

SADLERIANA BAVARICA BOETERS, 1989, A YOUNGER SYNONYM OF *S. FLUMINENSIS* (KÜSTER, 1852) (TRUNCATELLOIDEA: HYDROBIIDAE)

ALEKSANDRA JASZCZYŃSKA^{1,3}, SEBASTIAN HOFMAN², ANDRZEJ FALNIOWSKI¹

¹Department of Malacology, Institute of Zoology and Biomedical Research, Jagiellonian University, ul. Gronostajowa 9, 30–387 Kraków, Poland

²Department of Comparative Anatomy, Institute of Zoology and Biomedical Research, Jagiellonian University, ul. Gronostajowa 9, 30–387 Kraków, Poland

³Department of Invertebrate Evolution, Institute of Zoology and Biomedical Research, Jagiellonian University, Kraków, Poland

Abstract The shell and genetic interpopulation differences (for mitochondrial cytochrome oxidase subunit I and nuclear histone 3) were studied for 21 localities of *Sadleriana Clessin, 1890*, representing nominal species: *S. fluminensis* (Küster, 1852), *S. sadleriana* (Frauenfeld, 1863), and *S. robici* (Clessin, 1890), all from the Balkans, and for *S. bavarica* Boeters, 1989, known only from one short stream within a park in Munich in Bavaria. Species distinctness was confirmed for *S. robici*, but not for *S. sadleriana*. The Bavarian *S. bavarica* was found to form a clade within the widely distributed and genetically variable *S. fluminensis*, also the shell and soft part morphology were the same for both taxa. Thus, *Sadleriana bavarica* Boeters, 1989 should be considered a younger synonym of *S. fluminensis* (Küster, 1853). The origin of the isolated Bavarian population is more likely to be explained by human transportation.

Key words endemism, mtDNA, COI, H3, genetic differences, shell, human transportation

INTRODUCTION

Sadleriana Clessin, 1890, with its type species *Paludina fluminensis* Küster, 1853, described from Močilnik Spring in Slovenia (Fig. 1A) inhabits springs and upper parts of the streams in Slovenia, Croatia, Bosnia and Herzegovina (Radoman, 1967, 1978, 1983, 1985; Kabat & Hershler, 1993; Falniowski *et al.*, 2021). Reports of *Sadleriana* from Bulgaria (Georgiev, 2011; Georgiev & Glöer, 2013, 2022) remain doubtful. Frauenfeld (1863) described another species, *S. sadleriana* (Frauenfeld, 1863) and Clessin (1890) described *S. robici* (Clessin, 1890), whose distinctness reflected in the cytochrome oxidase subunit I (COI) sequences was confirmed by Szarowska & Falniowski (2013). Schütt (1969) described *S. supercarinata* (Schütt, 1969) (as *Pseudamnicola*) with a strong keel on the shell. The genus was revised by Bole (1972). Radoman (1978) described the stygophile *S. cavernosa* Radoman, 1987, whose distinctness was supported molecularly by Delicado (2018). The Central European *S. pannonica* (Frauenfeld, 1865), inhabiting springs in Hungary and Slovakia, was found to represent the genus *Bythinella* Moquin-Tandon, 1856 (Szarowska & Wilke, 2004; Szarowska 2006),

considering both anatomy and molecular data.

Unexpectedly, Seidle & Colling (1986) found what they considered to be the Balkan *S. fluminensis* within the city limits of Munich, Bavaria, occurring only in a short (approximately 3 kilometres long) cool stream flowing from a small spring Brunnbach (in Herzogpark area: Fig. 1B) into the Isar river (Seidl & Colling, 1986; Boeters, 1989; Glöer, 2002; Szarowska & Wilke, 2004). This habitat is regarded as an isolated remnant of glacial deposits from the Riß period and is thus older than similar habitats around it, which were remodelled by moraines during the subsequent Würm glaciation (Koller *et al.*, 2014), which perhaps influenced the idea of narrow endemism of this taxon. Boeters (1989) considered this population to represent a distinct species and described it as *S. bavarica* Boeters, 1989. Koller *et al.* (2014) presented aspects of the 3D microanatomy of *S. bavariaca*, which is the most detailed anatomical study of a representative of the family Hydrobiidae.

The aim of our study is to resolve the phylogenetic relationships and species status of *Sadleriana bavarica*, *S. fluminensis*, *S. sadleriana* and *S. robici*, applying molecular markers: mitochondrial cytochrome oxidase subunit I (COI) and nuclear histone 3 (H3). Especially we consider



Figure 1 Type localities: A – Močilnik Spring, type locality of *S. fluminensis* (Küster, 1853); B – Brunbach Spring, Munich, type locality of *Sadleriana bavariaca* Boeters, 1989.

two alternative explanations of the origin of the population of *S. bavarica* in Germany. Either this population represents a north-easternmost relict of a wider distribution of *Sadleriana* in the past, or it has been introduced by passive transportation (human or bird).

MATERIAL AND METHODS

The snails were collected by hand or with a net at 21 localities (Fig. 2, Table 1). Samples were sieved through a 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 illumination. The dissections were done under a NIKON SMZ18 microscope.

DNA was extracted from whole specimens; tissues were hydrated in 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 tris-EDTA (TE) buffer. The extracted DNA was stored at -80°C at the Department of Malacology,

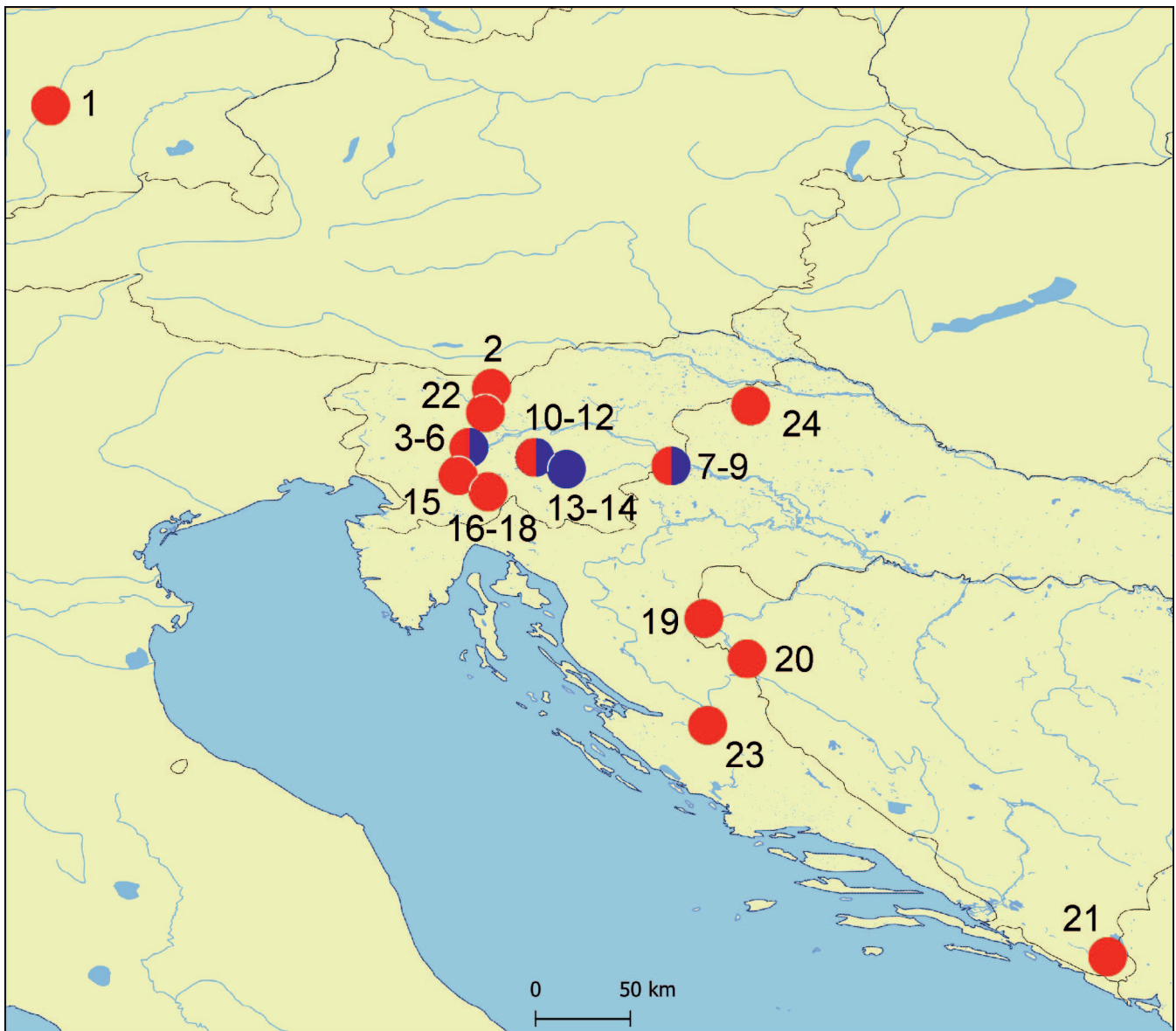


Figure 2 Localities of origin of the sequenced specimens. Numbers correspond to Table 1. Colours correspond to genetic lineages in the phylogram (Fig. 4).

Table 1 Sampling localities with geographical coordinates.

Id	Localities	Coordinates	
1	Munich, Germany	48.1604	11.6169
2	Potoče river, Slovenia, S29	46.3012	14.4428
3	Vrhnica, Slovenia, S34	45.9607	14.2920
4	Močilnik, Slovenia, S32	45.9544	14.2923
5	Retovje 1, Slovenia, S24	45.9516	14.2966
6	Retovje 2, Slovenia, S25	45.9508	14.2960
7	Dvorce, Slovenia, S18	45.8868	15.6101
8	Krska vas, Slovenia, S19	45.8927	15.5858
9	Kraška vas, aqueduct, Slovenia, S22	45.8624	15.5505
10	Krka spring, Slovenia, S2	45.8897	14.7714
11	Krka 1, Slovenia, S3	45.8862	14.7734
12	Krka 2, Slovenia, S4	45.8827	14.7815
13	Klečec, Slovenia, S7	45.8536	14.8841
14	Žužemberk, Slovenia, S8	45.8287	14.9304
15	Planina, Slovenia, S17	45.8225	14.2480
16	Žerovnica 1, Slovenia, S9	45.7631	14.4356
17	Žerovnica 2, Slovenia, S10	45.7619	14.4342
18	Žerovnica 3, Slovenia, S11	45.7603	14.4260
19	Izvor Klokot, Bihač district, Bosnia & Hercegovina	44.8244	15.8024
20	Orašac, Bihač district, Bosnia & Hercegovina	44.6217	16.0679
21	Confluence of Trebišnjica River with the Potok Blace	42.7154	18.3508
reference sequences			
1	Munich, Germany	48.1494	11.5996
4	Močilnik, Slovenia, S32	45.9544	14.2923
12	Krka 2, Slovenia, S4	45.8827	14.7815
22	Sava River, Slovenia,	46.1734	14.4151
23	Zrmanja River, near Radmilovići, Croatia	44.1968	15.7680
24	spring next to the Tounjčica River, Kamenica, Croatia	46.2415	16.0292

Institute of Zoology and Biomedical Research, Jagiellonian University in Kraków (Poland). A fragment of mitochondrial cytochrome oxidase subunit I (COI) and 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 was performed in Genomed Company in Warsaw, Poland.

Sequences were initially aligned in the MUSCLE (Edgar, 2004) program 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 translate of sequences and check for reading frame and stop codons. Uncorrected p-distances were calculated in MEGA 7. The estimation of the proportion of invariant sites and the saturation test (Xia, 2000; Xia *et al.*, 2003) were performed using DAMBE (Xia, 2013). In the phylogenetic analysis additional sequences from GenBank were used (Table

2). The phylogenetic analysis was performed applying two approaches: Bayesian inference (BI) and maximum likelihood (ML). In the BI analysis, the GTR +I + Γ 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 of most 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). FigTree v.1.4.4 (Rambaut, 2010) was used to visualise the trees. The maximum likelihood analysis was conducted in RAxML v. 8.2.12 (Stamatakis, 2014) using the 'RAxML-HPC v.8 on XSEDE (8.2.12) tool via the

Table 2 Reference sequences used in phylogenetic analyses.

Species	COI GB numbers	References
<i>Agrafia wiktoria</i> Szarowska & Falniowski, 2011	JF906762	Szarowska & Falniowski, 2011
<i>Alzoniella finalina</i> Giusti & Bodon, 1984	AF367650	Wilke <i>et al.</i> , 2001
<i>Anagastina zetaevallis</i> (Radoman, 1973)	EF070616	Szarowska, 2006
<i>Avenionia brevis berenguieri</i> (Draparnaud, 1805)	AF367638	Wilke <i>et al.</i> , 2001
<i>Belgrandia thermalis</i> (Linnaeus, 1767)	AF367648	Wilke <i>et al.</i> , 2001
<i>Belgrandiella cf. kuesteri</i> (Boeters, 1970)	MG551325	Osikowski <i>et al.</i> , 2018
<i>Daphniola lousi</i> Falniowski & Szarowska, 2000	KM887915	Szarowska <i>et al.</i> , 2014
<i>Dalmatinella fluviatilis</i> Radoman, 1973	KC344541	Falniowski & Szarowska, 2013
<i>Ecrobia maritima</i> (Milaschewitsch, 1916)	KX355835	Osikowski <i>et al.</i> , 2016
<i>Fissuria boui</i> Boeters, 1981	AF367654	Wilke <i>et al.</i> , 2001
<i>Graecoarganiella parnassiana</i> Falniowski & Szarowska, 2011	JN202352	Falniowski & Szarowska, 2011
<i>Graziana alpestris</i> (Frauenfeld, 1863)	AF367641	Wilke <i>et al.</i> , 2001
<i>Grossuana codreanui</i> (Grossu, 1946)	EF061919	Szarowska <i>et al.</i> , 2007
<i>Islamia zermanica</i> (Radoman, 1973)	KU662362	Beran <i>et al.</i> , 2016
<i>Montenegrospeum bogici</i> (Pešić & Glöer, 2012)	KM875510	Falniowski <i>et al.</i> , 2014
<i>Radomaniola curta</i> (Küster, 1853)	KC011814	Falniowski <i>et al.</i> , 2012
' <i>Sadleriana bavarica</i> Boeters, 1989'	AY273997	Szarowska & Wilke, 2004
<i>Sadleriana cavernosa</i> Radoman, 1978	MG922562	Delicado, 2018
<i>Sadleriana fluminensis</i> (Küster, 1853)	AY273996	Szarowska & Wilke, 2004
	KF193077-81	Szarowska & Falniowski, 2013
<i>Sadleriana robici</i> (Clessin, 1890)	KF193071-73	Szarowska & Falniowski, 2013
' <i>Sadleriana sadleriana</i> (Frauenfeld, 1863)'	MG922569	Delicado, 2018
<i>Sarajana apfelbecki</i> (Brancsik, 1888)	MN031432	Hofman <i>et al.</i> , 2019
<i>Tanousia zrmanjajae</i> (Brusina, 1866)	KU041812	Beran <i>et al.</i> , 2015

CIPRES Science Gateway (Miller *et al.*, 2010). We chose the GTR +G model, using jMODEL-TEST2 via CIPRES. In the ML inference based on the concatenated sequences the model was estimated separately for each partition. For COI, two species delimitation methods were used: Poisson Tree Processes (PTP) (Zhang *et al.*, 2013) and Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.*, 2011). The bPTP approach was run using the web server <https://species.h-its.org/ptp/>, with 100,000 MCMC generations, a thinning interval of 100 and 0.1 burn-in. We used the RAxML output phylogenetic tree. For the ABGD approach the web server (<https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html>) with the default parameters was used.

RESULTS

The shells of some of the sequenced *Sadleriana bavarica*, *S. fluminensis*, *S. sadleriana* and *S. robici* (Fig. 3) showed slight differences between the nominal taxa. In particular, the shells of *S. sadleriana* were somewhat smaller but nearly identical

with the ones of *S. fluminensis*. No differences between *S. bavarica* and *S. fluminensis* were found in the morphology of their shells. Three males and three females of each of the two species were dissected. Neither the penes, nor the female reproductive organs showed differences between these two taxa.

56 new sequences of cytochrome oxidase subunit I (COI) (GenBank no. OQ575653-OQ575708) from 21 localities, and 25 sequences of histone 3 (H3) (GenBank no. OQ607596-OQ607621) were acquired. For histone H3 all the sequences were identical. The saturation test (Xia, 2000; Xia *et al.*, 2003) showed no saturation for COI. Results from the substitution saturation analysis showed an ISS (0.74) significantly smaller than its critical value (ISSC: 0.95), indicating that all the sequences are useful in phylogenetic reconstruction. The topologies of the trees inferred with ML and BI approaches were identical in every last detail. Genetic p-distances between the taxa (Table 3) approached 0.12 between *S. cavernosa* and the other *Sadleriana*. Lower values, but still above 0.05, were calculated for *S. robici*. The

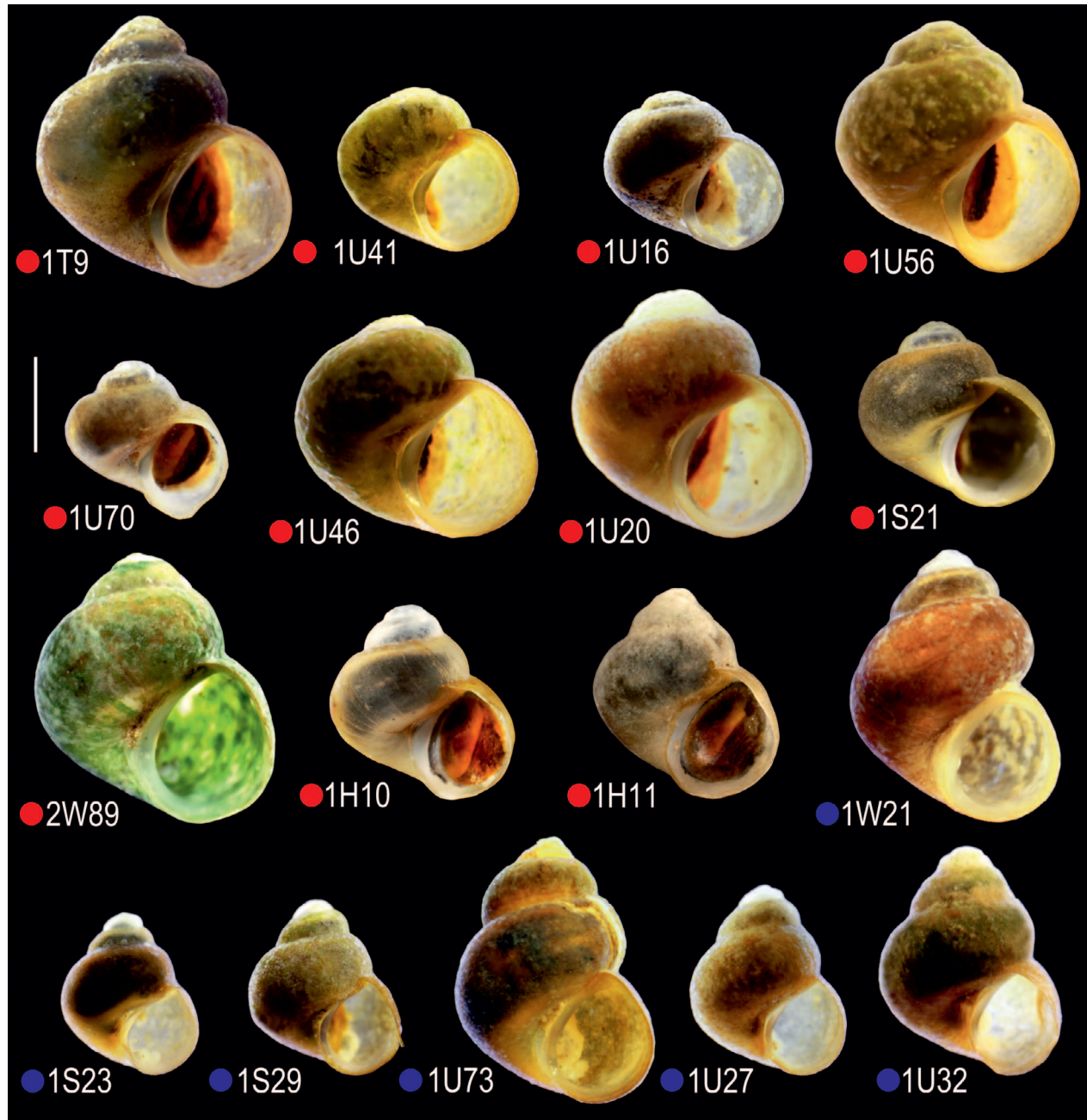


Figure 3 Shells of *Sadleriana*: 1T9 – locality 6, 1U41 – locality 16, 1U16 – locality 5, 1U56 – locality 18, 1U70 – locality 15, 1U46 – locality 17, 1U20 – locality 11, 1S21 – locality 10, 2W89 – locality 1, 1H10 – locality 19, 1H11– locality 20, 1W21 – locality 3, 1S23 – locality 10, 1S29 – locality 12, 1U73 – locality 7, 1U27 – locality 13, 1U32 – locality 14. Bar equals: 1mm, dots colour the same as in Fig. 2 and 4.

Table 3 p-distances for COI between (below diagonal) and within (diagonal, bold) *Sadleriana* putative species.

	<i>S. fluminensis</i>	' <i>S. bavarica</i> '	' <i>S. sadleriana</i> '	<i>S. robici</i>	<i>S. cavernosa</i>
<i>S. fluminensis</i>	0.020				
' <i>S. bavarica</i> '	0.032	0.000			
' <i>S. sadleriana</i> '	0.032	0.031	0.003		
<i>S. robici</i>	0.069	0.070	0.053	0.003	
<i>S. cavernosa</i>	0.120	0.119	0.116	0.117	-

distances between the other three studied taxa: *S. fluminensis*, *S. sadleriana* and *S. bavarica* (Table 3) were 0.031–0.032, comparable with 0.020 found between the populations of *S. fluminensis*.

The phylogram inferred for COI (Fig. 4) confirmed distinctness of *S. cavernosa*. Identity of the sequences for H3 in *S. bavarica*, *S. fluminensis*, *S. sadleriana* and *S. robici* reflected close relationships of these four nominal taxa. For COI both p-distances (Table 3) and the phylogram (Fig. 3) confirm the species distinctness of *S. robici* (the clade with the bootstrap support 99%, Bayesian probability 0.99) and the other clade grouping the other three studied nominal species (bootstrap support 93%, Bayesian probability 0.99), although the distinctness of *S. robici* is less evident than the one of *S. cavernosa*. The delimitation methods confirmed the distinctness of only three *Sadleriana* species: *S. cavernosa*, *S. fluminensis* and *S. robici*. *S. robici* was found only in Slovenia, whereas *S. fluminensis* in all the study area (Fig. 1). *S. fluminensis* and *S. robici* were found sympatrically at four localities (3, 10, 11 and 12).

DISCUSSION

Slight differences in the shell morphology between *S. sadleriana* and *S. fluminensis* were also noticed by Radoman (1983). Morphological differences between congeneric truncatelloid species often does not exist (Falniowski, 2018). Our results confirm the ones of Szarowska & Falniowski (2013), and of Delicado (2018), that *S. cavernosa* and *S. robici* are distinct species, although the species distinctness of *S. robici* is less obvious. Unfortunately, such estimates of the threshold values of genetic distances justifying the distinction of a species, like the ones presented for *Bythinella* by Bichain *et al.* (2007), are neither certain nor universal. In each group of species, the threshold values must be estimated. Usually, comparison of the intragroup and intergroup distances is helpful. As we could see in the COI tree (Fig. 4), within the big clade grouping *S. bavarica*, *S. fluminensis* and *S. sadleriana* the diversity within *S. fluminensis* is nearly as high as between the three nominal taxa. Therefore, we conclude that *S. bavarica* and *S. sadleriana* belong to the same genetically variable species: *S. fluminensis*. Distinguishing *S. bavarica* as a distinct species, not supported by low p-distances, would result in rejection of the monophyly of

S. fluminensis (Fig. 4). Both applied methods of species delimitation distinguished only two species, additionally supporting the hypothesis of synonymy of *S. bavarica*.

“*Sadleriana bavarica*” is evidently an isolated population of *S. fluminensis*. The divergence about 3% between it and the other populations of *S. fluminensis* falls within the infraspecific divergence in the latter. Also, neither the morphology of the shells and the soft parts anatomy nor the H3 sequences confirm interspecies differences. Considering the long geographic distance outside of the remaining range of the genus *Sadleriana*, as well as the occurrence only in one spring and short stream within a park within a big German city, coupled with the thousands of the German tourists visiting Yugoslavia in 1960s – 1980s, one could simply imagine somebody taking snails from some spring in former Yugoslavia and putting them in a spring in a park in his town. Accidental introduction with plants, fish or other material is likely as well, although in the case of spring and stream this is less probable than for, say, a pond or lake. The conditions in southern Germany have proved good enough for the survival but not enough for further expansion of the snail, thus a “man-made endemite” was created. With the available genetic data we cannot indicate which of the Balkan populations was the source of the Bavarian one. The absence of genetic variation in the Bavarian population may reflect the founder effect, although the number of sequenced specimens was too low for certain estimation.

The second scenario, that “*S. bavarica*” represents a north-easternmost relict of a wider distribution of *Sadleriana* in the past, is much less likely, especially since the occurrence of this snail, easily identifiable and usually present in large numbers, has not been reported anywhere between Munich and the remaining known range of *Sadleriana*, (approximately 200km distance). Also, no fossil record is known from southern Germany.

The anthropogenic transportation of snails is extremely common (Preston *et al.* 2022). Classic examples include repeated human-mediated translocations of the *Helix pomatia* Linnaeus, 1758 (e.g., Lubell, 2004, Peltanová *et al.*, 2011), some introductions of *Physella acuta* (Draparnaud, 1805) were intentional, through ponds and aquaria. Worldwide introductions of

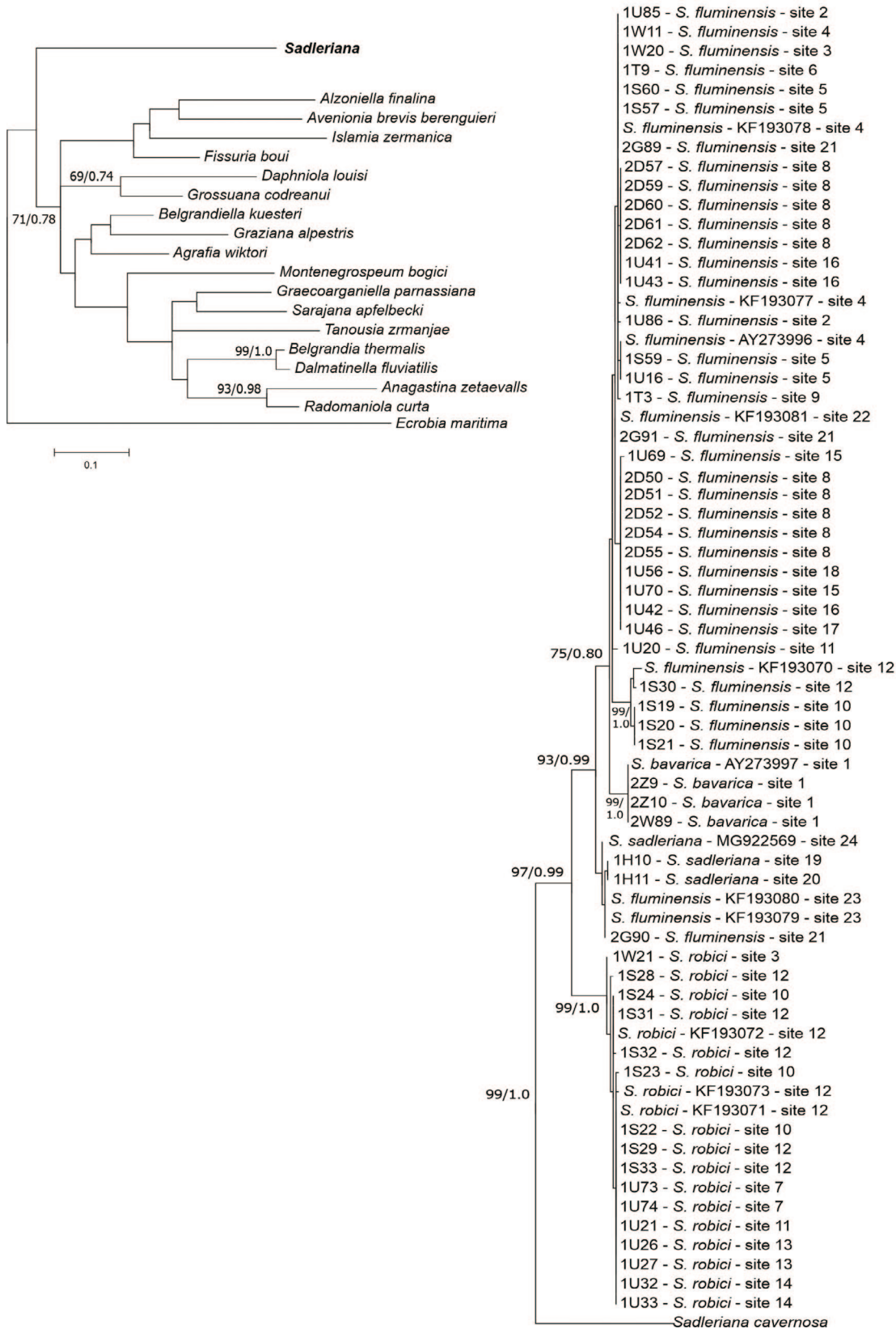


Figure 4 Maximum likelihood tree computed for COI sequences; bootstrap support and Bayesian posterior probabilities were shown when bootstrap supports >60%. Results of delimitation analysis are also shown.

Potamopyrgus antipodarum (J. E. Gray, 1843) were accidental (e.g., Ponder, 1988; Dillon *et al.*, 2005). *Bithynia tentaculata* (Linnaeus, 1758), common Palaearctic species, was first recorded in Lake Michigan in 1871, but was probably introduced in 1870 (Mills *et al.* 1993), and now is common in North America. South American brackish water *Heleobia haruana* (d'Orbigny, 1841) invaded northwest European estuaries (Van Haaren *et al.* 2021). Among nearly 500 alien species in Europe, more than 20 are molluscs (Nentwig *et al.*, 2018). However, these large-scale introductions differ from a local relocation of the *Sadleriana*. Such a transfer of several individuals does not have to be only the result of human activity, but also accidental introduction by birds (Rees, 1965, Cadée, 1988, 1994, Wesselingh *et al.*, 1999, Charalambidou & Santamaria, 2002, Figuerola & Green, 2002 Wada *et al.*, 2012) or other organisms.

To conclude, we contend that *Sadleriana bavaria* Boeters, 1989 should be considered a younger synonym of *S. fluminensis* (Küster, 1853).

ACKNOWLEDGMENTS

The study was supported by a grant from the National Science Centre 2017/25/B/NZ8/01372 to Andrzej Falniowski. We would like also to express our gratitude to Dr Ben Rowson and two anonymous reviewers for their useful corrections and comments.

REFERENCES

- BERAN L, HOFMAN S & FALNIOWSKI A 2015 *Tanousia zрманjae* (Brusina, 1866) (Caenogastropoda: Truncatelloidea: Hydrobidae): A living fossil *Folia Malacologica* **23**: 263–271.
- BERAN L, OSIKOWSKI A, HOFMAN S & FALNIOWSKI A 2016 *Islamia zermanica* (Radoman, 1973) (Caenogastropoda: Hydrobidae): morphological and molecular distinctness *Folia Malacologica* **24**: 25–30.
- BICHAIN JM, GAUBERT P, SAMADI S & BOISSELIER-DUBAYLE MC 2007 A gleam in the dark: Phylogenetic species delimitation in the confusing spring-snail genus *Bythinella* MoquinTandon, 1856 (Gastropoda: Rissooidea: Amnicolidae) *Molecular Phylogenetics and Evolution* **45**: 927–941.
- BOETERS HD 1989 Unbekannte westeuropäische Prosobranchia 8. *Heldia* **1**: 169–170.
- BOLE J 1972 Taksonomija i zoogeografija rodu *Sadleriana* Clessin, 1890 (Gastropoda, Prosobranchia)/ Taxonomie und Zoogeographie der Gattung *Sadleriana* Clessin, 1890 (Gastropoda, Prosobranchia). *Razprave, Slovenska Akademija Znanosti i Umetnosti, Razred za Rrirodoslovne i Medicinske Vede, Ljubljana* **15**: 49–74.
- CADÉE GC 1988 Levende wadslakjes in bergeend faeces. *Correspondentieblad van de Nederlandsche Malacologische Vereeniging* **243**: 443–444.
- CADÉE GC 1994 Eider, shellduck and other predators, the main producers of shell fragments in the Wadden Sea: palaeoecological implications. *Palaeontology* **37**: 181–202.
- CHARALAMBIDOU I & SANTAMARIA L 2002 Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecologica* **21**: 165–176.
- CLESSIN S 1887–1890 *Die Mollusken-Fauna Mitteleuropas, II. Theil: Die Molluskenfauna Österreich-Ungarns und der Schweiz* Bauer und Raspe, Nürnberg.
- DELICADO D 2018 A rare case of stygophily in the Hydrobiidae (Gastropoda: *Sadleriana*) *Journal of Molluscan Studies* **84**: 480–485.
- DILLON RT, WETHINGTON AR, RHETT JM & SMITH TP 2005 Populations of the European freshwater pulmonate *Physa acuta* are not reproductively isolated from American *Physa heterostropha* or *Physa integra* *Invertebrate Biology* **121**: 226–234. doi.org/10.1111/j.1744-7410.2002.tb00062.x
- EDGAR RC 2004 MUSCLE: multiple sequence alignment with high accuracy and high throughput *Nucleic Acids Research* **32**: 1792–1797.
- FALNIOWSKI 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>
- FALNIOWSKI A, PEŠIĆ V & GLÖER P 2014 *Montenegro-speum* PEŠIĆ et Glöer, 2013: a representative of Moitessieriidae? *Folia Malacologica* **22**: 263–268.
- FALNIOWSKI A & SZAROWSKA M 2011 A new genus and new species of valvatiform hydrobiid (Rissooidea; Caenogastropoda) from Greece *Molluscan Research* **31**: 189–199.
- FALNIOWSKI A & SZAROWSKA M 2013 Phylogenetic relationships of *Dalmatinella fluviatilis* Radoman, 1973 (Caenogastropoda: Rissooidea) *Folia Malacologica* **21**: 1–7.
- FALNIOWSKI 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.
- FALNIOWSKI A, LEWARNE B, RYSIEWSKA A, OSIKOWSKI A & HOFMAN S 2021 Crenobiont, stygophile and stygobiont molluscs in the hydrographic area of the Trebišnjica River Basin *ZooKeys* **1047**: 61–89.
- FIGUEROLA J & GREEN AJ 2002 Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshwater Biology* **47**: 483–494.
- FRAUENFELD G VON 1863 Die Arten der *Lithoglyphus* Mhlf., *Paludinella* Pf., *Assimineae* Gray, in der kaiserlichen und Cuming's Sammlung *Verhandlungen*

- der Kaiserlich-königlichen Zoologisch-botanischen Gesellschaft in Wien, *Abhandlungen* **13**: 193–212, available online at <https://www.biodiversitylibrary.org/page/54757330>
- FRAUENFELD G VON 1865 Zoologische Miscellen. V *Verhandlungen der Kaiserlich-königlichen Zoologisch-botanischen Gesellschaft in Wien, Abhandlungen* **15**: 525–536, pl: 8–12. Wien., available online at <https://www.biodiversitylibrary.org/page/16400966>
- GEORGIEV D 2011 Check list of the Bulgarian minor freshwater snails (Gastropoda: Rissooidea) with some ecological and zoogeographical notes *ZooNotes* **24**: 1–4.
- GEORGIEV D & GLÖER P 2013 Identification key of the Rissooidea (Mollusca: Gastropoda) from Bulgaria with a description of six new species and one new genus *North-Western Journal of Zoology* **9**: art.131301.
- GLÖER P 2002 *Mollusca I. Süßwassergastropoden Nord und Mitteleuropas. Bestimmungsschlüssel, Lebensweise, Verbreitung*. 2. neubearbeitete Auflage. In: *Die Tierwelt Deutschlands, 73*, ConchBooks, Hackenheim.
- GLÖER P 2022 *The Freshwater Gastropods of the West-Palaearctis, Volume II: Moitessieriidae, Bythinellidae, Stenothyridae*. Published by the author, Hetlingen.
- VAN HAAREN T, WORSFOLD TM, STELBRINK B, COLLADO A, GONÇALVES ICB, SERRA, WS, SCARABINO F, GITTENBERGER A & GITTENBERGER E 2021 *Heleobia charuana* (Gastropoda, Truncatelloidea, Cochliopidae), a South American brackish water snail in northwest European estuaries. *Basteria* **85**: 82–91.
- HALL TA 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, OSIKOWSKI A, RYSIEWSKA A, GREGO J, GLÖER P, DMITROVIĆ D & FALNIOWSKI A 2019 *Sarajana Radoman, 1975* (Caenogastropoda: Truncatelloidea): premature invalidation of a genus *Journal of Conchology* **43**: 407–418.
- KABAT AR & HERSHLER R 1993 The prosobranch snail family Hydrobiidae (Gastropoda: Rissooidea): review of classification and supraspecific taxa *Smithsonian Contribution to Zoology* **547**: 1–94.
- KOLLER K, BRENZINGER B & SCHRÖDL M 2014 A caenogastropod in 3D: microanatomy of the Munich endemic springsnail *Sadleriana bavarica* Boeters, 1989 (Caenogastropoda, Hydrobiidae) *Spixiana* **37**: 1–19.
- 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.
- KÜSTER HC 1852 Die Gattungen *Paludina*, *Hydrocaena* und *Valvata* *Abbildungen nach der Natur mit Beschreibungen. Systematisches Conchylien-Cabinet von Martini und Chemnitz* **1** (21), Bauer und Raspe, Nürnberg.
- LUBELL D 2004 Prehistoric edible land snails in the circum Mediterranean: the archaeological evidence. In JJ. Brugal and J. Dese (eds.), *Petits Animaux et Sociétés Humaines. Du Complément Alimentaire Aux Ressources Utilitaires. XXIVe rencontres internationales d'archéologie et d'histoire d'Antibes*: pp. 41–62.
- MILLER MA, PFEIFFER W & SCHWARTZ T 2010 Creating the CIPRES Science Gateway for inference of large phylogenetic trees *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov., New Orleans, LA: 1–8.
- MILLS EL, LEACH JH, CARLTON JT & SECOR CL 1993 Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. *Journal of Great Lakes Research* **19**:1–54.
- NENTWIG W, BACHER S, KUMSCHICK S, PYŠEK P & VILA M 2018 More than “100 worst” alien species in Europe *Biological Invasions* **20**: 1611–1621.
- NYLANDER JAA 2004 *MrModeltest v.2. Program distributed by the author*. Uppsala: Evolutionary Biology Centre, Uppsala University.
- 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.
- 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.
- PELTANOVÁ A, PETRUSEK A, KMENT P & JUŘIČKOVÁ L 2011 A fast snail's pace: colonization of Central Europe by Mediterranean gastropods *Biological Invasions* **14**: 759–764.
- PONDER WF *Potamopyrgus antipodarum* – a molluscan colonizer of Europe and Australia *Journal of Molluscan Studies* **54**: 271–285. doi:10.1093/mollus/54.3.271
- PRESTON DL, CRONE ER, MILLER-TER KUILE A, LEWIS CD, SAUER EL, & TROVILLION DC 2022 Non-native freshwater snails: a global synthesis of invasion status, mechanisms of introduction, and interactions with natural enemies *Freshwater Biology* **67**: 227–239. <https://doi.org/10.1111/fwb.13848>
- PULLANDRE N, LAMBERT A, BROUILLET S & ACHAZ G 2011 ABGD, Automatic Barcode Gap Discovery for primary species delimitation *Molecular Ecology* **21**: 1864–1877. doi:10.1111/j.1365-294X.2011.05239.x
- RADOMAN P 1967 Das Genus *Sadleriana* *Glasnik Prirodnjackog Museja, Beograd series B* **20**: 121–126.
- RADOMAN P 1978 Neue Vertreter der Gruppe Hydrobioidea von der Balkanhalbinsel *Archiv für Molluskenkunde* **109**: 27–43.
- RADOMAN P 1983 Hydrobioidea a superfamily of Prosobranchia (Gastropoda). I. Systematics *Monographs Serbian Academy of Sciences and Arts, DXLVII, Department 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, Institute of Zoology Beograd 1: 1–173.
- RAMBAUT A 2010 FigTree v1.3.1. <<http://tree.bio.ed.ac.uk/software/figtree>>.
- RAMBAUT A & DRUMMOND AJ 2009 Tracer v1.5. <http://beast.bio.ed.ac.uk/Tracer>.
- REES WJ 1965 The aerial dispersal of Mollusca. *Proceedings of the Malacological Society of London* **36**: 269–282.
- RONQUIST F, TESLENKO M, VANDER MP, AYRES DL, DARLING A, HÖHNA S & HUELSENBECK JP 2012 Mr. Bayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space *Systematic Biology* **61**: 539–542.
- SCHÜTT H 1969 Eine rezente gekielte *Pseudamnicola*. *Archiv für Molluskenkunde* **99**: 187–192.
- SEIDL F JUN & COLLING M 1986 Ein Vorkommen von *Sadleriana fluminensis* (Küster) in der Bundesrepublik Deutschland *Mitteilungen der Zoologischen Gesellschaft, Braunau* **4**: 345–354.
- STAMATAKIS 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>
- SZAROWSKA M 2006 Molecular phylogeny, systematics and morphological character evolution in the Balkan Rissooidea (Caenogastropoda) *Folia Malacologica* **14**: 99–168.
- SZAROWSKA M & FALNIOWSKI A 2011 An unusual, flagellum-bearing hydrobiid snail (Gastropoda: Rissooidea: Hydrobiidae) from Greece, with descriptions of a new genus and a new species *Journal of Natural History* **45**: 2231–2246.
- SZAROWSKA M & FALNIOWSKI A 2013 Species distinctness of *Sadleriana robici* (Clessin, 1890) (Gastropoda: Rissooidea) *Folia Malacologica* **21**: 127–133.
- 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: Rissooidea) *Hydrobiologia* **579**: 379–391.
- SZAROWSKA M, HOFMAN S, OSIKOWSKI A & FALNIOWSKI A 2014 *Daphniola* Radoman, 1973 (Caenogastropoda: Truncatelloidea) at east Aegean islands *Folia Malacologica* **22**: 269–75.
- 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. <http://dx.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.
- WADA S, KAWAKAMI K & CHIBA S 2012 Snails can survive passage through a bird's digestive system *Journal of Biogeography* **39**: 69–73.
- WESSELINGH FP, CADÉE GC & RENEMA W 1999 Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*. *Geologie en Mijnbouw* **78**: 165–174.
- WILKE T, DAVIS GM, FALNIOWSKI A, GIUSTI F, BODON M & SZAROWSKA M 2001 Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships *Proceedings of the Academy of Natural Sciences of Philadelphia* **151**: 1–21.
- XIA X 2018 DAMBE7: New and Improved Tools for Data Analysis in Molecular Biology and Evolution *Molecular Biology and Evolution* **35**: 1550–1552.
- 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.
- ZHANG J, KAPLI P, PAVLIDIS P & STAMATAKIS A 2013 A general species delimitation method with applications to phylogenetic placements *Bioinformatics* **29**: 2869–2876. doi:10.1093/bioinformatics/btt499

