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Article

Lampreys (Petromyzontidae) in the Almopaios River (Greece): New data on distribution and phylogenetic position

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Abstract
Eudontomyzon lampreys were recently discovered in the Almopaios River's main stem approximately 30 river kilometers downstream of Aridea river tributary, where specimens are known to have a stronghold in the past and have been collected recently as well. Molecular analyses assert that these lampreys belong to the taxon provisionally named *Eudontomyzon* sp. Almopaios, a brook lamprey; however, this species has not yet been formally described. Our genetic analysis provided a firm phylogenetic position for this population showing that their nearest relative is *Eudontomyzon danfordi* which has a center of distribution in the mid-Danube tributary basin, the River Tisza's catchment area. With the discovery and molecular confirmation of new specimens, this taxon's known distribution is presented for the first time; and particularly, the southernmost distribution area is located within a Natura 2000 protected area. However, this area is planned to be altered by a dam and river diversion. Conservation initiatives and steps towards further study are proposed.

Key words lampreys, *Eudontomyzon* sp. Almopaios, distribution, molecular analyses, conservation, Greece.

Introduction

A critical pitfall in conservation is the loss of undescribed species, sometimes referred to as the "dark diversity" (Pärtel et al. 2011). These species fall victim to taxonomic neglect, where delays in their scientific description make them invisible to conservation policy (Hortal et al. 2015). This is a silent tragedy in conservation and it is still unfolding even in well-studied areas such as Southeastern Europe. Here we present an example of such a neglected, range-restricted *Eudontomzyon* brook lamprey taxon from Northern Greece.

Freshwater lampreys are rare in Greece, geographically localized and understudied (Economou et al. 2007; Barbieri et al. 2015; Xanthopoulou et al. 2025). Two species of brook lampreys in the genus *Caspiomyzon* are described, in northeastern and western Greece (Vladykov et al. 1982; Renaud and Economidis, 2010; Gubili et al. 2025). And there is also a single population of a *Eudontomzyon,* known to be located solely in one river, the Almopaios, and provisionally referred to as the Almopaios Brook Lamprey, *Eudontomyzon* sp. Almopaios (Barbieri et al. 2015; Pereira et al. 2021). The discovery of this lamprey population was first published in a paper by Economidis and Banarescu (1991) which roughly sketches the population of Almopaios near Aridea town. In the same paper, Economidis and Banarescu (1991) also mention another location where lampreys may exist; they state: "an unidentified larva has been recently found in Loudias River basin" (p. 280). No further reference to the exact geographic range of this taxon or any other lampreys in this area was ever published. The lamprey of the Almopaios does not have a valid scientific name so it has not been assessed during Greece’s recent Red List review (NECCA 2024). Interestingly, even in Economidis’s 1995 review of endangered fishes of Greece, there is no mention of this range-restricted population, although he mentioned the other “named” lamprey populations (Economidis 1995).

This paper provides new data on this lamprey’s limited distribution, aspects of the genetic positioning of the collected specimens and documentation of current anthropogenic threats. Since so little is known about this *Eudontomyzon* species, the only one in Greece, any new knowledge of its status is important for conservation. As part of this endeavor, two tissue samples of this lamprey specimen were supplied to an international team coordinated by the University of Debrecen, Hungary, who are working on the Europe-wide molecular phylogeography of the genus *Eudontomyzon*. While this work is ongoing, the phylogenetic placement of the known samples from Greece was determined with high certainty, and given the urgency of this matter (i.e., conservation threats), we decided to refer to these preliminary results to argue for the unique phylogenetic placement of the brook lampreys of the Almopaios River.

Study Area and Methods

The Almopaios river (also known as the Moglenitsa) has an interesting biogeographical and hydrological history (Ghilardi et al. 2008; Economidis et al. 1981). Its ichthyofauna is closely related to the nearby rivers of Aliakmon, Loudias and Axios (Vardar) but it does have some distinctions, holding at least two species of fish that are unique to it; this includes an unidentified *Phoxinus*, genetically closely related or similar to *Phoxinus lumaireul* (Šanda et al. 2019) and the lamprey which is part of the current research note (Economidis et al. 1981). The Almopaios river originally flowed into a huge inland delta lake and the estuarine area of the upper Thermaikos Gulf, the lake being known as Giannitson Lake (Figure 1). In the 1930s this lake was drained as were the vast wetlands and the lower part of Almopaios was totally diverted to form an artificial channel and confluence with the lower Aliakmon. The diversion was made possible by the construction of a diversion channel (T66 Canal) and this has made the Almopaios a *de facto* artificial tributary of the Aliakmon. In management and assessment studies it is considered part of the Aliakmon (Lazaridou-Dimitriadou et al. 1999) and its biological aquatic assemblages are similar to the lower Aliakmon river basin (Economidis et al. 1981).

We reviewed the available bibliography and geographical fish records and compiled additional electrofishing investigations in the Almopaios River in 2022 and early 2023. Lampreys are known from a spring-fed tributary next to Aridea village and next to the city of Aridea (Sampling Site #1; Figure 1). The Aridea River site is a cold-water spring-fed tributary of the Almopaios where populations have been collected in 2023 by the first and last author (40°58'57.8"N 22°03'12.1"E). Aridea stream has excellent silt-sand habitat for ammocetes and usually at least ten specimens can be found within 30 m. of river stretch while sampling with electricity; locally the population is quite dense (Zogaris, S. unpublished personal observations). Samples from the Aridea area where also used within the paper of Geiger et al. (2014) which genetically positions the population for the first time. Although the known distribution is concentrated in the Aridea River and near Aridea on the Almopaios main stem, its total distribution has never been charted. In this paper we refer to a new discovery of lampreys 30 km to the south of Aridea (Figure 1).

Figure 1. Sampling of *Eudontomyzon* including: known distribution at Aridea (Site #1) and the discovery downstream; collected at two downstream locations at the lower Moglenitsa Gorge during this study (Site #2). The river hydrology shows current conditions (dark blue lines) and presumed past conditions (dotted lines). Before the 1930s, the Almopaios (in dotted blue line, #3), entered wetlands of the former Giannitson Lake (approximate extent delineated, when drainage works commenced in 1930). The Almopaios's flow is now artificially diverted (#4) to the Aliakmon river. A dam is planned exactly at the new *Eudontomyzon* collection locations (Site #2).

Fish sampling at the Aridea Tributary site and the downstream locations where the discovery was made consisted of electrofishing, following standardized approaches used through the European Union Water Framework Directive in Greece. A battery-powered backpack electrofishing unit was used (Smith Root 24 L DC pulsed, 1.5 kW, 35–100 Hz, max 980 V) and a single pass of a river stretch at least 100 m long was completed (one transect per locality; average fishing time approximately 45 minutes). In order to search specifically for lampreys, at the river's slow flowing habitats (i.e. river pools) with fine substrates (silt, sand) the electronic frequency of the electrofishing was lowered below 30 hertz. Experience has shown that lower frequencies are more effective at stimulating burrowed larvae or adult lampreys to emerge (Jolley et al. 2017).

Once the lampreys were caught, they were photographed alive in a glass field aquarium. Anesthesia using a clove oil solution was performed to keep the specimens relatively still. Later with an overdose of the clove oil and/or electrocution the specimens were put to death and preserved in 96% ethanol solution for laboratory investigation; specimens were preserved in order to explore possibilities for species description in the near future. A total of three specimens were stored at the Department of Ichthyology and Aquatic Environment, University of Thessaly in Volos, Greece (see acknowledgements). Electrofishing and collection was undertaken by license issued by the Hellenic Ministry of Environment license ΩΧΨΙ4653Π8-ΤΜ0 (no. ΥΠΕΝ/ΔΔΔ/68311/2115/28/06/2023) which mentions the first author among others.

To identify the new population through molecular techniques, a fin clip (~0.1 g) was preserved in silica gel and transported to co-authors in Hungary for DNA extraction. The samples were included in a single-digest RADseq library (Szatmári et al. 2021) with specimens from 35 European rivers across seven countries. RADseq was used to overcome the limited phylogenetic resolution of conventional markers (Pereira et al. 2021), providing thousands of loci across the genome for evolutionary analysis. The phylogenetic tree was constructed using a maximum likelihood approach in iqtree v.2.0.3 (Minh et al. 2020), where branch robustness was assessed.

Results

Distribution and documentation

Our survey has identified a new river site with *Eudontomyzon* brook lampreys on the lower main-stem of the Almopaios river. On the 7th of February 2023 we collected two specimens of *Eudontomyzon* from two locations approximately 30 river kilometers south of the Aridea tributary confluence (Site 2; Figure 1): Location 1 is situated below Kalli Weir near Kalli village (40°51'07.6"N 22°09'10.7"E) and Location 2 within the Moglenitsa Gorge (40°52'57.4"N 22°08'00.1"E); both are within a Natura 2000 protected area at 49 m. and 79 m. elevation (a.s.l.) respectively. We provide the specific positions of these sites since, to the best of our knowledge, this is the most southernmost known distribution for this species and we consider it a range extension.

Since only single adults were found, this population may maintain a low-density, much of the river being fairly fast-flowing (in winter) with specific habitats for ammocetes (the larval form) being quite rare in the area of the Moglenitsa Gorge. In both of the new locations, the lampreys inhabited relatively slow-flowing lotic habitats (side-arms) where fine sand bends were also present. However, most of the river habitats where rocky, dominated by boulders and cobble beds. The following seven fish species co-occurred in the sampled stretch of the main stem of the lower Almopaios at Kalli and the Moglenitsa Gorge: *Barbus balcanicus*, *Romanogobio cf. elimeius*, *Sabanejewia balcanica*, *Gobio bulgaricus*, *Squalius vardarensis*, *Rhodeus meridionalis* and *Alburnoides thessalicus*.

The lamprey taxon identification – to the genus level - was based on external morphology and to species level through molecular confirmation (see below). Our photographs (Fig. 2 and 3) of one adult and its head structure with oral disc details support identification. Externally, the adults show generic brook lamprey characteristics of the *Eudontomyzon* genus. There is no knowledge of this species being parasitic (feeding on live fish) but our photo shows mouth parts evident in parasitic lampreys of the *Eudontomyzon* genus (Kottelat and Freyhof 2007). These are obviously not the distinctively reduced tooth-like structures and patterns found on the non-parasitic *Caspiomyzon* species of Greece (Vladykov et al. 1982). Evidence of the sucker disc with tooth-plates is provided in our photograph and the keratinous-like tongue structure inside the mouth is apparent. Finally, the outer lips are soft and fringed, with sensory papillae.

Figure 2. The Almpaios Brook Lamprey, *Eudontomyzon sp.* Almopaios (TL: 185 mm), an adult collected immediately below the Moglenitsa Gorge (Below Kalli Weir).

Figure 3. *Eudontomyzon* sp. Almopaios (TL: 185 mm); showing oral disc as its sucks on the aquarium glass (same individual as in Figure 2).

Phylogenetic data

The molecular work confirms that the specimens are of the undescribed taxon *Eudontomyzon* sp. Almopaios (Perreira et al. 2021). The ongoing phylogeographic study of European brook lampreys (see introduction) using the RADseq approach has produced a maximum likelihood phylogenetic tree based on 7150 variable SNPs in iqtree v.2.0.3 (Minh et al. 2020) with statistical support of branch robustness assessed by 1000 replicate of SH-aLRT test (Guindon et al. 2010) and 1000 ultrafast bootstrap (UFboot) replicates (Minh et al. 2013). We accepted a branch as supported if aLRT ≥ 80% and UFboot ≥ 95% at the same time. In this respect, the resulting phylogenetic tree is well-resolved at the backbone of the tree and recovered the samples from the same waterbodies as monophyletic tips on the tree (with a few exceptions). While we regard our results as preliminary in respect to taxonomic interpretation and sampling spectrum, the phylogenetic placement of the samples of *Eudontomyzon* sp. Almopaios was unequivocal: it is placed at the base of a clade that contains *Eudontomyzon* samples from the Tisza River catchment area from Romania and Hungary (Fig. 4). This means that the Almopaios population represents a unique genetic lineage in the Balkans, its closest relation being the *Eudontomyzon danfordi* complex of the Danube's Tisza catchment area. The basal position of the Almopaios samples within this lineage argues for this being a relict population of the lineage. The analysis also implies that we exclude the possibility of anthropogenic introduction that would require the Almopaios samples to be in a more "tip position" on the phylogenetic tree, close to a putative donor population's sample.

Discussion

Taxonomic difficulties and the research context

The taxonomy of closely related lampreys is hindered by their morphological similarity, one exception being the details of the feeding apparatus of fully metamorphosed adults (Docker et al. 1999). However, care must be taken on making identification from such characters when few specimens are considered. In most lamprey samplings in Greece, ammocetes are usually found, not adults; metamorphosis takes place just before reproduction and adults presumably die rather soon after this (i.e. in non-parasitic forms; Maurakis and Economidis 2003). The information we share in terms of identification characters is necessarily limited since morphological description is not sanctioned due to the possible variations in the metamorphosed adults, for example we observed variations due to the degree of keratinization of disc teeth as is well known from earlier studies (Vladykov et al. 1982). We have only inspected two adults from the new sites and necessarily we decided to limit our morphological diagnosis to this brief snap-shot documentation (further taxonomic research on this is underway). Moreover, until recently, taxonomic difficulties also existed since there is a lack of molecular phylogenetic resolution that conventional genetic markers can provide (e.g., the *cytochrome oxidase I* gene of the mitochondrion) (McCauley et al. 2015). This leaves taxonomists with few morphological clues and complex genetic patterns for a natural classification. Finally, in spite of their rarity and biogeographical interest, lamprey species have been sorely neglected in natural history collections and conservation research in southern Europe (Stefanov and Holčík, 2007; Mateus et al. 2013).

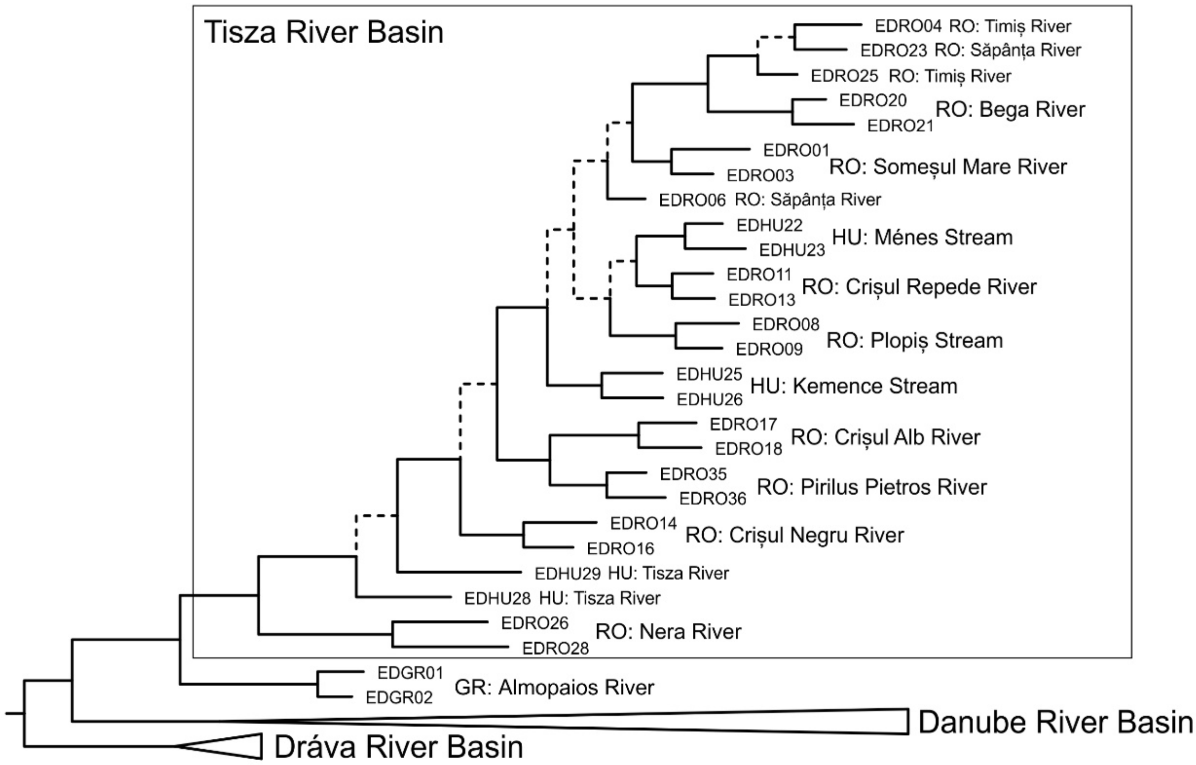

Figure 4. Phylogenetic placement of the brook lamprey samples from the Almopaios River, Greece; phylogenetic tree using a maximum likelihood approach in iqtree. Robust branches (where aLRT ≥ 80% and UFboot ≥ 95% at the same time) are indicated by continuous lines above, while unsupported branches are dashed. The clades containing samples from the Danube and Drava rivers catchment area collapsed.

Despite its initial discovery in 1991, the unnamed taxon of *Eudontomyzon* from the Almopaios river was first analyzed within a phylogeographic study in Geiger et al. (2014) and scientists consider that this probably represents a new undescribed species, native to Northern Greece (Barbieri et al. 2015; Pereira et al. 2021). However, the species status of this population has never been specifically detailed, nor can the analysis of Pereira et al. (2021) establish this since their Almopaios sample falls into the basal polytomy within the genus. These authors used two mitochondrial and nuclear markers to gain insight into the family-level taxonomy of lampreys, but they could report only limited phylogenetic resolution within the genera (Pereira et al. 2021). Despite the wide-ranging work in the aforementioned paper, this result of the analyses in Pereira et al. (2021) is particularly interesting as the Greek taxon is understood to be the basal member of a lineage containing *E. danfordi* and *E. vladykovi*, although without statistical support.

Our phylogenomic results support the unique nature of the Almopaios population, presumably as a relict population of the *Eudontomyzon* species complex related to species inhabiting the mid-Danubian Tisza river catchment area. Although this report does not provide a definitive description of the lamprey population of the Almopaios River, the premise of our study is based on this position and we believe that even if a species has not yet been “named”, every effort must be made to promote its conservation as a significant natural taxonomic unit.

In this paper we also provide initial known distributional data: the species known population is distributed at least within a 30 km river area ranging from Aridea to the village of Kalli. To the best of our knowledge, the species distribution has never been charted, the only previous mention of this being a rather vague map within the original biogeographical review paper by Economidis and Banarescu (1991).

Conservation insights
There are several issues of conservation concern in relation to the lamprey population under study. Initially, species within the *Eudontomyzon* genus are to be protected in the European Union as the genus is listed in Appendix II of the EU Habitats Directive (92/43/EC), however the taxon in our study is still not valid. Since it is not a described species, scant research into its distribution and ecology have been pursued in Greece. We may assume that the species is potamodromous (i.e., migratory) as are other related *Eudontomyzon* brook lampreys, and that anthropogenic barriers to longitudinal connectively in rivers are a serious threat to dispersal and/or potential distributional range cover. The species (or some lamprey species) may very possibly exist (or have existed) beyond the Almopaios river, as has been suggested by Economidis and Banarescu (1991; see introduction). However, based on our review, no lampreys have ever been found in any other river sites in the wider area of the Central and Western Macedonia Region, despite the occurrence of suitable habitats. Although brook lamprey habitats in rivers and lakes are specific and discernible to trained researchers (Zvezdin et al. 2021), little is known about specific ecology, life-history, habitat-use and movement patterns by this taxon in Greece. A major pitfall in conservation research is the failure to adequately inventory a species' full potential range (Vavalidis et al. 2021). Such poor attention to distributional details is a classic example of a sampling pitfall, leading to misallocated resources and potentially neglecting key habitats crucial for protection and species recovery. Comprehensive, systematic surveys at the inventory level are essential to avoid these errors and ensure accurate assessments (Economou et al. 2016).

Furthermore, human activities have drastically changed the natural conditions and hydrology in both the Almopaios valley and adjacent Thessaloniki plain (as shown in Figure 1) resulting in catastrophic habitat changes and ongoing reduction of available water resources (Moutsiakis and Yiannakou 2023). Specific areas where *Eudontomyzon* sp. Almopaios exist are now potentially threatened by water development and irrigation intensification projects. As irrigation demands increase, new dams and river diversions are being developed. In the Almopaios River, at the site of the newly discovered *Eudontomyzon* population, a 61 m high dam is being planned (Stamou et al. 2025) and it is foreseen to inundate part of a Natura 2000 protected area (specifically, listed as site GR1240005, Stena Apsalou – Moglenitsas). The Almopaios dam will have a capacity of about 45 million m^3/year and will be constructed in front of the exit of the river from the Moglenitsa Gorge upstream of Kalli village; exactly where the range *Eudontomyzon* extension described here was discovered. This kind of large-scale irrigation project could produce ecological problems (Destouni & Prieto 2018) and may specifically impact the lamprey population or other assemblages of aquatic biodiversity. This particular area of the Central Macedonia region has seen a rapid increase of many water development projects, including many that potentially fragment connectivity (Panagiotou et al. 2022) and degrade waterbody conditions (Moutsiakis and Yiannakou 2023). Attention to spatial planning and biodiversity protection initiatives are called for.

In view of the discovery of the lamprey population currently above and below the exact location of a proposed dam on the Almopaios river, specific conservation initiatives and mitigation measures should be initiated. In this paper we reiterate that this lamprey is a native and potentially range-restricted species. The aim of our study is to publish and publicize our new data and analyses in order to call attention to this important species and to help resolve its taxonomic status as soon as possible.

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