



# PHYLOGENETIC RELATIONSHIPS OF *TERRANIGRA* RADOMAN, 1978 (TRUNCATELLOIDEA: HYDROBIIDAE)

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**ABSTRACT:** *Terranigra kosovica* Radoman, 1978, was known from four localities in Kosovo. The monotypic genus was described on the basis of genital morphology. We collected *T. kosovica* at a new locality, about 40 km from its type locality. The shell morphology, as well as the soft part morphology and anatomy were identical to that described by Radoman. The molecular markers mitochondrial cytochrome oxidase subunit I (COI) and nuclear histone (H3) resolved phylogenetic position of *Terranigra* as a sister clade to *Agrafia* Szarowska et Falniowski, 2011.

**KEY WORDS:** cytochrome c oxidase; COI; histone H3; Gastropoda

## INTRODUCTION

RADOMAN (1978) described a new genus of the truncatelloid snail *Terranigra* Radoman, 1978, with its type species *Terranigra kosovica* Radoman, 1978. The genus still remains monotypic (RADOMAN 1983, 1985, KABAT & HERSHLER 1993). The genus was characterised by a big bursa copulatrix with a short duct, two seminal receptacles, with the distal ( $rs_1$ ) seminal receptacle very small, nearly vestigial, and the proximal ( $rs_2$ ) seminal receptacle big, and the penis simple without outgrowths. The type locality of *T. kosovica* is a spring by Crna Zemlja (which means black soil, in Latin *terránigra*), near Mala Reka, about 6 km west of Nerodimlje (=Nerodime e Epërme) and 12–13 km west of Uroševac (=Ferizaj) town (Table 1, Fig. 1, locality 2). The species was reported by RADOMAN (1983) from three other additional localities (Table 1, Fig. 1): a small spring at the village of Pridvorica, near the place Velji Breg on the road

Ribarić-Kosovska Mitrovica (locality 3); the spring below the rock in Crnoljevo village (=Carralevë), Gornja Mahala, a little over the road Štimlje-Prizren

Table 1. Sampling localities with geographical coordinates

Id	Locality	Coordinates
1	Ponorc/Ponorac village, Ponorc Cave	42°29'17.5"N, 20°37'17.8"E
2	spring by Crna Zemlja (type locality)	42°21'56.5"N, 21°01'36.5"E
3	Pridvorica village	42°55'21.7"N, 20°41'25.1"E
4	Carralevë/Crnoljevo village	42°27'27.7"N, 20°58'42.2"E
5	Nerodime e Epërme/Gornje Nerodimlje	42°21'58.0"N, 21°03'28.4"E

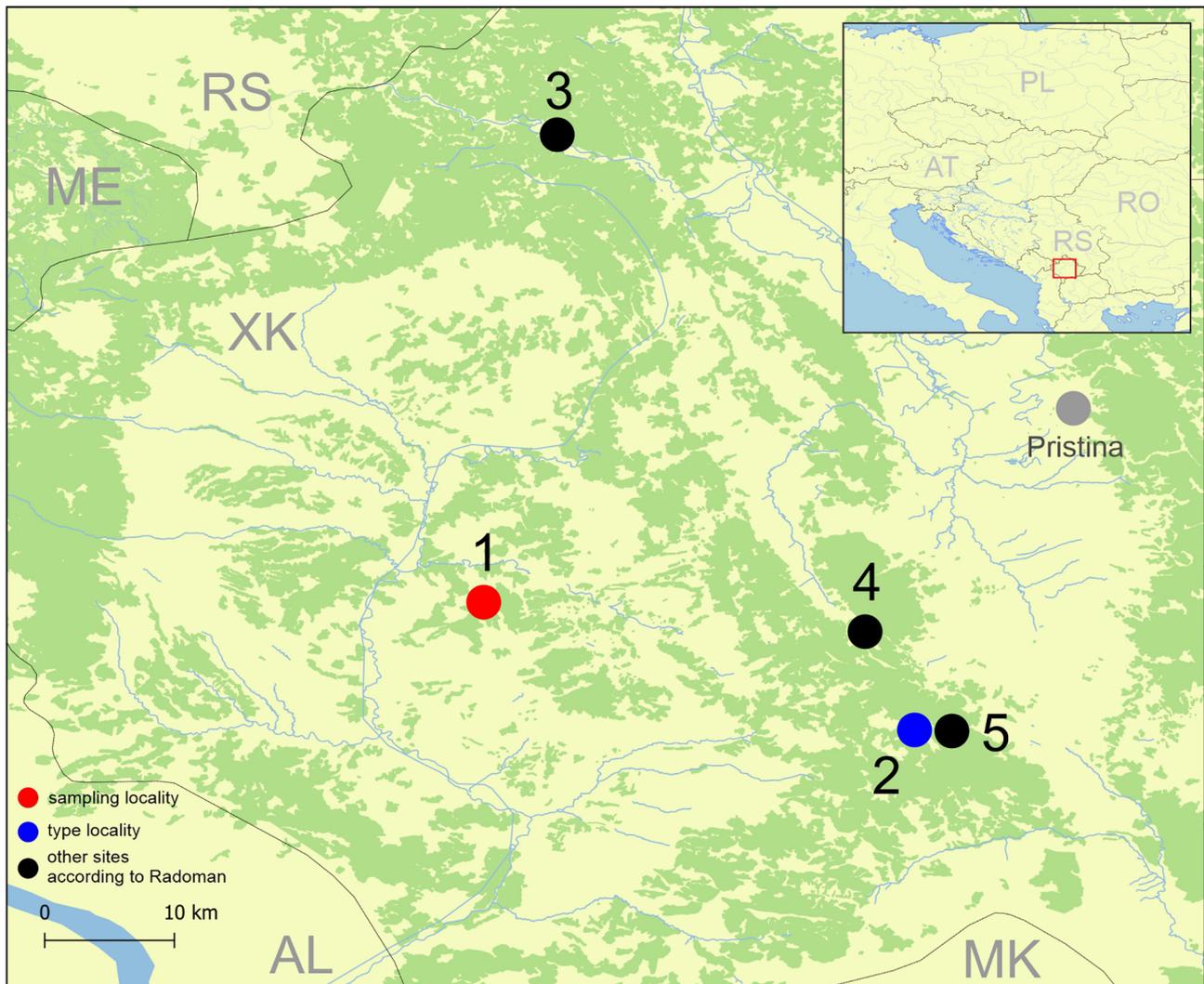


Fig. 1. Geographic distribution of the known localities of *Terranigra kosovica*. Inset indicates the location of the study area. For country identification we used the officially assigned code ISO (ISO 3166 alpha-2)

(locality 4); the spring (fountain) at the forester's hut, near the confluence of the Mala and Velika Reka, at the beginning of Nerodimka River (locality 5) (RADOMAN 1978). This species, with an unpigmented body and with eyespots present, was reported as a "subterranean form" inhabiting also epigeal springs (RADOMAN 1978, 1983). To our knowledge, there are no more published data on *Terranigra*, except imprecise information about 10 sites in The IUCN Red List of Threatened Species (SEDDON 2011).

In the autumn of 2018, a new attempt was made to find this species in some of its known localities.

## MATERIAL AND METHODS

Our field activities in Kosovo in years 2015–2018 includes a freshwater gastropod diversity survey over 96 springs of the region, many of them repeatedly sampled. During the end of September 2018

As in previous years, we were unsuccessful in our attempt to find the locus typicus as described by Radoman. We had equally negative results in two other localities listed by RADOMAN (1983), but we did discover a previously unknown *Terranigra* population near Ponorc/Ponorac village.

The aim of the present study was to collect material for genetic analysis to resolve issues with the systematics of these snails. The availability of living specimens has allowed us to use DNA-based methods to identify the position of the species (and the monotypic genus) in the phylogenetic tree.

field trip, we sampled springs at 20 different locations. Two of which were thought to correspond to localities known from the literature for *Terranigra kosovica* (Table 1, Fig. 1). One was the locality west



Figs 2–3. Ponorc Cave: 1 – distant view of the hillside where Ponorc Cave is located, 2 – one of the small springs beneath Ponorc Cave (locality 1)

of Nerodime e Epërme/Gornje Nerodimlje, at beginning of the Nerodime/Nerodimka River (some springs along a ca. 500 m section downstream from the confluence with Mala Reka), 690 m a.s.l., 42°21'58.0"N, 21°03'28.4"E (locality 5). The other one was at Carralevë/Crnoljevo village from the large karstic spring near the mosque, 640 m a.s.l., 42°27'27.7"N, 20°58'42.2"E (locality 4). Despite careful searching (including digging and filtering in spring zone, picking underside of the stones and fine sandy sediment sieving), *T. kosovica* was not found at these historical localities. This of course does not provide conclusive evidence, but strongly suggests that the species has become extirpated at these localities since 1978. At one of the other 18 sampled springs at this field trip we found a population that we could identify as *T. kosovica*. This locality was south of Ponorc/Ponorac village (Prizren District), in side-springs beneath Ponorc Cave, 575 m a.s.l., 42°29'17.5"N, 20°37'17.8"E (Table 1, Figs 1–3, locality 1). Some animals were hand collected from the bottom side of larger stones lying in the spring, some others were found in by sieving the sandy sediment of the spring head as described in GREGO *et*

al. (2017a). Sediment samples were sieved through a 3 mm and 500 µm sieve and fixed in 80% analytically pure ethanol, replaced two times, and later the samples were sorted. Next, the snails were put in fresh 80% analytically pure ethanol and kept in –20 °C temperature in a freezer. The shells were photographed with a CANON EOS 50D digital camera, under a NIKON SMZ18 microscope with dark field.

DNA was extracted from whole two specimens; tissues were hydrated in tris-EDTA (TE) buffer (3 × 10 min); then total genomic DNA was extracted with the SHERLOCK extraction kit (A&A Biotechnology), and the final product was dissolved in 20 µl of TE buffer. The extracted DNA was stored at –80 °C at the Department of Malacology, Institute of Zoology and Biomedical Research, Jagiellonian University in Kraków (Poland). Fragments of the mitochondrial cytochrome oxidase subunit I (COI) and the nuclear histone H3 (H3) were sequenced. Details of PCR conditions, primers used, and sequencing technique were given in SZAROWSKA *et al.* (2016). The Sanger sequencing, in both directions, was performed at Genomed Company in Warsaw, Poland.

Table 2. Reference sequences used in phylogenetic analyses

Species	COI GB numbers	H3 GB numbers	References
<i>Agrafia wiktoriae</i> Szarowska et Falniowski, 2011	JF906762	MG543158	SZAROWSKA & FALNIOWSKI 2011 GREGO et al. 2017b
<i>Alzoniella finalina</i> Giusti et Bodon, 1984	AF367650	–	WILKE et al. 2001
<i>Anagastina zetaevallis</i> (Radoman, 1973)	EF070616	–	SZAROWSKA 2006
<i>Avenionia brevis berenguieri</i> (Draparnaud, 1805)	AF367638	–	WILKE et al. 2001
<i>Belgrandiella cf. kuesteri</i> (Boeters, 1970)	MG551325	MG551366	OSIKOWSKI et al. 2018
<i>Daphniola lousi</i> Falniowski et Szarowska, 2000	KM887915	–	SZAROWSKA et al. 2014
<i>Dalmatinella fluviatilis</i> Radoman, 1973	KC344541	OP617253	FALNIOWSKI & SZAROWSKA 2013 HOFMAN et al. 2022
<i>Ecrobia maritima</i> (Milaschewitsch, 1916)	KX355835	MG551322	OSIKOWSKI et al. 2016 GREGO et al. 2017b
<i>Fissuria boui</i> Boeters, 1981	AF367654	–	WILKE et al. 2001
<i>Graecoarganiella parnassiana</i> Falniowski et Szarowska, 2011	JN202352	–	SZAROWSKA & FALNIOWSKI 2011
<i>Graziana alpestris</i> (Frauenfeld, 1863)	AF367641	–	WILKE et al. 2001
<i>Grossuana codreanui</i> (Grossu, 1946)	EF061919	–	SZAROWSKA et al. 2007
<i>Horatia klecakiana</i> Bourguignat, 1887	KJ159128	–	SZAROWSKA & FALNIOWSKI 2014
<i>Islamia zermanica</i> (Radoman, 1973)	KU662362	MG551320	BERAN et al. 2016 GREGO et al. 2017b
<i>Montenegrospeum bogici</i> (Pešić et Glöer, 2012)	KM875510	MG880218	FALNIOWSKI et al. 2014 GREGO et al. 2018
<i>Radomaniola curta</i> (Küster, 1853)	KC011814	–	FALNIOWSKI et al. 2012
<i>Sarajana apfelbecki</i> (Brancsik, 1888)	MN031432	–	HOFMAN et al. 2019
<i>Sadleriana fluminensis</i> (Küster, 1853)	AY273996	OQ607596	SZAROWSKA & WILKE 2004 JASZCZYŃSKA et al. 2023

In the phylogenetic analysis additional, most similar sequences from GenBank were used (Table 2). Sequences of both loci were initially aligned with MUSCLE (EDGAR 2004) program implemented in MEGA 7 (KUMAR et al. 2016). The correctness of the alignment was checked in BIOEDIT 7.2.5 (HALL 1999), this program was also used to check for reading frame and stop codons. Uncorrected mean p-distances were calculated in MEGA 7. We analysed COI and H3 datasets individually, as well as concatenated dataset (COI+H3). For all datasets, the estimation of the proportion of invariant localities and the saturation test (XIA 2000, XIA et al. 2003) were performed using DAMBE (XIA 2018). The phylogenetic analysis was performed applying two approaches: Bayesian Inference (BI) and Maximum Likelihood (ML). In the BI analysis, the GTR+I+ $\Gamma$  model of nucleotide substitution was applied. Model was selected using

MRMODELTEST 2.3 (NYLANDER 2004). The Bayesian analyses were run using MrBayes v. 3.2.3 (RONQUIST et al. 2012) with defaults priors. Two simultaneous analyses were performed, each with 10,000,000 generations, with one cold chain and three heated chains, starting from random trees and sampling the trees every 1,000 generations. The first 25% of the trees were discarded as burn-in. The analyses were summarised as a 50% majority-rule tree. Convergence was checked in Tracer v. 1.5 (RAMBAUT & DRUMMOND 2009); in all cases the effective sample size exceeded 200. FigTree v.1.4.4 (RAMBAUT 2010) was used to visualise the trees. The maximum likelihood analysis was conducted in RA $\times$ ML v. 8.2.12 (STAMATAKIS 2014) using the 'RA $\times$ ML-HPC v.8 on XSEDE (8.2.12) tool via the CIPRES Science Gateway (MILLER et al. 2010). We used the GTR+G model, using jModelTest2 via CIPRES.

## RESULTS

The examined animals and their anatomy were nearly identical with the one described by RADOMAN (1978); the unpigmented body (Figs 4–5), the soft part morphology and anatomy confirmed identification as *T. kosovica*. We obtained two new sequences of COI (457 bp, GenBank accession numbers OR373065-OR373066) and two of H3 (310 bp, GenBank accession numbers OR471608-OR471609). The tests by



Figs 4–5. Shells of *Terranigra kosovica*: 4 – 2A73, 5 – 2M24. Scale bar equals 1 mm

XIA et al. (2003) revealed no saturation. Results from the substitution saturation analysis showed an ISS (0.76 for COI; 0.50 for H3) substantially smaller than the critical ISS value (ISSC: 0.96 for COI; 0.62 for H3), indicating that all sequences are useful in phylogenetic reconstruction. The topologies of the trees inferred with ML and BI approaches were identical (Figs 6–8). At each tree (for COI, H3 and concatenated sequences) the sister genus of *Terranigra* was *Agrafia* Szarowska et Falniowski, 2011 (p-distance for COI was 0.074 and for H3 was 0.010). The bootstrap support and Bayesian posterior probability for concatenated sequences were high (98%, and 1.0 respectively). *Islamia* Radoman, 1973 was placed far from these two sister species in each tree, although in the COI tree (Fig. 6), as expected, basal nodes are not supported. In the H3 tree (Fig. 7), however, *Islamia* was outside of the well supported (bootstrap 72%) clade including *Terranigra*, *Agrafia*, *Dalmaninella* Radoman, 1973, *Sadleriana* Clessin, 1890, *Montenegrospeum* Pešić et Glöer, 2013, and *Belgrandiella* A. J. Wagner, 1928. Nearly the same relationships are present in the tree based on the concatenated sequence (Fig. 8), only the bootstrap is lower (68%), and *Sadleriana* does not belong to this clade.

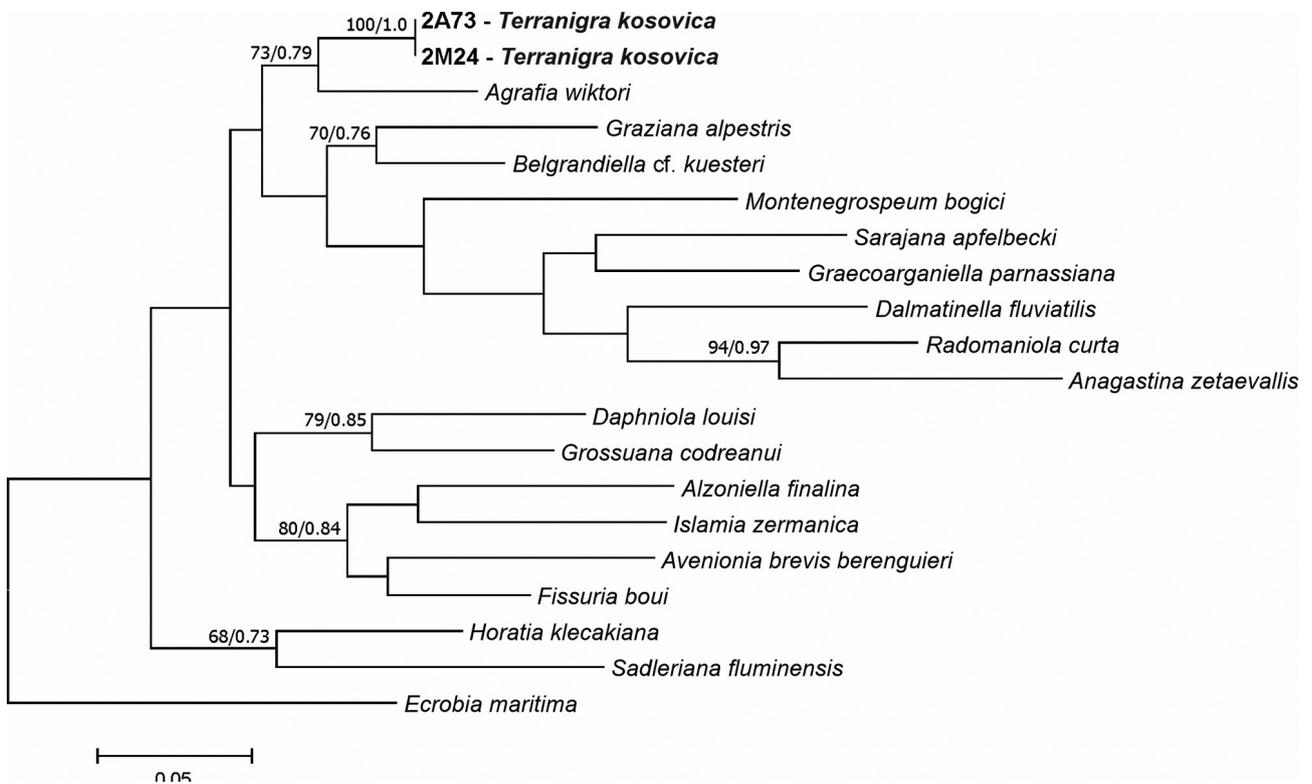


Fig. 6. Molecular phylogenetic tree inferred by Bayesian inference (BI) and Maximum likelihood (ML) of COI (457 bp). The support of the branches is indicated by maximum likelihood bootstrap values and Bayesian posterior probabilities, always when bootstrap values >60%

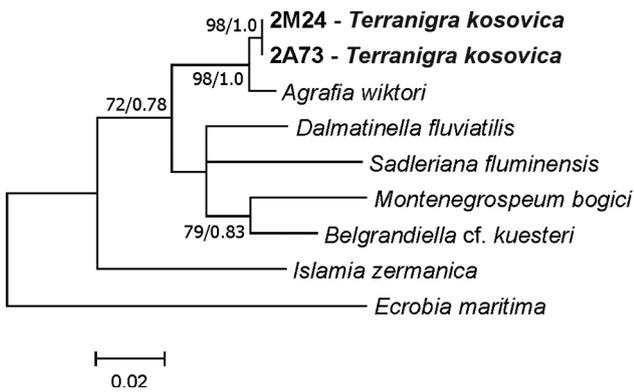


Fig. 7. Molecular phylogenetic tree inferred by Bayesian inference (BI) and Maximum likelihood (ML) of H3 (310 bp). The support of the branches is indicated by maximum likelihood bootstrap values and Bayesian posterior probabilities, always when bootstrap values >60%

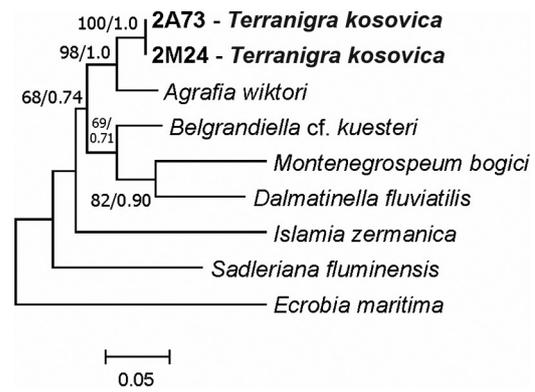


Fig. 8. Molecular phylogenetic tree inferred by Bayesian inference (BI) and Maximum likelihood (ML) of COI + H3 (767 bp). The support of the branches is indicated by maximum likelihood bootstrap values and Bayesian posterior probabilities, always when bootstrap values >60%

## DISCUSSION

As stressed in many publications, in Truncatelloidea, morphological data are sufficient neither for species distinction (FALNIOWSKI 2018, CHERTOPRUD et al. 2023), nor higher classification (e.g. SZAROWSKA & FALNIOWSKI 2008). Despite several efforts to apply molecular data (e.g. WILKE et al. 2001, 2013) we are still far from a well-supported phylogeny of the Truncatelloidea, including the Hydrobiidae. Our study confirmed the genus level status of *Terranigra*: genetic divergence between this species and its sister genus was 7.4%. This value is higher than interspecies level in many Hydrobiids (e.g. 1.5 to 3.5% estimate for interspecies divergence for *Bythinella*: BICHAIN et al. 2007). In our trees *Terranigra* clearly belongs to the family Hydrobiidae Stimpson, 1865. The well supported clade based on H3 represents the subfamily Sadlerianinae sensu Szarowska, 2006 (not Sadlerianinae Radoman, 1973). This name was proposed by SZAROWSKA (2006) as a provisional replacement name for Horatiinae D. W. Taylor, 1966, since the specimen whose sequence was the only one available at that time in GenBank for “*Horatia klecakiana*” was the one used in the phylogeny of the Rissooidea by WILKE et al. (2001), and this specimen was misidentified (SZAROWSKA & FALNIOWSKI 2014). It has to be pointed out that Sadlerianinae sensu Szarowska, 2006 was used for the clade sister to the Hydrobiinae (the latter including also *Pyrgula* and *Pseudamnicola*), grouping most of the genera of the Hydrobiidae. The more recent systematics of WILKE et al. (2013) followed by BOUCHET

et al. (2017) lists several subfamilies within the Horatiinae sensu Szarowska, 2006, Belgrandiellinae Radoman, 1973, Horatiinae D. W. Taylor, 1966 and Islamiinae Radoman, 1973 among them, but not resolving the relationships between them, showing either polytomy or paraphyletic Islamiinae. Clearly, our phylogeny based on COI and H3, is not congruent with the one presented in WoRMS (2022), which without any justification classify *Agrafia* within the subfamily Islamiinae Radoman, 1973, and *Terranigra* within the subfamily Belgrandiinae de Stefani, 1877, thus sister taxa in our tree classifying in two subfamilies, confirming that a credible phylogeny of the Truncatelloidea is badly needed.

The last published IUCN Red List of Threatened Species (SEDDON 2011) ranked this species as Near Threatened (NT). At that time, the number of locations was thought to be 10 and the Extent of Occurrence (EOO) were estimated as the whole area of Kosovo. The fact that there is good reason to believe that some populations have been extirpated since 1978 and that the main threats to the species' habitats, namely habitat conversion and water abstraction, will continue in the future, would qualify this species as Endangered (EN) based on criteria B1ab(ii, iii, iv) and B2ab(ii, iii, iv). On the other hand, the relatively large EOO (1,700 km<sup>2</sup>) and the recent discovery of a new subpopulation implies that there might be some more undiscovered subpopulations within its potential range.



## REFERENCES

- BERAN L., OSIKOWSKI A., HOFMAN S., FALNIEWSKI A. 2016. *Islamia zermanica* (Radoman, 1973) (Caenogastropoda: Hydrobiidae): morphological and molecular distinctness. *Folia Malacologica* 24: 25–30.  
<https://doi.org/10.12657/folmal.024.004>
- BICHAIN J. M., BOISSELIER-DUBAYLE M. C., BOUCHET P., SAMADI S. 2007. Species delimitation in the genus *Bythinella* (Mollusca: Caenogastropoda: Rissooidea): a first attempt combining molecular and morphometrical data. *Malacologia* 49: 293–311.  
<https://doi.org/10.4002/0076-2997-49.2.293>
- BOUCHET P., ROCROI J.-P., HAUSDORF B., KAIM A., KANO Y., NUTZEL A., PARKHAEV P., SCHRÖDL M., STRONG E. E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. *Malacologia* 61: 1–526.  
<https://doi.org/10.4002/040.061.0201>
- CHERTOPRUD E., GREGO J., MUMLADZE L., HOFMAN S., PALATOV D., OSIKOWSKI A., JASZCZYŃSKA A., FALNIEWSKI A. 2023. Revealing the stygobiotic and crenobiotic molluscan biodiversity hotspot in the Caucasus: Part IV. Crenobiotic Belgrandiellinae Radoman, 1983 (Mollusca, Hydrobiidae) from Georgia. *Diversity* 15: 450 (1–63).  
<https://doi.org/10.3390/d15030450>
- CLESSIN S. 1890. Die Mollusken-Fauna Mitteleuropa's. II. Teil. Die Molluskenfauna Oesterreich-Ungarns und der Schweiz, 858 pp. [part 5: 625–858 (1890)]. Bauer & Raspe, Nürnberg.  
<http://biodiversitylibrary.org/page/39745274>
- DE STEFANI C. 1877. Molluschi continentali fino ad ora notati in Italia nei terreni pliocenici, ed ordinamento di questi ultimi. *Atti della Societa Toscana di Scienze Naturali Residente in Pisa* 3: 274–325.
- EDGAR R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.  
<https://doi.org/10.1093/nar/gkh340>
- FALNIEWSKI A. 2018. Species distinction and speciation in hydrobioid gastropods (Mollusca: Caenogastropoda: Truncatelloidea). *Archives of Zoological Studies* 1: 003.  
<https://doi.org/10.24966/AZS-7779/100003>
- FALNIEWSKI A., SZAROWSKA M. 2011. A new genus and new species of valvatiform hydrobiid (Rissooidea; Caenogastropoda) from Greece. *Molluscan Research* 31: 189–199.
- FALNIEWSKI A., SZAROWSKA M. 2013. Phylogenetic relationships of *Dalmanella fluviatilis* Radoman, 1973 (Caenogastropoda: Rissooidea). *Folia Malacologica* 21: 1–7.  
<https://doi.org/10.12657/folmal.021.001>
- FALNIEWSKI A., SZAROWSKA M., GLÖER P., PEŠIĆ V. 2012. Molecules vs morphology in the taxonomy of the *Radomaniola/Grossuana* group of Balkan Rissooidea (Mollusca: Caenogastropoda). *Journal Conchology* 41: 19–36.
- FALNIEWSKI A., PEŠIĆ V., GLÖER P. 2014. *Montenegrospeum* Pešić et Glöer, 2013: a representative of Moitessieriidae? *Folia Malacologica* 22: 263–268.  
<https://doi.org/10.12657/folmal.022.023>
- GREGO J., GLÖER P., ERŐSS Z. P., FEHÉR Z. 2017a. Six new subterranean freshwater gastropod species from northern Albania and some new records from Albania and Kosovo (Mollusca, Gastropoda, Moitessieriidae and Hydrobiidae). *Subterranean Biology* 23: 85–107.  
<https://doi.org/10.3897/subtbiol.23.14930>
- GREGO J., GLÖER P., RYSIEWSKA A., HOFMAN S., FALNIEWSKI A. 2018. A new *Montenegrospeum* species from south Croatia (Mollusca: Gastropoda: Hydrobiidae). *Folia Malacologica* 26: 25–34.  
<https://doi.org/10.12657/folmal.026.004>
- GREGO J., HOFMAN S., MUMLADZE L., FALNIEWSKI A. 2017b. *Agrafia* Szarowska et Falniowski, 2011 (Caenogastropoda: Hydrobiidae) in the Caucasus. *Folia Malacologica* 25: 237–247.  
<https://doi.org/10.12657/folmal.025.025>
- HALL T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- HOFMAN S., GREGO J., BERAN L., JASZCZYŃSKA A., OSIKOWSKI A., FALNIEWSKI A. 2022. *Kerkia* Radoman, 1978 (Caenogastropoda: Hydrobiidae): endemism, apparently morphostatic evolution and cryptic speciation. *Molluscan Research* 42: 295–319.  
<https://doi.org/10.1080/13235818.2022.2129943>
- HOFMAN S., OSIKOWSKI A., RYSIEWSKA A., GREGO J., GLÖER P., DMITROVIĆ D., FALNIEWSKI A. 2019. *Sarajana* Radoman, 1975 (Caenogastropoda: Truncatelloidea): premature invalidation of a genus. *Journal of Conchology* 43: 407–418.
- JASZCZYŃSKA A., HOFMAN S., FALNIEWSKI A. 2023. *Sadleriana bavarica* Boeters, 1989, a younger synonym of *S. fluminensis* (Küster, 1852) (Truncatelloidea: Hydrobiidae). *Journal of Conchology* 44: 439–449.  
<https://doi.org/10.5281/zenodo.8081266>
- KABAT A. R., HERSHLER R. 1993. The prosobranch snail family Hydrobiidae (Gastropoda: Rissooidea): review of classification and supraspecific taxa. *Smithsonian Contribution to Zoology* 547: 1–94.  
<https://doi.org/10.5479/si.00810282.547>
- KUMAR S., STECHER G., TAMURA K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33: 1870–1874.  
<https://doi.org/10.1093/molbev/msw054>
- MILLER M. A., PFEIFFER W., SCHWARTZ T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. In *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov., New Orleans, LA: 1–8.  
<https://doi.org/10.1109/GCE.2010.5676129>



- NYLANDER J. A. A. 2004. MrModeltest v.2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.
- OSIKOWSKI A., HOFMAN S., GEORGIEV D., KALCHEVA S., FALNIOWSKI A. 2016. Aquatic snails *Ecrobia maritima* (Milaschewitsch, 1916) and *E. ventrosa* (Montagu, 1803) (Caenogastropoda: Hydrobiidae) in the east Mediterranean and Black Sea. *Annales Zoologici* 66: 477–486.  
<https://doi.org/10.3161/00034541ANZ2016.66.3.012>
- OSIKOWSKI A., HOFMAN S., RYSIEWSKA A., SKET B., PREVORČNIK S., FALNIOWSKI A. 2018. A case of biodiversity overestimation in the Balkan *Belgrandiella* A. J. Wagner, 1927 (Caenogastropoda: Hydrobiidae): molecular divergence not paralleled by high morphological variation. *Journal of Natural History* 52: 323–344.  
<https://doi.org/10.1080/00222933.2018.1424959>
- PEŠIĆ V., GLÖER P. 2013. *Montenegrospeum*, a new genus of hydrobiid snails (Gastropoda: Rissoidae) from Montenegro. *Acta Zoologica Bulgarica* 65: 565–566.
- RADOMAN P. 1973. New classification of fresh and brackish water Prosobranchia from the Balkans and Asia Minor. *Posebna Izdanja, Prirodnjacki Musej u Beogradu* 32: 1–30.
- RADOMAN P. 1978. Neue Vertreter der Gruppe Hydrobioidea von der Balkanhalbinsel. *Archiv für Molluskenkunde* 109: 27–44.
- RADOMAN P. 1983. Hydrobioidea a superfamily of Prosobranchia (Gastropoda). I. Systematics. Serbian Academy of Sciences and Arts, Monograph 547, Department of Sciences 57: 1–256.
- RADOMAN P. 1985. Hydrobioidea, a superfamily of Prosobranchia (Gastropoda). II. Origin, zoogeography, evolution in the Balkans and Asia Minor. Faculty of Sciences – Department of Biology Monographs 1, Institute of Zoology Beograd 1: 1–173.
- RAMBAUT A. 2010. Molecular evolution, phylogenetics and epidemiology: FigTree v1.3.1. Institute of Evolutionary Biology, University of Edinburgh. Available online at <http://tree.bio.ed.ac.uk/software/figtree/> (accessed 15 December 2022)
- RAMBAUT A., DRUMMOND A. J. 2009. Tracer v1.5. Available online at <http://beast.bio.ed.ac.uk/Tracer> (accessed 15 December 2022).
- RONQUIST F., TESLENKO M., VANDER M. P., AYRES D. L., DARLING A., HÖHNA S., HUELSENBECK J. P. 2012. Mr. Bayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542.  
<https://doi.org/10.1093/sysbio/sys029>
- SEDDON M. B. 2011. *Terranigra kosovica*. The IUCN Red List of Threatened Species 2011: e.T155681A4823068.  
<https://doi.org/10.2305/IUCN.UK.2011-2.RLTS.T155681A4823068.en>
- STAMPATAKIS A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313.  
<https://doi.org/10.1093/bioinformatics/btu033>
- STIMPSON W. 1865. Diagnoses of newly discovered genera of gasteropods, belonging to the sub-fam. Hydrobiinae of the family Rissoidae. *American Journal of Conchology* 1(1): 52–54.  
<https://www.biodiversitylibrary.org/page/16084571>
- SZAROWSKA M. 2006. Molecular phylogeny, systematics and morphological character evolution in the Balkan Rissoidae (Caenogastropoda). *Folia Malacologica* 14: 99–168.  
<https://doi.org/10.12657/folmal.014.014>
- SZAROWSKA M., FALNIOWSKI A. 2008. There is no philosopher's stone: *coup de grace* for the morphology-based systematics in the rissoidae gastropods? 5th Congress of the European Malacological Societies, Ponta Delgada: 28.
- SZAROWSKA M., FALNIOWSKI A. 2011. An unusual, flagellum-bearing hydrobiid snail (Gastropoda, Rissoidae, Hydrobiidae) from Greece, with descriptions of a new genus and a new species. *Journal of Natural History* 45: 2231–2246.  
<https://doi.org/10.1080/00222933.2011.591067>
- SZAROWSKA M., FALNIOWSKI A. 2013. Species distinctness of *Sadleriana robici* (Clessin, 1890) (Gastropoda: Rissoidae). *Folia Malacologica* 21: 127–133.  
<https://doi.org/10.12657/folmal.021.016>
- SZAROWSKA M., FALNIOWSKI A. 2014. *Horatia* Bourguignat, 1887: is this genus really phylogenetically very close to *Radomaniola* Szarowska, 2006 (Caenogastropoda: Truncatelloidea)? *Folia Malacologica* 22: 31–39.  
<https://doi.org/10.12657/folmal.022.003>
- SZAROWSKA M., GRZMIL P., FALNIOWSKI A., SIRBU I. 2007. *Grossuana codreanui* (Grossu, 1946) and the phylogenetic relationships of the East Balkan genus *Grossuana* (Radoman, 1973) (Gastropoda: Rissoidae). *Hydrobiologia* 579: 379–391.  
<https://doi.org/10.1007/s10750-006-0530-4>
- SZAROWSKA M., HOFMAN S., OSIKOWSKI A., FALNIOWSKI A. 2014. *Daphniola* Radoman, 1973 (Caenogastropoda: Truncatelloidea) at East Aegean islands. *Folia Malacologica* 22: 269–275.  
<https://doi.org/10.12657/folmal.022.021>
- SZAROWSKA M., OSIKOWSKI A., HOFMAN S., FALNIOWSKI A. 2016. *Pseudamnicola* Paulucci, 1878 (Caenogastropoda: Truncatelloidea) from the Aegean Islands: a long or short story? *Organisms Diversity and Evolution* 16: 121–139.  
<https://doi.org/10.1007/s13127-015-0235-5>
- SZAROWSKA M., WILKE T. 2004. *Sadleriana pannonica* (Frauenfeld, 1865): A lithoglyphid, hydrobiid or amnicolid taxon? *Journal of Molluscan Studies* 70: 49–57.  
<https://doi.org/10.1093/mollus/70.1.49>
- TAYLOR D. W. 1966. A remarkable snail fauna from Coahuila, Mexico. *Veliger* 9: 152–228.
- WAGNER A. J. 1928. Studien zur Molluskenfauna der Balkanhalbinsel mit besonderer Berücksichtigung Bulgariens und Thraziens, nebst monographischer Bearbeitung einzelner Gruppen. *Annales Zoologici (Musei Polonici Historiae Naturalis)* 6: 263–399.
- WILKE T., DAVIS G. M., FALNIOWSKI A., GIUSTI F., BODON M., SZAROWSKA M. 2001. Molecular systematics of



- Hydrobiidae (Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships. *Proceedings of the Academy of Natural Sciences of Philadelphia* 151: 1–21.  
[https://doi.org/10.1635/0097-3157\(2001\)151\[0001:MSOHMG\]2.0.CO;2](https://doi.org/10.1635/0097-3157(2001)151[0001:MSOHMG]2.0.CO;2)
- WILKE T., HAASE M., HERSHLER R., LIU H. P., MISOF B., PONDER W. 2013. Pushing short DNA fragments to the limit: Phylogenetic relationships of 'hydrobioid' gastropods (Caenogastropoda: Rissooidea). *Molecular Phylogenetics and Evolution* 66: 715–736.  
<https://doi.org/10.1016/j.ympev.2012.10.025>
- WORMS (EDITORIAL BOARD) 2022. World Register of Marine Species. Available online at <https://www.marinespecies.org> (accessed 26 October 2022)  
<https://doi.org/10.14284/170>
- XIA X. 2018. DAMBE7: New and improved tools for Data Analysis in Molecular Biology and Evolution. *Molecular Biology and Evolution* 35: 1550–1552.  
<https://doi.org/10.1093/molbev/msy073>
- XIA X. 2000. *Data analysis in molecular biology and evolution*. Kluwer Academic Publishers, Boston, Dordrecht & London.
- XIA X., XIE Z., SALEMI M., CHEN L., WANG Y. 2003. An index of substitution saturation and its application. *Molecular Phylogenetics and Evolution* 26: 1–7.  
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