floor consists of sandy clastic sediments at least 10 m thick; along the accessible section, stones and gravel are virtually absent, except for breakdown cones (Novel et al. 2007; Pennos et al. 2017; Skoglund et al. 2023). The system is fed mainly by the swallow sinkholes of the Kato Nevrokopi polje, 10 km away and 360 m higher (Novel et al. 2007). Heat exchange with the sandy streambed dampens and warms the water downstream: the annual temperature amplitude falls from 16.2 °C at the uppermost monitoring station to 7.4 °C near the entrance, and dry-season temperatures stabilise between about 15 and 16.6 °C in the middle and lower reaches (Skoglund et al. 2023). Spring discharge averaged 4.66 $m^3\ s^{-1}$ over 1949–2008 but ranges from 0.14 $m^3\ s^{-1}$ in droughts to 35 $m^3\ s^{-1}$ in floods. The water is of Ca–HCO_3 type, weakly mineralised

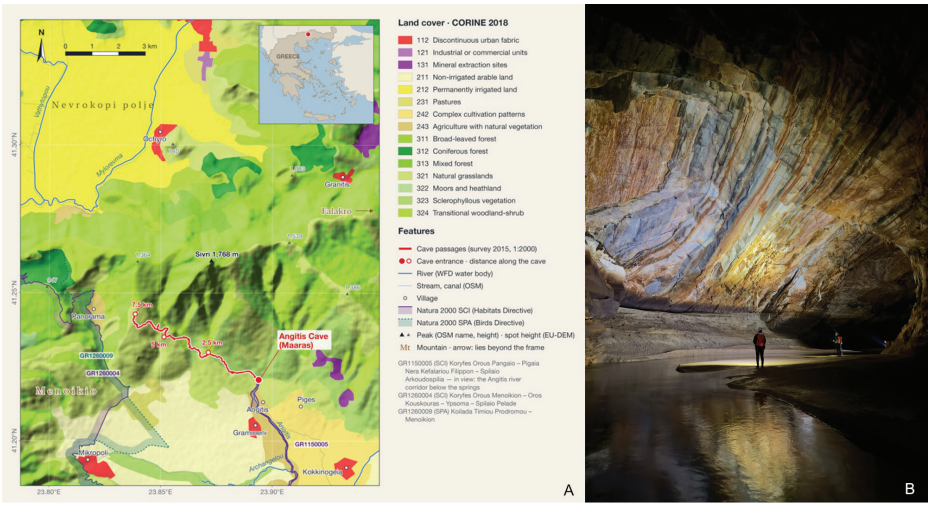


Figure 1. The Angitis (Maaras) river cave, Drama, northern Greece. **A.** Location of the cave between the Kato Nevrokopi polje and the Angitis spring, showing relief, CORINE 2018 land cover, Natura 2000 sites, rivers and the surveyed cave passages (red line, with distances along the cave from the entrance); inset: position in Greece. Data sources are given in Methods; **B.** The subterranean river with its sandy banks and banded marble walls, 4 km from the entrance. Map and photograph by S. Paragkamian.

and slightly alkaline (pH 7.0–7.7), but rich in nitrate (mean 16.4 mg L^{-1} $N–NO_3$) from agriculture in the Kato Nevrokopi plain (Petalas and Moutsopoulos 2019).

The cave is protected under Greek archaeological legislation (Law 3028/2002, codified by Law 4858/2021), while the spring and the Angitis River downstream lie within the Special Area of Conservation "Koryfes Orous Pangaio – Pigaia Nera Kefalariou Filippon – Spilaio Arkoudospilia" (Natura 2000 code: GR1150005). The cave fauna reported so far includes 24 species (Paragamian 2026). The aquatic fauna includes a blue-tinged population of the stone crayfish *Austropotamobius torrentium* (von Paula Schrank, 1803), a priority species of Annexes II and V of the Habitats Directive, recorded up to 7,100 m from the entrance (Koutrakis et al. 2005). Ongoing surveys have yielded at least 12 additional taxa, three of which appear restricted to this cave (K. Paragamian, unpublished data).

The map in Fig. 1A was prepared in the GGRS87 / Greek Grid projection (EPSG:2100). Relief was derived from the EU-DEM v1.0 digital elevation model (25 m; Copernicus) and shaded with the R package rayshader (Morgan-Wall 2026) on a 10 m grid. Land cover is from CORINE Land Cover 2018 (v2020_20u1; European Environment Agency), Natura 2000 boundaries from the Greek end-2021 submission (v32), rivers from the Water Framework Directive river water bodies of the Ministry of Environment and Energy (1:50,000), and villages and streams from OpenStreetMap (© OpenStreetMap contributors, ODbL). The cave passages were digitised from the 1:2,000 survey plan of C. Pennos, Y. Sotiriadis, E. Kiourexidou, and N. Kortimanitsis (with data from Theodosiadis; Therion plan, 2015), with the entrance georeferenced at 41.2207°N, 23.8939°E.

Field survey

The cave was surveyed on 24–26 July 2026 under low-flow conditions, which allowed passage of the siphons up to 6.5 km from the entrance. Fish were searched for visually using head torches. Specimens were captured with aquarium dip nets (18 × 24 cm) in residual pools in the streambed, measured to total length (T.L.), photographed in a small aquarium, and released alive *in situ*; no voucher material was retained.

Results

Pseudorasbora parva was observed repeatedly at the remote parts of cave, singly or in small groups, mostly in residual pools. Five specimens were captured in pools 3–6 km from the entrance: one adult or subadult of 7.5 cm total length (Fig. 2) and four younger specimens of 3–5 cm.

Accompanying aquatic fauna

Along the same 6.5 km section, we also recorded the native barbel *Barbus strumicae* Karaman, 1955, stone crayfish *A. torrentium*, Mediterranean medicinal leech *Hirudo verbana*, and amphipods of the genera *Niphargus* and *Turcogammarus*, whose species-level identification is in progress. The amphipods and leach are new records for the cave.



Figure 2. Live specimen of *Pseudorasbora parva* (adult, 7.5 cm TL) captured in a residual pool 3–6 km from the entrance of the Angitis (Maaras) river cave, July 2026, and photographed in a small aquarium. Photograph by K. Paragamian.

Material examined

GREECE • 1 adult/subadult, 7.5 cm T.L.; Eastern Macedonia and Thrace, Regional Unit of Drama, Municipality of Prosotsani, Angitis (Maaras) river cave, 3–6 km from the natural entrance; [41.2207°N, 23.8939°E]; ca. 130 m a.s.l.; 24–26 Jul. 2026; S. Paragkamian, I. Mylona, P. Karakoulakis, and A. Salmoda leg.; aquarium dip net, residual pools; photographed and released, no voucher retained • 4 individuals, 3–5 cm T.L.; same data as for preceding.

Discussion

The record extends the range of one of Europe's most invasive freshwater fishes into a wholly subterranean setting and shows that Greek caves are not buffered from biological invasions. The most plausible pathway is passive transport from the surface waters of the Kato Nevrokopi polje through the swallow sinkholes: transit times of 15–30 h (Novel et al. 2007; Skoglund et al. 2023) allow fish to arrive alive, and the species is widespread in the Strymon basin (Koutsikos et al. 2019; Kalogianni et al. 2024). Since the species has also recently been found immediately downstream of the cave outlet, within the receiving sub-catchment (Sapounidis et al. 2025), it may also be true that the fish may be able to swim upstream within the cave system.

The five specimens captured 3–6 km inside the cave demonstrated that more than one size class of *P. parva* occurred deep within the subterranean system, although the presence of multiple age classes could not be confirmed from body length alone (Kirczuk et al. 2021). *P. parva* lays adhesive eggs on hard surfaces, which are guarded by the male, and such substrates are scarce on the sandy cave floor. Repeated passive input of individuals of different sizes, potentially representing successive cohorts, is therefore a plausible explanation for their occurrence in the cave. However, the available observations do not establish whether the cave population is sustained by recurrent introductions or by reproduction within the subterranean system. Distinguishing a sink population from a self-sustaining, potentially more difficult-to-manage population will require seasonal sampling, age determination, and targeted searches for eggs and larvae.

Cave temperatures of approximately 12–17 °C lie within the tolerance of the species, and nitrate from the polje suggests a nutrient subsidy that may support populations. In this energy-limited system, an omnivorous fish may prey on amphipods and early stages of the stone crayfish and compete with *B. strumicae* for scarce organic matter. Recurrent droughts, which can reduce spring discharge to 0.14 $m^3 s^{-1}$ (Petalas and Moutsopoulos 2019) and, as during our survey, leave the river as isolated pools, are likely to intensify these interactions.

Pseudorasbora parva is also a potential carrier of the parasite *Sphaerothecum destruens* Arkush et al., 2003, which causes mortality and inhibits spawning in cyprinids and salmonids (Gozlan et al. 2005; Spikmans et al. 2020). In the Oder catchment,

Czerniejewski et al. (2023) found no *S. destruens* but recorded five parasite taxa new for the species in Poland, among them a co-introduced Asian monogenean. Thus, founder populations carry a twofold risk: parasites translocated with the host, and spillback of local parasites onto native hosts. A susceptible cyprinid, *B. strumicae*, is already present in the cave. Downstream of the resurgence, the Angitis and the karst springs of the Drama basin hold fishes of high conservation concern, including the Greek brook lamprey *Eudontomyzon hellenicus* Vladykov, Renaud, Kott & Economidis, 1982, and *Cobitis punctilineata* Economidis & Nalbant, 1996 (Economidis 1995; Economidis and Nalbant 1996; Economou et al. 2007).

The species is listed as a Union concern under Regulation (EU) No 1143/2014 and Implementing Regulation (EU) 2016/1141 (Kalogianni et al. 2024), which prohibit its keeping, transport, and release and require surveillance, early detection, and rapid eradication. In Greece, Law 3937/2011 on biodiversity conservation provides the national framework, and the species is included in the national inventory of invasive alien species (Arianoutsou et al. 2023). Early eradication of isolated populations is feasible and benefits native fish (Britton et al. 2009), whereas control at the catchment scale rarely succeeds. In Greece, such basic inventory and monitoring work is poorly developed, despite the remarkable recent rise of alien and translocated fish; many species that may be invading frequently go unnoticed (Economou et al. 2016; Zogaris et al. 2023). Furthermore, basic systematic monitoring of non-indigenous fish has yet to be developed (Koutsikos et al. 2021), and such initiatives do not explicitly address subterranean habitats or the swallow sinkhole systems through which invaders may reach them.

Conclusions

The presence of *P. parva* up to 6 km inside the Angitis cave is the first documented occurrence of an alien animal species in a Greek cave, where the invader shares the subterranean river with a native cyprinid, a conservation priority crayfish species, and two amphipod genera. Swallow sinkholes connecting invaded surface waters to karst conduits thus may act as unmonitored invasion pathways; however, further research is required to determine whether the species can enter from the cave outlet. We recommend targeted monitoring of the cave using visual census, netting, and environmental DNA; parasite screening of retained specimens; surveys of the Kato Nevrokopi swallow holes as the likely source; and the inclusion of groundwater-dependent ecosystems in national invasive alien species action plans.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

Fish were handled alive for the minimum time needed for measurement and photography and released at the point of capture; no animal was killed. The field research was authorised by the Ministry of Culture (18516-16/01/2006) and the Ministry of Environment and Energy (ΥΠΕΝ/ΔΔΔ/109858/4024-20/10/2025).

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
Regarding the use of AI in the preparation of this manuscript, the authors declare the following: Claude.
Used for: Other.
Claude (Anthropic) was used to assist English language editing and formatting; the authors reviewed all text and take full responsibility for the content.

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Author contributions

Conceptualisation: KP, SP. Investigation: KP, SP, SZ. Writing – original draft: KP. Writing – review and editing: KP, SP, SZ.

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Data availability

All of the data that support the findings of this study are available in the main text.