


ORIGINAL ARTICLE

Taxonomic revision and dissolution of the genus *Monachoides* (Gastropoda, Stylommatophora)

Tereza Adamcová¹  | Lucie Juříčková¹  | Małgorzata Proćków²  |
Eike Neubert^{3,4}  | Adam Petrussek⁵  | Ondřej Korábek¹ 

¹Department of Zoology, Faculty of Science, Charles University, Praha 2, Czechia

²Museum of Natural History, University of Wrocław, Wrocław, Poland

³Naturhistorisches Museum Bern, Bern, Switzerland

⁴Institute of Ecology and Evolution, University of Bern, Bern, Switzerland

⁵Department of Ecology, Faculty of Science, Charles University, Praha 2, Czechia

Correspondence

Tereza Adamcová, Department of Zoology, Faculty of Science, Charles University, Viničná 7, Praha 2 12800, Czechia.

Email: terez.kosova@gmail.com

Funding information

Grantová Agentura, Univerzita Karlova, Grant/Award Number: 244120

Abstract

Monachoides is a genus of medium-sized European land snails in the family Hygromiidae. Systematics of this family was until recently based on traits of the genital system that were shown to be uninformative, resulting in revisions of classifications at the genus and family levels. Up to six species were recognized in *Monachoides* lately, but the inclusion of three of these species was questionable. Our phylogenetic analysis and morphological examinations show that the genus includes species previously classified in two different Hygromiidae subfamilies. After transferring three Balkan species to the unrelated genus *Xerocampylaea*, *Monachoides* emerged as a group that diversified relatively northerly, at the boundary between the Balkans and Central Europe. One species, *Monachoides bacescui*, is synonymized here and a previously overlooked one is redescribed, leaving only three valid species in *Monachoides* as currently understood: *M. incarnatus*, *M. vicinus* and *M. welebitanus*. These can be distinguished from other hygromiid species by their distinctive microsculpture of the shell surface, which also allows for identification of juveniles or fragmented fossil material. However, the clade comprising the three above species was found to also include the two species currently classified in *Perforatella*. As a result, the two genera are synonymized, with *Perforatella* having priority.

KEYWORDS

Balkans, Hygromiidae, land snail, *Perforatella*, phylogeny, *Xerocampylaea*

1 | INTRODUCTION

Even in Europe, where the study of land snail diversity has a three-century-long tradition, their species diversity remains insufficiently known in many cases, and the phylogenetic relationships among species as well as the higher level taxonomy are only slowly being clarified

with molecular phylogenetic studies. Such issues also affect seemingly familiar taxa, as was the case of splitting *Helix pomatia* Linnaeus, 1758, a broadly distributed, very abundant and widely known land snail, into two species (Korábek et al., 2016). Similarly, the common and conspicuous *Fruticicola fruticum* (Müller, 1774) was recently split into three species (Hofman et al., 2022). Here, we

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studied the systematics of the genus *Monachoides* Gude & Woodward, 1921, whose type species is not as well known to the public as *H. pomatia*, but is equally widely distributed and highly abundant in Central Europe.

Monachoides belongs to Hygromiidae Tryon, 1866, a diverse and genus-rich family of land snails, widely distributed across the Palearctic region, and even reaching sub-Saharan Africa (Neiber et al., 2017). The systematics of Hygromiidae from the division into subfamilies down to the assignment of species to genera relied for a long time on the structure of the reproductive system (Forcart, 1946; Hesse, 1921, 1931; Nordsieck, 1987, 1993; Schileyko, 1970, 1972a, 1972b, 1978, 1991, 2006; von Ihering, 1892; Wagner, 1915; Watson, 1919). The number and arrangement of dart sacs were among the most important characters; a single sac with a developed dart was one of the defining characters for the group into which *Monachoides incarnatus* (Müller, 1774) was classified. However, the morphology-based classifications were always controversial, and in many cases were eventually overturned by molecular phylogenetic analyses (Neiber et al., 2017; Razkin et al., 2015). Several characters traditionally used for systematics, including the number of dart sacs, were found to have evolved several times independently (Neiber et al., 2018; Neiber & Hausdorf, 2017).

The results of molecular phylogenetic studies led to a re-definition of the family and its subfamilies (Neiber et al., 2017), a new classification into tribes (Neiber et al., 2017), and revisions of the generic placement of many species (e.g., Neiber, 2019; Pročków et al., 2019) including the description of new genera (Caro et al., 2019; Kneubühler et al., 2022; Neiber et al., 2017). Finally, molecular phylogenetic and genetic studies also prompted revisions of the species-level taxonomy of several hygromiid genera (e.g., Bamberger et al., 2020; Duda et al., 2011; Pieńkowska et al., 2022; Pročków et al., 2013, 2019).

The genus *Monachoides* (tribe Perforatellini Neiber, Razkin & Hausdorf, 2017; Figure 1) is among the genera that have not been re-examined with the help of molecular phylogenetics yet. The name was introduced in 1921, with *M. incarnatus* as its type species (Gude & Woodward, 1921a, 1921b), originally as a subgenus of a broadly (and incorrectly) interpreted genus *Fruticicola* Held, 1838. *Monachoides incarnatus* has a long history of changing (sub)generic placements: from the description in *Helix* Linnaeus, 1758 in the early years of land snail taxonomy through placements in *Monacha* Fitzinger, 1833, *Bradybaena* Beck, 1837, *Fruticicola* Held 1838, *Theba* Risso, 1826, or *Hygromia* Risso, 1826 (see Locard, 1882 for references) to more recent classifications in *Zenobiella* Gude & Woodward, 1921 (Likharev & Rammel'meyer, 1952; Lindholm, 1927) and *Perforatella* Schlüter, 1838 (Forcart, 1946; Hudec, 1963; Kerney

et al., 1983). This wide array of assignments to different genera was not only due to the uncertainty regarding natural relationships but also because of purely nomenclatural issues (Lindholm, 1927).

Hesse (1921) proposed a system of Hygromiidae that was based mainly on the anatomy of the reproductive system. He placed *M. incarnatus* in *Monacha* (not in the current sense of the genus), which was defined as follows: the right eye retractor muscle crosses the genitalia, a penis retractor muscle is always developed and a single dart sac is present (Hesse, 1921: 61). He distinguished two subgenera, *Monacha* and *Perforatella*. *Monacha* sensu Hesse (1921) comprised a range of species, some of which are currently classified in other genera (here in original combinations with current classification in parentheses): *Helix incarnata* Müller, 1774, *Helix vicina* Rossmässler, 1842, *Monacha fallax* Wagner, 1914 (*Monachoides*), *Helix fusca* Montagu, 1803 (*Zenobiellina* Holyoak & Holyoak, 2018), *Helix glabella* Draparnaud, 1801, *Helix umbrosa* Pfeiffer, 1828 (*Urticicola* Lindholm, 1927), *Helix inchoata* Morelet, 1845 (*Portugala* Gittenberger, 1980), *Helix rubiginosa* Rossmässler, 1838 (*Pseudotrachia* Schileyko, 1970), *Helix ruscadensis* Letourneux, 1870 (*Ganula* Gittenberger, 1970), *Helix (Trichia) transsilvanica* Westerlund, 1876 (*Lozekia* Hudec, 1970) and *Fruticicola (Monacha) veselyi* Frankenberger, 1919 (*Circassina* Hesse, 1921). *Perforatella* contains two species that are characterized by having two teeth on the apertural lip. Hesse of course did not develop the system from scratch but built on earlier anatomical research and classifications (Kobelt, 1904; von Ihering, 1892; Wagner, 1915; Westerlund, 1902), but his systematic studies were particularly influential. The confrontation of Hesse (1921) system based on genital anatomy with molecular phylogenetics nicely highlights the limitations of a morphological approach based on the investigation of a single organ system. The phylogenetic study of Neiber et al. (2017) places the 11 species listed above into six different tribes.

A sister group relationship of *Monachoides* and *Perforatella* is fully supported by molecular phylogenetics (Neiber et al., 2017). Forcart (1946) considered *Perforatella* (Figure 1a) and *Monachoides* (Figure 1b–i) congeneric, with the former name having priority and the latter being its subgenus (see, e.g., Kerney et al., 1983). However, from today's perspective, Forcart's concept of this genus was too wide, as two taxa he considered as belonging to *Monachoides* (*Perforatella (Monachoides) ventouxiana* Forcart, 1946, *Fruticicola (Trichia) memnonis* Sturany, 1904) are now placed in *Urticicola* and *Pseudotrachia*, respectively. Which species belong to *Monachoides* and which do not has never been the subject of a targeted discussion. Instead, species were moved from the *Perforatella* + *Monachoides* group on several occasions



FIGURE 1 Live animals of *Monachoides* (as currently interpreted) and its closest relative, *Perforatella*. (a) *Perforatella dibothrion* (SK: Prešov Region, Renčišov). (b) *Monachoides vicinus* (SK: Košice Region, Vihorlat Mts). (c) *Monachoides vicinus* (CZ: Pardubice Region, nature reserve Rohová near Moravská Třebová). (d) *Monachoides* sp. (HR: Primorje-Gorski Kotar County, Vrbovsko). (e) *Monachoides* sp. (HR: Lika-Senj County, Švica). (f) *Monachoides incarnatus* (HR: Primorje-Gorski Kotar County, Vrbovsko). (g) *Monachoides incarnatus* (CZ: Moravian-Silesian Region, Staré Hamry). (h) *Monachoides incarnatus* (HR: Zagreb, Podsused; within-population colour variability). (i) *Monachoides taraensis* (NMP P6M 30,775; ME: Pljevlja, Donja Dobrilovina). (a–g): photo R. Coufal. NMP: Národní muzeum (National Museum), Prague, Czechia.

(Hudec, 1970: *H. transsilvanica* to *Lozekia*; Schileyko, 1970: *H. rubiginosa* to *Pseudotrichia*; Gittenberger, 1980: *H. inchoata* to *Portugala*; Nordsieck, 1993: *M. fallax*, *H. glabella* and *P. ventouxiana* to *Urticola*, *F. memnonis* to *Pseudotrichia*, *Helix stuxbergi* Westerlund, 1876 and *Zenobiella aculeata* Uvalieva, 1964 to *Stygius* Schileyko, 1970). Schileyko (1970) quite correctly identified the closest relatives of the sister genera *Monachoides* and *Perforatella*, as later shown by molecular phylogenetic investigations (Neiber et al., 2017). However, while he listed *M. incarnatus* and *M. vicinus* as representatives of *Monachoides*, he did not try to resolve which other species belonged to that genus. Later, Schileyko (1978) listed in *Monachoides* species now placed in *Leptaxis* Lowe, 1852 and indicated a geographic range of the genus that also included Northern Africa (information repeated also in Welter-Schultes, 2012).

At present, six species are considered members of *Monachoides* (MolluscaBase, 2023a; Welter-Schultes, 2012). *Monachoides incarnatus* (Central Europe,

Balkans; Figure 1f–h) and *M. vicinus* (Eastern and Central Europe, Carpathians; Figure 1b,c) form the undoubted core of the genus. Clearly close to *M. incarnatus* is also *Monachoides bacescui* Grossu, 1979, described from western Romania. Besides these, there are three mutually similar species from the western Balkans (former Yugoslavia) whose genus-level placement is more problematic. *Monachoides fallax* is the most widely distributed of them (reported from Bosnia to North Macedonia, but the range is uncertain; Dhora & Welter-Schultes, 1996; Fehér & Eröss, 2009; Welter-Schultes, 2012), while the others have small ranges in the surroundings of their respective type localities: *Monachoides taraensis* de Winter & Maassen, 1992 is known from a part of the Tara river valley in Montenegro (Figure 1i), *Monachoides kosovoensis* de Winter & Maassen, 1992 was described from the eastern side of the Čakor Pass on the border of Montenegro and Kosovo. As already mentioned, Nordsieck (1993) proposed to transfer *M. fallax* to *Urticola*, and de Winter & Maassen (1992) admitted that the placement of their two

new species in *Monachoides* is provisional and is actually questioned by the presence of a small accessory sac in *M. kosovoensis*. De Winter and Maassen (1992) also noted a great conchological similarity of *M. taraensis* and *M. kosovoensis* to taxa that were recently shown to belong to the genus *Xerocampylaea* Kobelt, 1871 in the tribe Urticicolini Neiber, Razkin & Hausdorf, 2017 (*Semifruticicola serbica* Wagner, 1914 and *Helix erjavecii* Brusina, 1870; Neiber et al., 2017; Pročków et al., 2019) as well as to the type species of that genus, *Xerocampylaea zelebori* (Pfeiffer, 1853).

On the intraspecific level, two subspecies of *M. incarnatus*, aside from the nominotypical subspecies, were considered valid in recent decades (Falkner, 1990; MolluscaBase, 2023b; Štamol, 2010). One is currently called *Monachoides incarnatus armatus* (Stabile, 1859) and was described from near Lugano on the Swiss-Italian frontier and is characterized by a tooth on the lower apertural lip. The second subspecies is *Monachoides incarnatus welebitanus* (Pfeiffer, 1847) for which no type locality was indicated, and the original description mentions only a more solid [than typical *M. incarnatus*] and opaque shell with a straight lower apertural margin. Falkner (1990) newly characterized the taxon, stating among others that the surface microstructure of the shell is about twice as fine and dense as in *M. incarnatus* samples from north of the Alps. This subspecies should be distributed in the northwestern part of former Yugoslavia (*welebitanus* refers to the Velebit Mountains in western Croatia). Its status needs reassessment, also because of a passing note of Nordsieck (2017: inside of the back cover) on the syntopic presence of *M. incarnatus* and an unidentified, possibly undescribed *Monachoides* species (Figure 1d,e) in the Velebit Mountains.

We revise here the delimitation of the genus *Monachoides* and the species-level taxonomy of the taxa belonging to the genus, that is, *M. incarnatus* and its closest relatives as revealed by molecular phylogenetic analyses. While the current delimitation of *Monachoides* based on the presence of a single dart sac is rejected, we show that morphological characters, which were previously given less weight, support the new genus-level taxonomy or are informative for species identification.

2 | MATERIALS AND METHODS

2.1 | Note on sampling

We include here samples of five of the six species presently classified in *Monachoides*. We failed to obtain a sample of *M. kosovoensis*, although we included an unidentified juvenile collected near its type locality. *Monachoides fallax*

is represented here only by samples from the type locality (Mt. Trebević near Sarajevo). On the intraspecific level, we did not sample marginal, postglacially colonized areas; we focused on the areas potentially relevant for the diversification of the genus. However, samples from the Romanian parts of the Carpathian Arc are largely missing due to logistic reasons.

The original data were supplemented by sequences from Neiber et al. (2017), who laid the foundations of the modern, phylogeny-based classification of Hygromiidae, and from Pročków et al. (2019), who focused on *Xerocampylaea*. We included all representatives of the tribes Perforatellini and Urticicolini with available sequences, which allowed for testing the hypothesis that *M. fallax*, *M. taraensis* (and by extension also *M. kosovoensis*) actually belong to the latter clade, as would hold if they are related to *Xerocampylaea*.

2.2 | Laboratory procedures

Total DNA was extracted using a spin column-based extraction kit for animal tissues (Tissue Genomic DNA Mini Kit, Geneaid) from ethanol-preserved pieces of the foot. Three loci were targeted: two partial mitochondrial genes (cytochrome c oxidase subunit I and 16S rRNA; *cox1* and *rrnL* hereafter) and the nuclear internal transcribed spacer 2 (ITS2) with the flanking parts of the genes for 28S and 5.8S rRNA (hereafter 28S and 5.8S respectively). The nuclear marker was only sequenced for selected samples representing the major mitochondrial lineages.

The primer pairs LCO1490+HCO2198 (producing 655bp long amplicon; Folmer et al., 1994) and 16Scs1+16Scs2 (~850–860bp; Chiba, 1999) were used for the amplification of *cox1* and *rrnL* respectively. In a few samples where amplification of the *rrnL* fragment failed, we assembled it from two overlapping fragments using the primer pairs 16Sar+16Scs2 (Palumbi et al., 1991) and 16Scs1+16S_MN3R (Neiber et al., 2017). For ITS2, we used the primer pair LSU1+LSU3 (Wade & Mordan, 2000) for both PCR and sequencing. ITS2 is present in the genome in multiple copies that may differ in length (Nekola et al., 2023), preventing simple sequencing of the PCR product. We initially attempted to use internal primers (Neiber et al., 2017) to assemble the sequences from multiple reads positioned between the indels, but this turned out impractical in most cases due to the presence of more than one variant. We, therefore, performed the PCR and sequencing for multiple specimens per clade and kept those, for which the product could be sequenced in whole using the LSU1 and LSU3 primers or with the 1–2 internal primers in addition (MN2-F, MN3-F, MN2-R, MN4-R; Neiber et al., 2017).

PCR was mostly done with Platinum II Taq Hot-Start DNA Polymerase (Thermo Scientific) following the manufacturer's recommendations except for annealing temperature (50°C) and addition of 1.5 mM MgCl₂. PCR products were purified with ExoSAP-IT™ (Thermo Scientific) and Sanger sequencing was performed in both directions by capillary electrophoresis (at Faculty of Science, Charles University, Prague or MacroGen Europe, Amsterdam).

All sequences were deposited in GenBank, and accession numbers are listed in Appendix S1. Most of the mitochondrial data from *M. incarnatus* were already reported in Korábek et al. (2023).

2.3 | Phylogenetic analyses

The sequences were aligned with MAFFT 7.520 (Katoh & Standley, 2013; --genafpair) and the mitochondrial sequences were concatenated. Mitochondrial and nuclear data were analysed separately. We used IQ-TREE 2.2.0 (Nguyen et al., 2015) for substitution model selection (Kalyaanamoorthy et al., 2017) and maximum likelihood phylogenetic analyses, and MrBayes 3.2.7a (Ronquist et al., 2012) for Bayesian phylogenetic analyses.

For model and partitioning scheme selection, the *cox1* was split into three partitions by codon position; *rrnL* and ITS2 were treated as a single partition each. The best scheme selected was GTR + F + I + G4 (*rrnL*; in IQ-TREE notation), TIM2 + F + I + G4 (*cox1* 1st), K3Pu + F + I + G4 (*cox1* 2nd) and K3Pu + F + G4 (*cox1* 3rd) for the mtDNA alignment and TIM3 + F + G4 for ITS2. GTR model was specified for all partitions for analyses in MrBayes. Branch support was assessed with 500 bootstrap replicates with IQ-TREE. Analyses in MrBayes were performed in two replicates, each of six heated chains for 25.5 million generations (i.e., until the average standard deviation of split frequencies dropped below 0.01), sampling each 10,000th; the first 25% of the runs were discarded as burn-in.

Average p-distances between species and major intraspecific lineages, and maximum p-distances within them, were calculated for *cox1* with MEGA 11 (Tamura et al., 2021).

2.4 | Morphological and anatomical observations

2.4.1 | General conchological characteristics

We examined the general shape of the shells, the umbilicus, colouration and the surface sculpture. Whorl count follows the method favoured by Ehrmann (1933). Shell

diameter and height in selected individuals were measured, as shown in Kerney et al. (1983), to assess size ranges of studied taxa.

2.4.2 | Surface microsculpture

We photographed the surface microsculpture of 118 individuals of *Monachoides*, *Xerocampylaea* and several other genera of the family Hygromiidae (Appendix S1) with a light microscope and a scanning electron microscope (SEM). *Monachoides* individuals were selected to represent all major intraspecific mitochondrial lineages.

The shell surface was studied primarily on the upper shell surface of adult shells, on the last three-quarters of the body whorl, but a few juveniles were also used. We also examined the structure of the shell in cross-section by studying the fracture surfaces of the mechanically broken wall of the last whorl and measured the thickness of the periostracum, the height of the periostracal scales and the scale density. This also allowed studying the periostracal (organic) versus ostracal (mineral) origin of the structure. The shell fragments were attached using double-sided adhesive carbon or copper tape on metal supports, dried in a desiccator and gold-plated. Scanning electron micrographs were taken with a SEM JEOL 6380VL device. We also photographed the surface structures under a stereomicroscope, as that is how they are typically examined during species identification.

The density of the tubercles/scales was counted from photos within a 200 × 200 μm square. A feature was counted if more than half of it was within the delimited area.

2.4.3 | Genital system morphology

Dissections of ethanol-preserved bodies were performed in search of characters that would allow for distinguishing *M. incarnatus* from the Croatian clade of *Monachoides* revealed here (see Results). A total of 21 *M. incarnatus* individuals representing five major mitochondrial clades (from Czechia, Croatia, Italy, Bosnia and Herzegovina and France; Appendix S1), 10 individuals belonging to the Croatian clade and four *M. vicinus* individuals were dissected.

Love darts of 22 specimens of *M. incarnatus*, 11 specimens belonging to the Croatian clade and six *M. vicinus* specimens were examined. Dart sacs were carefully cut out of the reproductive system and, following Koene and Schulenburg (2005), placed overnight in 1-M NaOH, which dissolved all the tissue and mucus but left the love dart intact. We would like to highlight, however, that the darts were very fragile after overnight incubation and it

seems better to extract the dart from the tissue remnants immediately when it becomes visible in the dissolving dart sac. The love darts were prepared for scanning electron microscopy in the same way as the shell fragments.

3 | RESULTS

3.1 | Phylogeny

The mitochondrial phylogeny (Figure 2) divides the presently accepted *Monachoides* species into two groups. *Monachoides incarnatus*, *M. vicinus* and *M. bacescui* are embedded within the Perforatellini (“Perforatellini *Monachoides*” hereafter). These are split into three clades, of which only two correspond to accepted species (*M. incarnatus* and *M. vicinus*). *Monachoides bacescui* is found to be nested within *M. incarnatus*, specifically within its shallowly differentiated, widely distributed clade ranging from the southern Balkans to Poland in the north and France in the west. Besides these two species, there is a third clade comprising some of the samples from north-western Croatia (“Croatian clade” hereafter). Specimens of this clade occur sympatrically and even syntopically with *M. incarnatus* and represent a morphologically distinct form. The division into these three clades is supported also by the ITS2 phylogeny (Figure 3), which shows three *Monachoides* lineages matching the three mitochondrial clades.

The sample from the type locality of *M. fallax*, collected on the top of the Trebević Mountain in Bosnia, groups alongside *M. taraensis* with *Xerocampylaea* and *Semifruticicola* in the Urticicolini clade (“Urticicolini *Monachoides*” hereafter). That is the case also for the juvenile hygromiid collected near the type locality of *M. kosovoensis*. The sequence of the latter sample is close to that of a specimen collected almost precisely at the type locality of *M. kosovoensis*, identified as *Xerocampylaea erjavecii floerickae* in Neiber et al. (2017). In addition to the samples reported here, we analysed a number of samples of *Trochulus*- or *Monachoides*-like samples from within the possible range of *M. fallax* (Welter-Schultes, 2012), but these all also turned out to be close to *Xerocampylaea* (Pročków et al., unpublished data) and will be treated in detail elsewhere. We did not detect any lineage related to *M. incarnatus* in Bosnia, Serbia, Montenegro and Kosovo.

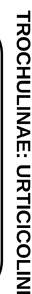
Our results show *Monachoides*, in the restricted sense comprising only the species related to *M. incarnatus* and placed in Perforatellini, as paraphyletic. Both species of *Perforatella* (*P. bidentata* and *P. dibothrion*) form a clade with *M. vicinus* in the mitochondrial phylogeny (Figure 2) and *P. bidentata* also in the ITS2 phylogeny (*P. dibothrion* ITS2 sequences could not be obtained; Figure 3).

3.2 | Morphology and anatomy

3.2.1 | Overall appearance

The three clades of the “Perforatellini *Monachoides*” group correspond to three morphotypes that can in most cases be distinguished by outer appearance (Figure 1). Two of them are *M. incarnatus* (Figure 1f–h) and *M. vicinus* (Figure 1b,c); the differences between these species were described in great detail by Pawłowska-Banasiak (2008). They often differ in the colouration: *M. vicinus* tends to be paler and yellowish, *M. incarnatus* is often somewhat darker and with a reddish shell. The colour of the foot of *M. incarnatus* varies from pink to dark grey. The mantle is usually densely covered by a fine network of dark grey, rarely red spots. The foot of *M. vicinus* is yellow to grey and the mantle usually has large, widely spaced black spots. The shell of *M. vicinus* typically has no umbilicus, unlike *M. incarnatus*, in which the umbilicus is developed. The shells of *Monachoides* have a thickened rim inside the aperture, which is visible from the outside where it forms a yellowish to ochre band; from the inside, it is typically white in *M. vicinus*, in *M. incarnatus* also reddish. There is often an inconspicuous elongate tooth-like protuberance on the lower apertural margin in *M. vicinus*, but this may also be present in *M. incarnatus*. None of these differences is, however, entirely reliable by itself due to inter-individual and geographic variation. *Monachoides vicinus* may have brown shells, slightly open umbilicus, and dark bodies as is more typical for *M. incarnatus*, black spots on the mantle may be reduced in both species, *M. incarnatus* may be yellowish, with nearly (but never completely) missing umbilicus and well-separated, compact spots on the mantle. Despite these overlaps, the two species can usually be distinguished in the area where they occur sympatrically.

FIGURE 2 Mitochondrial phylogeny of *Monachoides*. Maximum likelihood tree based on concatenated partial *rrnL* and *cox1* sequences. Support values represent SHaLRT, standard bootstrap (both from the ML analysis) and posterior probabilities from a Bayesian analysis respectively. The supports are shown for branches where SHaLRT >95 or bootstrap >70 or posterior probability >0.95. Species classified so far in *Monachoides* and samples collected at or near the type localities of *Monachoides kosovoensis* are highlighted in bold. Revised taxonomic names (see Systematics) are shown in bold on the right. The colours correspond to those in Figures 3 and 5. * data from Neiber et al. (2017), ** data from Pročków et al. (2019), *** data from Pfenninger et al. (2005).



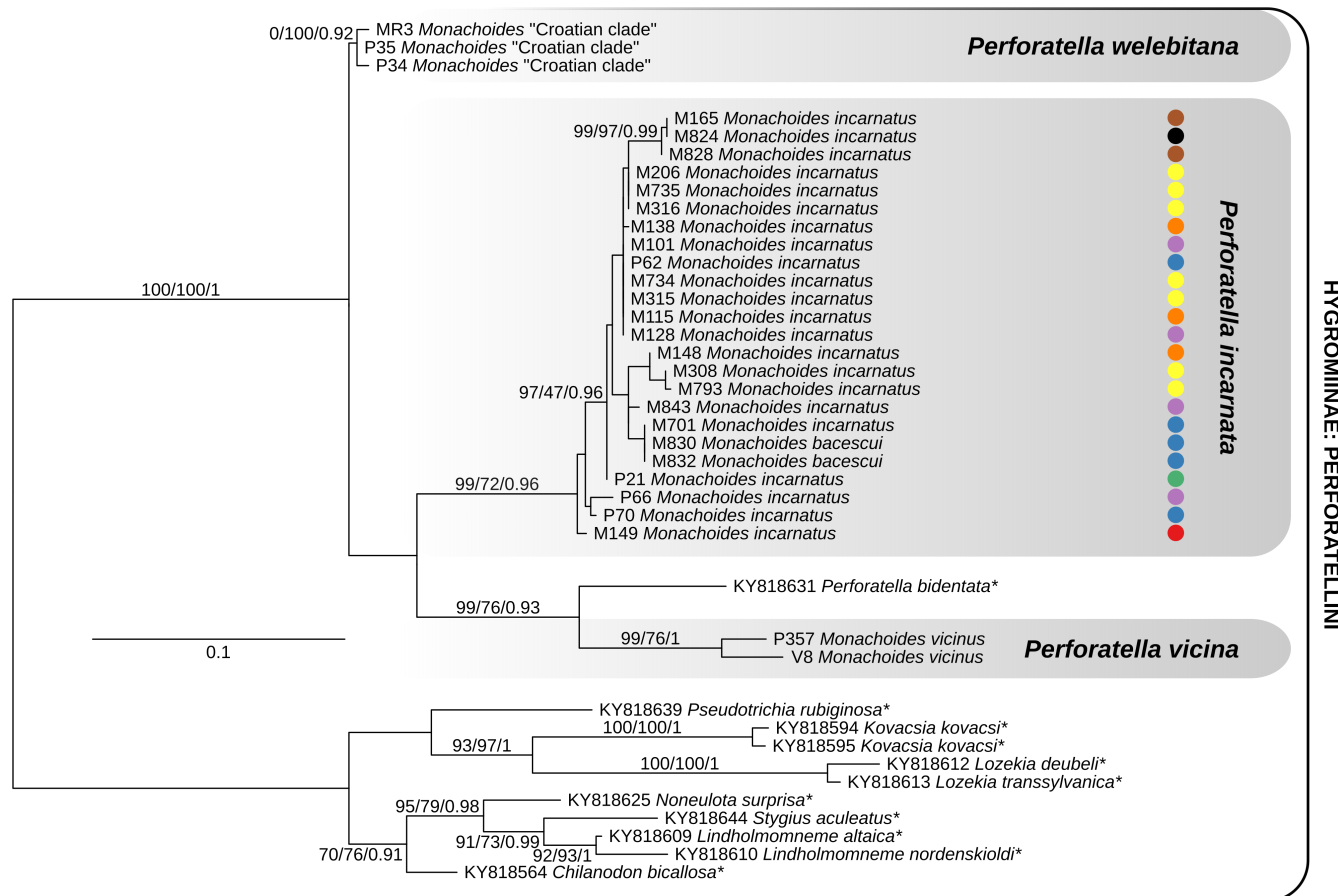


FIGURE 3 Nuclear phylogeny of *Monachoides* sp. (‘Perforatellini *Monachoides*’). Maximum likelihood tree based on the internal transcribed spacer 2 and the flanking parts of 5.8S rRNA and 28S rRNA genes. Support values represent SHaLRT, standard bootstrap (both from the ML analysis) and posterior probabilities from a Bayesian analysis respectively. The supports are shown for branches where SHaLRT >95 or bootstrap >70 or posterior probability >0.95. Coloured dots indicate intraspecific mitochondrial lineage of each analysed *M. incarnatus* individual. An asterisk indicates data from Neiber et al. (2017); *M. incarnatus* and *M. vicinus* sequences from that study were not used, as the former formed distinctively the longest branch within *M. incarnatus* and the latter branched off basally of a clade comprising our *M. vicinus* samples and *Perforatella bidentata*. Attempts to sequence *Perforatella dibothrion* failed. Revised taxonomic names (see Systematics) are shown in bold on the right.

The Croatian clade is also distinguishable by morphological traits. We examined the phenotypic differences particularly at three localities where specimens belonging to this clade occur syntopically with *M. incarnatus* in northwestern Croatia: Švica, Vrbovsko and Frketić Selo (Appendix S1). At these localities, the unidentified species was distinctly smaller than *M. incarnatus*, which largely holds for the species as a whole. Shells are flatter than those of *M. incarnatus*. The shell surface of the unidentified species is dull, the shell itself is yellowish or brown. The last whorl appears relatively broader than that of *M. incarnatus*, the lower part of the apertural margin is usually straighter and the apertural margins and the rim inside the aperture are white. The umbilicus is narrower than in *M. incarnatus* but present. The colouration of the body and mantle is similar to *M. vicinus*, but the spots on the mantle are smaller and denser; there is typically a larger, elongated, transverse dark spot close to the

aperture, which allows also for the identification of juveniles at the localities where this taxon occurs syntopically with *M. incarnatus*. We found no intermediate phenotypes at the syntopic sites.

The species grouping with *Xerocampylaea* (‘Urticolini *Monachoides*’) have an appearance different from *Monachoides* (Perforatellini group). Their shells are more opaque, they have a much wider umbilicus, and in *M. taraensis* there is a conspicuous white band on the periphery (Figure 1i). There is also no pattern formed by dark spots on the mantle visible through the shell wall in *M. taraensis* and *M. fallax*.

3.2.2 | Shell surface microsculpture

The three species of the ‘Perforatellini *Monachoides*’ group are well distinguished from each other by the

microsculpture of the shell surface. Their shells are covered with diamond-shaped to oval ostracal tubercles, whose density differs among species (least dense in *M. vicinus*, the most dense in the Croatian clade). On top of these, there are arched, slightly curved periostracal scales (Figure 4a–e); between the scales of some individuals, there are fine but distinctive transverse ridges (Appendix S4: Figure 5c,g,k). In *Monachoides vicinus*, the

scales are typically completely lost on adult shells but can be found well developed on juvenile shells. While in the other two species, the scales are typically lost when the whole periostracum peels off, in *M. vicinus* the periostracum appears to consist of two layers: a thin surface layer with the scales that peels off and a more persistent basal layer that remains on the shell even if there are no scales present anymore.

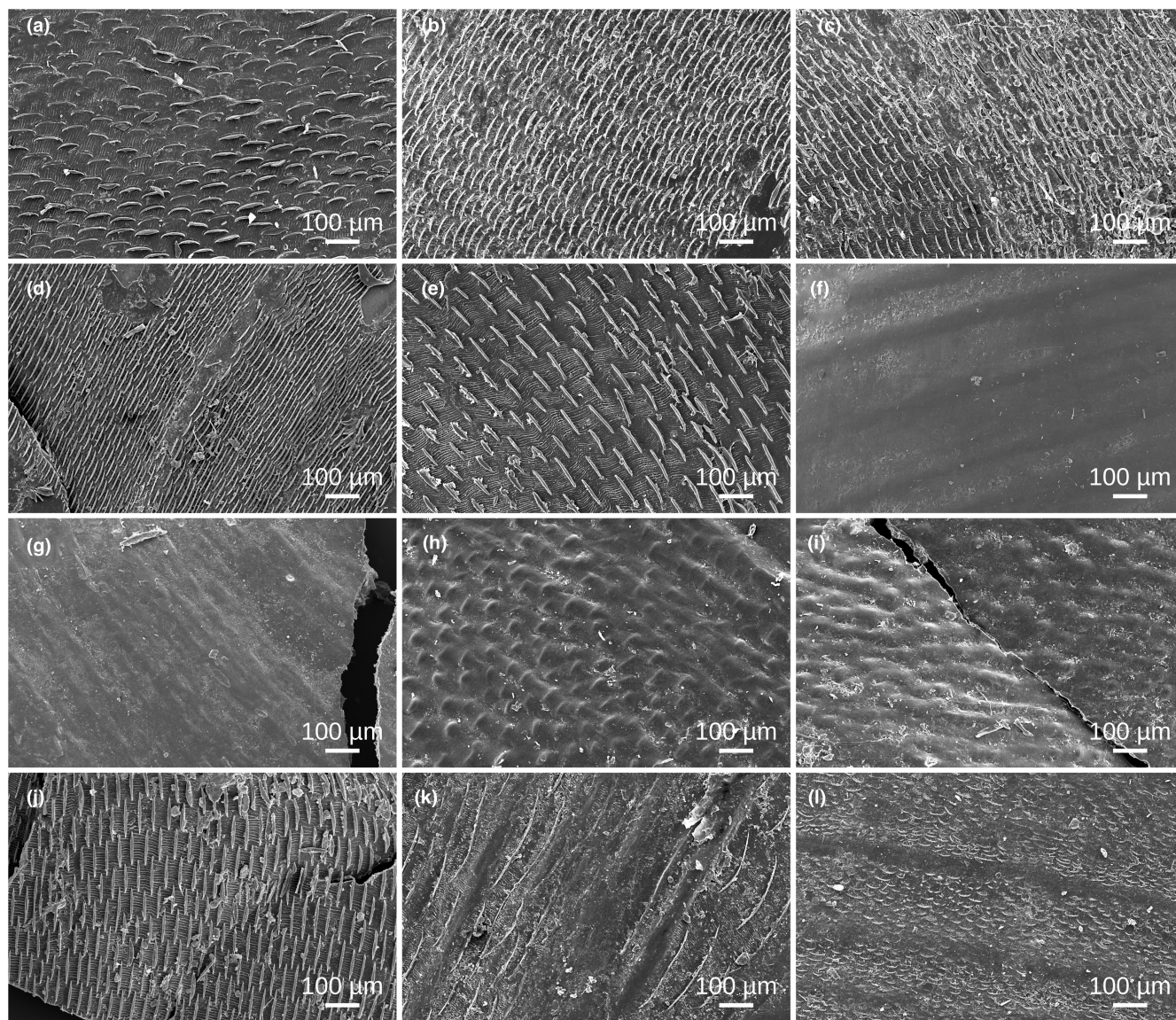


FIGURE 4 Comparison of shell surface structures of the species classified so far in *Monachoides* with *Xerocampylaea* and other selected Hygromiidae. Revised nomenclature is used. (a) *Perforatella incarnata* (NMP P6M 30,536; CZ: Praha, Sedlec). (b) *Perforatella incarnata*, topotype of *Monachoides bacescui* (NMP P6M 30,862; RO: Caraș-Severin County, Sasca Montană). (c) *Perforatella incarnata*, “*Monachoides incarnatus armatus*” morphotype (NMP P6M 30,860; IT: Piemonte, Biella, Santuario di Oropa). (d) *Perforatella welebitana* (NMP P6M 30,585; HR: Primorje-Gorski Kotar County: Vela Učka). (e) *Perforatella vicina* (NMP P6M 043229; SK: Košice Region, Brzotín); subadult individual, the scaly periostracal structure is missing in most adults. (f) *Xerocampylaea zelevori* (NMP P6M 30,925; RO: Caraș-Severin County, Sasca Montană). (g) *Xerocampylaea taraensis* (NMP P6M 30,775; ME: Pljevlja, Gornja Dobrilovina, canyon of Tara). (h) *Xerocampylaea* sp. from near the type locality of *M. kosovoensis* (XK: Peć Municipality, Bogë northwest of Pejë). (i) *Xerocampylaea fallax* (NMP P6M 30,756; BA: Sarajevo, top of Mt. Trebević). (j) *Lozekia deubeli* (juvenile, BG: Pazardzhik Province, Yundola east of Pazardzhik). (k) *Hiltrudia mathildae* (HR: Split-Dalmatia County, island Brač, Sumartin). (l) *Elbasania* cf. *occidentalis* (AL: Tirana County, Pëllumbas, cave). NMP: Národní muzeum (National Museum), Prague, Czechia.

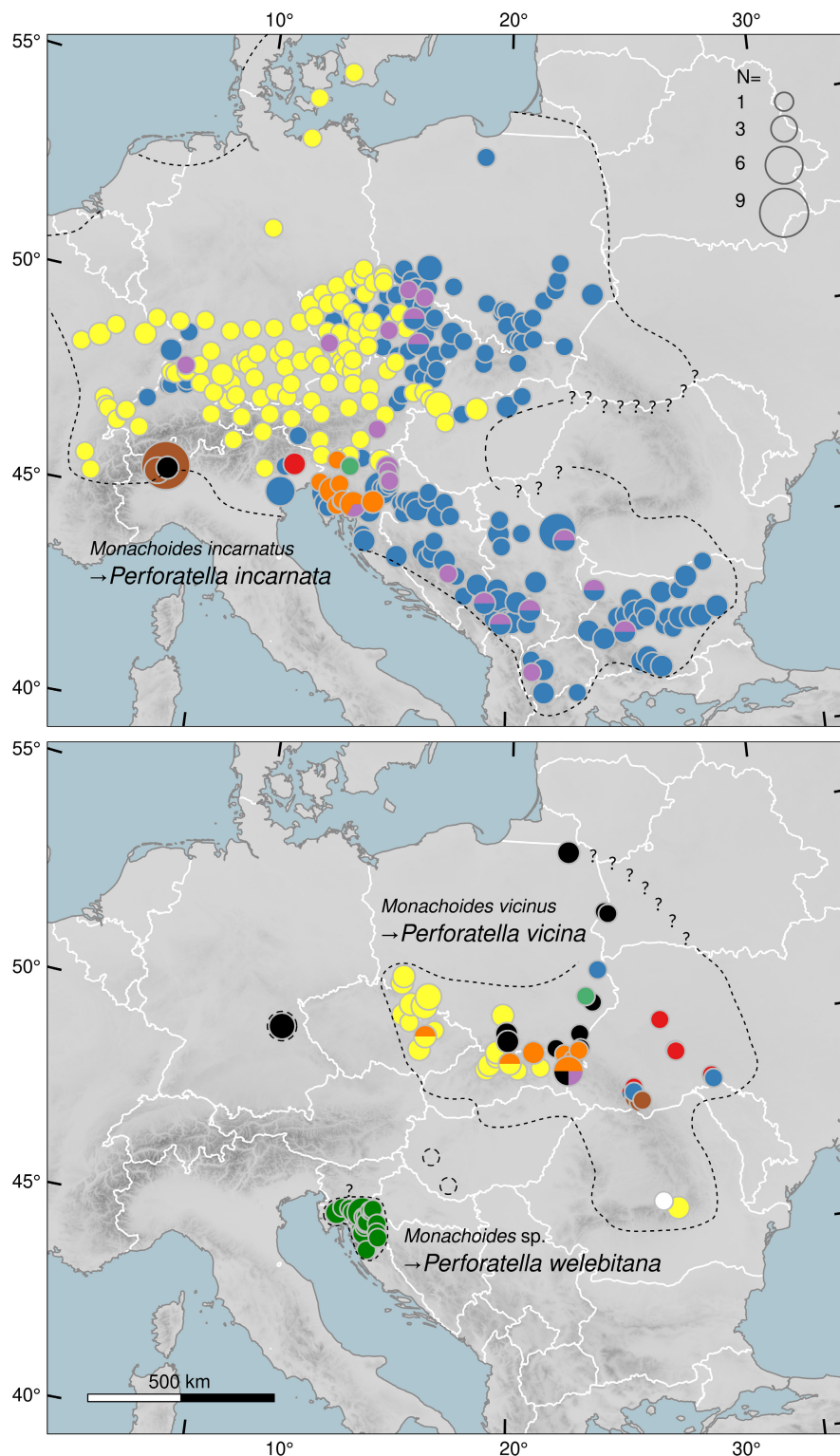


FIGURE 5 Approximate distributions of *Perforatella incarnata* (top), *Perforatella vicina* and *P. welebitana* (bottom), location of the sampling sites and the distribution of mitochondrial lineages. Revised nomenclature is used. Size of the dots reflects the number of individuals analysed; colours correspond to those in Figure 2. Eastern range limits of *P. incarnata* and *Perforatella vicina* are poorly documented. We did not check the reported occurrence of *P. vicina* in the south of Hungary. The range of *P. welebitana* likely extends into Slovenia.

While the density of the surface scales and tubercles usually allows for easy species identification, two things need to be noted. First, some of the western-most *M. incarnatus* samples from Italy had a relatively high density of sculptural elements, reaching that of some individuals of the unidentified species from Croatia. Second, the density seems to reflect the growth rate of the shell (scales are arranged in rows parallel to the direction of growth) and is thus slightly uneven.

Examination of the thickness of the periostracum, height of the periostracal scales and the surface of the protoconch did not reveal any interspecific differences.

The shell surface sculpture is different in the three species of the “Urticolini *Monachoides*” group, which lack the periostracal scales altogether. It is quite smooth in *M. taraensis*, with only weakly developed tubercles parallel to the growth lines (Figure 4g). In *M. fallax*, the shell is covered by rounded tubercles (Figure 4i). According to

de Winter & Maassen (1992), the surface of *M. kosovoensis* consists of irregularly placed and shaped nodules and ridges (as in Figure 4h,i).

3.2.3 | Genital system morphology

The genital system of *M. vicinus* has been repeatedly described in the literature (Grossu, 1983; Pawłowska-Banasiak, 2008; Schileyko, 1978; Schmidt, 1854) and the last author concluded that no character can reliably discriminate *M. vicinus* from *M. incarnatus*, although the flagellum is usually slightly shorter than the epiphallus in *M. incarnatus* and longer in *M. vicinus*.

We focused on finding differences in the anatomy of the genital system useful for discriminating between *M. incarnatus* and the Croatian clade. Most characters are variable (Appendix S2: Figure S1), but individuals of the Croatian clade tend to have much shorter penis than *M. incarnatus* (relative to female parts as well as epiphallus). The flagellum is shorter than in both *M. vicinus* and *M. incarnatus* (relative to penis+epiphallus; Appendix S4: Figure S5). The bursa copulatrix has a bulge on the sac (missing in some individuals), which appears to be positioned more or less apically in both *M. incarnatus* and *M. vicinus* (where it can be very prominent) and more laterally in the Croatian clade. More individuals with undamaged bursa should be examined, however, to confirm this. In contrast to the soft parts of the reproductive system, the shape of the love dart is very different between the two species. *M. incarnatus* has a spirally twisted, curved love dart (Appendix S3: Figure S2a–c; Appendix S4: Figure S6a). The love dart of the Croatian clade is straighter and not twisted (Appendix S3: Figure S2d–f; Appendix S4: Figure S6b). *Monachoides vicinus* has a love dart similar to the Croatian clade (Appendix S3: Figure S2g–i; Appendix S4: Figure S6c).

The tip of the dart bears two main and several less developed blades in *M. incarnatus*, *M. vicinus* and the Croatian clade, while in *M. kosovoensis* (drawing by de Winter & Maassen, 1992) and *M. fallax*, the dart is a simple spike that is circular in cross-section and has no blades, similar to the dart of *Xerocampylaea erjavecii* (Wagner, 1915). We failed to retrieve the dart of *M. taraensis*.

3.3 | Distribution and intraspecific diversity

Monachoides incarnatus is the most broadly distributed species assigned to this genus (Figure 5), occurring from

Bulgaria and Greece in the south across the Balkans and Central Europe to southern Scandinavia (Kerney et al., 1983; Welter-Schultes, 2012; Wiktor, 2004) in the north. The western limits of its range are reached in France (Kerney et al., 1983; Welter-Schultes et al., 2011) and northern Italy (Cossignani & Cossignani, 1995); the eastern limits are relatively poorly known. It occurs up to western Ukraine (Balashov, 2016) and Moldova (Balashov et al., 2013), but in Romania it lives only in the south and southwest of the country (Gheoca et al., 2024; Grossu, 1983; Poliński, 1924; Soós, 1943). There is a substantial intraspecific diversity of relatively deeply divergent mitochondrial lineages in *M. incarnatus* (Figure 2; intraspecific p-distance in the *cox1* fragment reaching 16%). The distribution of these lineages (Figure 5) has been detailed by Korábek et al. (2023), who inferred that the glacial refugia from which the present distributions derived were located mainly in northern Croatia and Slovenia. However, there was another refugium inferred in northwestern Italy ("*M. incarnatus armatus*").

Monachoides vicinus is a species with a primarily Carpathian distribution (Figure 5). Its range extends in a discontinuous manner to the Białowieża Forest and Masuria in Poland in the north (Cameron et al., 2010; Riedel, 1988), and to western Ukraine (Balashov & Gural-Sverlova, 2012) and Romania (Grossu, 1983) in the east. To the west, the range extends from the Carpathians to the Sudeten Mountains and along their northern edge (Wiktor, 2004). The species does not extend south of the Carpathians. Besides this more or less contiguous range, there are isolated populations in Bavaria, Germany (Häblein, 1960); additional isolated occurrences were reported from the southwest of Hungary (Pintér & Suara, 2004). Several earlier authors claim that this species also occurs in Croatia and Slovenia (Brusina, 1870; Clessin, 1879; Ehrmann, 1933; Erjavec, 1877; Hirc, 1881; Kormos, 1907; Poje & Rada, 1975) but these reports were likely due to misidentifications (Štamol, 2010). Among the sites listed by Brusina (1870), one is very close to our sampling site of the Croatian clade in Vrbovsko (Stubica) and at another one we sampled untypically coloured *M. incarnatus* with a nearly absent umbilicus (Podsused, Figure 1h).

Like in *M. incarnatus*, there are divergent intraspecific mitochondrial lineages within *M. vicinus* (p-distances in *cox1* exceeding 15%), but the sampling is insufficient to describe their distribution. Most crucially, we lacked samples from the Romanian Carpathians and, therefore, additional major lineages could have been missed. However, we were able to analyse samples from an isolated Bavarian population and found it to be very closely related to samples from Poland and Slovakia.

The Croatian clade was found only in Croatia (Figure 5). To the west, the occurrence of this species

extends to Vela Učka National Park, in the northeast we found it up to Karlovac, while the eastern-most record is close to Bihać. In the south, it was found in the Velebit Mts. southwest of Gospić. Its range lies completely within the range of *M. incarnatus*, but it is distributed southwest of the glacial refugia of *M. incarnatus* inferred by Korábek et al. (2023). Based on the material analysed so far, the Croatian clade has a very shallow intraspecific variation in the mitochondrial markers (p-distance in *cox1* under 2%).

Complete overview of the intraspecific (as well as interspecific) sequence variation of the studied *cox1* fragment is provided in Appendix S5.

3.4 | Validity of problematic taxa

Grossu (1979) distinguished *M. bacescui* largely based on characteristics of the genital system, but the only character that should differentiate it from *M. incarnatus* and is actually depicted in his comparative drawings are long mucous glands. Indeed, we collected two adult snails at its type locality and both had long mucous glands (Appendix S2: Figure S1e). The shell characters (size, colour, surface) were not unusual for *M. incarnatus* and the length of the mucous glands is variable in *M. incarnatus* (Appendix S2: Figure S1). Both the mitochondrial and ITS2 phylogenies place *M. bacescui* in *M. incarnatus*. We, thus, consider *M. bacescui* a synonym of the latter.

The probable syntype of *M. incarnatus armatus* (deposited in Museo cantonale di Storia naturale, Lugano) has the usual appearance of *M. incarnatus* and lacks the tooth on the lower apertural margin that should characterize the taxon. We did not analyse samples from the type locality of *M. incarnatus armatus* near Lugano, only from even more westerly locations in northern Italy; all eight fully developed adult shells had a tooth on the lip. The samples yielded two divergent, endemic mitochondrial lineages embedded within *M. incarnatus*. Shell and body colour are not unusual, but the surface microsculpture of the shell tends to be more dense than typical for *M. incarnatus* (Figure 4c). We do not recognize any subspecies here formally, but we acknowledge that the sampled populations from northwestern Italy exhibit some regionally specific characteristics. They have been probably geographically isolated at least since the last interglacial (Korábek et al., 2023).

The type material of *M. incarnatus welebitanus* was most probably destroyed with Pfeiffer's whole collection (Zilch, 1967) and the description (Pfeiffer, 1848) is useless for identification. Wohlberedt (1909) used the name, with doubt, for large and reddish individuals from Montenegro; generally, it was presumed to be a taxon from Velebit Mts.

or more broadly the western Balkans (von Möllendorff, 1873; Jaekel et al., 1957). Our *M. incarnatus* samples collected close to the Velebit were large but otherwise ordinary, and the molecular data show that these are closely related to central European *M. incarnatus* (Korábek et al., 2023). Falkner (1990) provided under the name *M. incarnatus welebitanus* a description that, apart from the larger size, fits the Croatian clade studied by us. We follow this interpretation and attribute the name to the Croatian clade by selecting a neotype for *Helix welebitana* Pfeiffer, 1847.

3.5 | Taxonomy and nomenclatural acts

ZooBank registration of the paper: urn:lsid:zoobank.org:pub:651B421D-474B-4A79-8AED-3E0632808144.

The following taxonomic changes are proposed based on our results:

- *Monachoides* Gude & Woodward, 1921 is synonymized with *Perforatella* Schlüter, 1838.
- *Monachoides bacescui* Grossu, 1979 is synonymized with *Helix incarnata* Müller, 1774 (as *Perforatella incarnata*).
- *Helix welebitana* Pfeiffer, 1847 is considered a valid species (as *Perforatella welebitana*)
- *Monacha fallax* Wagner, 1914 is transferred to *Xerocampylaea* Kobelt, 1871 (as *Xerocampylaea fallax*).
- *Monachoides taraensis* de Winter & Maassen, 1992 is transferred to *Xerocampylaea* Kobelt, 1871 (as *Xerocampylaea taraensis*).
- *Monachoides kosovoensis* de Winter & Maassen, 1992 is transferred to *Xerocampylaea* Kobelt, 1871 (as *Xerocampylaea kosovoensis*).

Detailed descriptions of the species of the “Perforatellini *Monachoides*” and information on types and synonymies are provided in Appendix S4.

We designate here a neotype for *Helix welebitana* Pfeiffer, 1847 to clarify its taxonomic status because the original description does not allow to identify the taxon (and in particular to distinguish it from *Perforatella incarnata*, which may occur syntopically), and also to fix the type locality of the taxon, which was originally not stated (Art. 75.3.1; ICZN, 1999). *Helix welebitana* is re-described (Art. 75.3.2) and the neotype figured (Art. 75.3.3) in Appendix S4 (Figure S8a). No type material of *Helix welebitana* Pfeiffer, 1847 could be found in major old collections (Appendix S4) and the author's collection is believed to have been destroyed (Zilch, 1967) (Art. 75.3.4). There are two species around the Velebit Mts. that the original description may refer to; by the neotype selection we have chosen the one that presumably

better fits to the characters given by the author of the description (see Appendix S4 for details) (Art. 75.3.5). The new type locality is close to the Velebit Mts., from where the Pfeiffer's material likely originated given the taxon name, the biological species to which the neotype belongs does occur in the Velebit, the neotype is not genetically different from the populations in Velebit, and the chosen type locality yielded a representative series of individuals (Art. 75.3.6). The selected individual was deposited in National Museum, Prague, Czechia under the number P6M 42979 (Art. 75.3.7).

4 | DISCUSSION

4.1 | Diversity and classification of *Monachoides*

Our phylogenetic analyses show that the genus *Monachoides* as recently recognized contained two groups of very distantly related species. On the one hand, there is the type species *M. incarnatus* and two related species, which together with the two species of *Perforatella* belong to the subfamily Hygromiinae, tribe Perforatellini. On the other hand, there are *M. fallax* and *M. taraensis*, which group with *Xerocampylaea* in Trochilinae, tribe Urticicolini. The placement of the latter group in *Monachoides* was uncertain already before our study. Nordsieck (1993) suggested transferring *M. fallax* to *Urticicola* (thus close to its actual position revealed by molecular phylogenetic analyses), and de Winter & Maassen (1992) were themselves not confident about the generic placement of the two species they described, *M. taraensis* and *M. kosovoensis*, and noted similarities to *Xerocampylaea*. Although we could not analyse samples unambiguously identified as *M. kosovoensis*, *Xerocampylaea* samples were found in the area of its type locality (which lies on the border between Kosovo and Montenegro on the east side of Čakor Pass) by us as well as by Neiber et al. (2017), and the similarities to *M. taraensis* and *M. fallax* leave little doubt that this species also belongs to *Xerocampylaea*. Its exclusion from *Monachoides* is supported also by the presence of a small accessory sac in the genital system (de Winter & Maassen, 1992).

The genus *Xerocampylaea* was, until the work of Neiber et al. (2017), considered a monotypic genus with a restricted range. Since then, *Xerocampylaea* emerged as a more diversified group widely distributed in the western Balkans and the southwest of the Pannonian Basin from Kosovo to Slovenia and Hungary (Pročków et al., 2019). It now includes taxa previously classified

in *Trochulus* Chemnitz, 1786 (Trochulinae: Trochulini Lindholm, 1927), and we here show that also taxa classified as *Monachoides* belong to this group (*X. fallax*, *X. taraensis* and *X. kosovoensis*). A more detailed study of *Xerocampylaea*, based on a broad sample of sequenced individuals, is in preparation.

We found three species in what remained of *Monachoides* after excluding the misclassified Balkan taxa. Of the three originally recognized, *Monachoides bacescui* is indistinguishable from *M. incarnatus* both morphologically and genetically, so we consider it a junior synonym of the latter. However, the number remains at three, as we confirmed the distinctness of another species from western Croatia, hitherto considered a subspecies or synonym of *M. incarnatus*. It is clearly differentiated in both mitochondrial and nuclear markers and can be reliably distinguished by its finer, more dense surface sculpture. Also, the overall appearance is different from the other two species. All three species appear to be reproductively isolated, as the range of *M. incarnatus* overlaps with the ranges of the other two, and frequently occurs with either of them syntopically. The Croatian clade is matched here with *M. welebitanus* (Pfeiffer, 1847) by designating a neotype for that taxon; this interpretation largely follows the description given by Falkner (1990).

However, as *M. vicinus* is shown here to be more closely related to both species of *Perforatella* than to the other two *Monachoides* species while sharing conchological characteristics with the latter, the two genera can no longer be treated as separate. *Perforatella* was characterized by shells with regular riblets but no periostracal structures and two large teeth on the lower apertural margin, traits which appear to be derived in light of our phylogenetic analyses. But apart from these differences, the two genera share similarities in the genital system, although these are not diagnostic: single dart sac without traces of an accessory sac (unlike *Lozekia*, *Kovacsia*, *Chilanodon*, *Lindholmomneme*; Schileyko, 1978; Fehér et al., 2009), and short, but not highly reduced flagellum. Furthermore, the shell morphology of *P. bidentata* and *P. dibothrion* is probably an ecological adaptation (a very similar morphology is seen in *Chilanodon bicallosa* (L. Pfeiffer, 1853)) and apparently derived, and as such taxonomically uninformative. Finally, the periostracal scales typical for *Monachoides* are present on the shells of *Perforatella* hatchlings (Kuźnik-Kowalska & Rokseła, 2009). We propose to reunite the two genera in *Perforatella* Schlüter, 1838 with five species: *Perforatella bidentata* (Gmelin, 1791), *Perforatella dibothrion* (Kimakowicz, 1884), *Perforatella vicina* (Rossmässler, 1842), *Perforatella incarnata* (Müller, 1774) and *Perforatella welebitana* (Pfeiffer, 1847).

4.2 | Biogeographic implications

We have previously shown that even though the range of *P. incarnata* includes also most of the non-Mediterranean Balkans, the diversification centre of the species is located more northerly, in Slovenia and Croatia (Korábek et al., 2023). *Perforatella vicina* is a primarily Carpathian species, not occurring south of the Carpathians. The newly defined *P. welebitana* lives north of 44.4° of latitude, and both *P. bidentata* and *P. dibothrion* are distributed exclusively north of the Balkans. The Balkan species previously included in *Monachoides* were transferred to the very distantly related genus *Xerocampylaea* (Trochulinae: Urticolini) here. *Perforatella*, thus, belongs to a group of several Hygromiidae genera that apparently diversified and persisted over the Quaternary glacial cycles north of the south European peninsulas in the Alps, Carpathians, and Central Europe. Other examples are *Petasina* Beck, 1847, *Plicutera* Schileyko, 1978, *Prostenomphalia* Baidashnikov, 1985 and *Trochulus* Chemnitz, 1786, after many species were excluded from the last-mentioned genus following molecular phylogenetic analyses (Neiber et al., 2017).

Snails with this type of distribution are interesting from the palaeoecological point of view, because they likely survived the glacial cycles rather northerly, yet are mostly still more dependent on woody flora and less tolerant to harsh climatic conditions than the typical land snail fauna of the cold stadials of Central Europe (Juříčková et al., 2014). These taxa could, therefore, be particularly informative about the location of the northern-most glacial refugia of the temperate invertebrate fauna in Europe, considering that the shells of land snails frequently leave a well-preserved and recognizable fossil record.

4.3 | Significance of the surface microsculpture

We found that the three “Perforatellini *Monachoides*” species are well distinguishable from each other based on the shell surface sculpture only. The periostracal structures differentiates them also from other hygromiids, even where similar structures can be found. Among Metafruticicolinae Schileyko, 1972, such structures were reported for *Hiltrudia kusmici* (Clessin, 1887), *Hiltrudia mathildae* (Westerlund, 1881), *Metafruticicola berytensis* (Pfeiffer, 1841), *Cyrnotheba corsica* (Shuttleworth, 1843) and *Elbasania occidentalis* (Subai, 1999). There are differences in the shape, length, density and regularity of the scales and in the transversal structures between them (Bank et al., 2013; Giusti & Manganelli, 1987; Maassen, 1995; Nordsieck, 1993). The transversal

structures may also be completely missing, as in *Hygromia limbata* (Draparnaud, 1805) (Hygromiini) (Giusti & Manganelli, 1987). However, periostracal scales very similar to those found in *Perforatella* are also developed in the genera *Kovacsia* Nordsieck, 1993 and *Lozekia* Hudec, 1970 (Perforatellini) (Fehér et al., 2009; Figure 4j), whose ranges overlap with those of “Perforatellini *Monachoides*”. They could be easily mistaken for juvenile *Monachoides*, as was initially the case for the individual in Figure 4j, which came from outside the previously known range of *Lozekia* (Fehér et al., 2009) and which we received as a presumed *Monachoides* sample.

Further studies are needed to confirm if the species of the “Perforatellini *Monachoides*” can be distinguished from all other hygromiids using the surface sculpture of the shell only. We found that the three “Perforatellini *Monachoides*” species differ from each other in the shell surface sculpture even after the periostracum is lost (Appendix S4: Figure S4d,h,l), which is important for species identification in the fossil record. The Quaternary fossil record of land snails is extensive, but medium-sized snails like *Perforatella* are typically found in the form of small shell fragments, which can often be identified only based on the surface structure (Ložek, 1964). It remains to be demonstrated that the surface sculpture of the “Perforatellini *Monachoides*” after periostracum loss is unique (e.g., with respect to *Lozekia* and *Kovacsia*). This is important because in the fossil record we cannot rely on present distributions when identifying the material.

The functional significance of periostracal surface sculptures in land snails remains virtually unexplored. There have been speculations on the function of periostracal hair in *Trochulus* (Trochulini) with regard to the water that can be held between the hairs (Pfenninger et al., 2005; Proćków et al., 2018; Shvydka et al., 2020). Such hairs occur in many unrelated lineages of land snails and was even reported from a Cretaceous caenogastropod land snail (Neubauer et al., 2019), suggesting some significant function, but there is no well-supported consensus on what advantage the hairs convey. Why species from different lineages have mutually similar sickle-like periostracal scales is then completely unclear. However, regardless of their possible functions, they can be a valuable character for taxonomy and for species identification from shell fragments.

5 | CONCLUSIONS

The land snail family Hygromiidae is an example where traditional morphology-based taxonomy was unable to uncover the true relationships among species, genera and family-group taxa. The earlier reliance on the genital

system morphology led to incorrect family- and genus-level systematics. A crucial defining character of *Monachoides* was thought to be a single dart sac, but our results show that this trait is shared by distantly related taxa in the family. Three species classified so far in *Monachoides* were found to belong to *Xerocampylaea*, a monophyletic clade that now contains species with one or two dart sacs (with or without accessory sacs). Conchological characters are also unreliable at the genus level. The remaining species of *Monachoides* share a typical microsculpture on the shell surface. However, as a group, they were found to be paraphyletic with respect to *Perforatella*, a genus comprising so far two species lacking the microsculpture and differing from *Monachoides* in having prominent teeth on the lower apertural margin. Based on the results of phylogenetic analyses, *Monachoides* is here synonymized with *Perforatella*, which is an older name.

The change in the taxonomic perspective is accompanied also by a change in the biogeographic perspective. As long as *Monachoides* included narrow-range endemics from the western Balkans, it was natural to expect that its diversity, both species-level and intraspecific, follows the pattern usual for mid- to large-sized land snails, for which the centre of diversity is located in the south of the taxon's range (e.g., Hofman et al., 2022; Korábek et al., 2022; Pinceel et al., 2005; Ramos-Gonzales et al., 2022; Welter-Schultes, 2012). We have shown previously that this is not true for the intraspecific diversity of *P. incarnata* (Korábek et al., 2023), and here we demonstrate the same for the whole genus. We did uncover an overlooked species, but not in the south of the distribution range of *Perforatella*. After our revision, *Perforatella* is a genus from southeastern Central Europe with five species. Being related to genera from the Carpathians and southern Siberia (Neiber et al., 2017), it is part of a group that diversified in relatively high latitudes and apparently never had any close relationship to the hotspot of land snail diversity in the Balkans.

ACKNOWLEDGEMENTS

We thank all of the many colleagues and friends who helped us with sampling or provided samples. We are also grateful to Dominika Mierzwa-Szymkowiak (Zoological Museum in Warsaw), Anita Eschner (Natural History Museum in Vienna), Christine Zorn (Museum of Natural History in Berlin), Tom Schiøtte (Natural History Museum of Denmark), Ronald Janssen and Sigrid Hof (Naturmuseum Senckenberg, Frankfurt am Main), Emmanuel Tardy (Natural History Museum of Geneva), Tom Hübner and Christian Göcke (Museum of Natural Gotha) and Melanya Stan ("Grigore Antipa" National Museum of Natural History, Bucharest) for providing photographs and information about museum specimens. Petr

Dolejš helped to obtain literature. We also thank Barna Páll-Gergely, Marco T. Neiber and Bernhard Hausdorf for advice and critical comments. Collecting permits were issued by Ministerstvo na okolnata sreda i vodite, Bulgaria (99-00-312/18.11.2019), Ministarstvo zaštite okoliša i energetike, Croatia (class UP/I-612-07/19-33/02 reg. no. 517-05-2-1-19-2; class UP/I-612-07/18-33/09 reg. no. 517-07-2-1-1-18-2; class UP/I-612-07/17-33/50 reg. no. 517-07-2-1-1-17-2) Ministère de la transition écologique, France (TREL2022990S/374, ABSCH-IRCC-FR-253278-1), Administrația Parcului Național Cheile Nerei – Beușnița (Nr. 1338 V.C. 29.10.2019). The authors acknowledge the Viničná Microscopy Core Facility (VMCF of the Faculty of Science, Charles University), an institution supported by the MEYS CR (LM2023050 Czech-BioImaging), for their support and assistance in this work. This study was funded by the Grant Agency of the Charles University (GAUK) project no. 244120. M.P. received financial support through the subsidy of the University of Wrocław. O.K. has been supported by Charles University Research Centre program No. UNCE/24/SCI/006. Open access publishing facilitated by Univerzita Karlova, as part of the Wiley - CzechELib agreement.

ORCID

Tereza Adamcová <https://orcid.org/0000-0003-4705-0737>

Lucie Juříčková <https://orcid.org/0000-0001-5163-1222>

Małgorzata Proćków <https://orcid.org/0000-0003-2240-7306>

Eike Neubert <https://orcid.org/0000-0002-0277-2894>

Adam Petrusek <https://orcid.org/0000-0001-5150-4370>

Ondřej Korábek <https://orcid.org/0000-0002-2522-9165>

REFERENCES

- Balashov, I. A., & Gural-Sverlova, N. (2012). An annotated checklist of the terrestrial molluscs of Ukraine. *Journal of Conchology*, 41, 91–109.
- Balashov, I. A. (2016). *Fauna Ukrainy. Tom 29, Mollyski. Vypusk 5, Stebel'chatoglazye (Stylommatophora)*. Kyiv, Naukova Dumka.
- Balashov, I. A., Son, M. O., Coadă, V., & Welter-Schultes, F. (2013). An updated annotated checklist of the molluscs of the Republic of Moldova. *Folia Malacologica*, 21, 175–181. <https://doi.org/10.12657/folmal.021.021>
- Bamberger, S., Duda, M., Tribsch, A., Haring, E., Sattmann, H., Macek, O., Affenzeller, M., & Kruckenhauser, L. (2020). Genome-wide nuclear data confirm two species in the alpine endemic land snail *Noricella oreinos* s.l. (Gastropoda, Hygromiidae). *Journal of Zoological Systematics and Evolutionary Research*, 58, 982–1004. <https://doi.org/10.1111/jzs.12362>
- Bank, R. A., Gittenberger, E., & Neubert, E. (2013). Radiation of an eastern Mediterranean landsnail genus: Revision of the taxa belonging to *Metafruticicola* von Ihering 1892. *Archiv für Molluskenkunde*, 142, 67–136. <https://doi.org/10.1127/arch.moll/1869-0963/142/067-136>

- Brusina, S. (1870). *Contribution à la malacologie de la Croatie*. Zagreb, C. Albrecht. <https://doi.org/10.5962/bhl.title.50295>
- Cameron, R. A., Pokryszko, B. M., & Horsák, M. (2010). Land snail faunas in polish forests: Patterns of richness and composition in a post-glacial landscape. *Malacologia*, 53, 77–134. <https://doi.org/10.4002/040.053.0105>
- Caro, A., Neiber, M. T., Gómez-Moliner, B. J., & Madeira, M. J. (2019). Molecular phylogeny and biogeography of the land snail subfamily Leptaxinae (Gastropoda: Hygromiidae). *Molecular Phylogenetics and Evolution*, 139, 106570. <https://doi.org/10.1016/j.ympev.2019.106570>
- Chiba, S. (1999). Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: Evidence from mitochondrial DNA sequences. *Evolution*, 53, 460–471. <https://doi.org/10.1111/j.1558-5646.1999.tb03781.x>
- Clessin, S. (1879). Zur Molluskenfauna Croatiens. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 11, 116–125.
- Cossignani, T., & Cossignani, V. (1995). *Atlante delle conchiglie terrestri e dulciacquicole italiane*. Ancona L'Informatore Picens.
- De Winter, A. J., & Maassen, W. J. M. (1992). Two new Hygromiidae from Crna Gora and Kosovo (Gastropoda Pulmonata), with a checklist of the hygromiid species described from western Balkan. *Basteria*, 56, 173–192.
- Dhora, D., & Welter-Schultes, F. W. (1996). List of species and atlas of the non-marine molluscs of Albania. *Schriften zur Malakozoologie*, 9, 90–197.
- Duda, M., Sattmann, H., Haring, E., Bartel, D., Winkler, H., Harl, J., & Kruckenhauser, L. (2011). Genetic differentiation and shell morphology of *Trochulus oreinos* (Wagner, 1915) and *T. hispidus* (Linnaeus, 1758) (Pulmonata: Hygromiidae) in the north-eastern Alps. *Journal of Molluscan Studies*, 77, 30–40. <https://doi.org/10.1093/mollus/eyq037>
- Ehrmann, P. (1933). Mollusca. In P. Brohmer, P. Ehrmann, & G. Ulmer (Eds.), *Die Tierwelt Mitteleuropas 2 (Lief. 1)*. Leipzig Quelle & Meyer.
- Erjavec, F. (1877). *Die malakologischen Verhältnisse der gefürsteten Grafschaft Görz im österreichischen Küstenlande*. Gorizia, Mailing.
- Falkner, G. (1990). Binnenmollusken. In R. Fechter & G. Falkner (Eds.), *Weichtiere. Europäische Meeres- und Binnenmollusken* (pp. 112–280). München, Mosaik Verlag.
- Fehér, Z., & Erőss, Z. (2009). Checklist of the Albanian mollusc fauna. *Schriften für Malakozoologie*, 25, 22–38.
- Fehér, Z., Varga, A., Deli, T., & Domokos, T. (2009). Geographic distribution and genital morphology of the genera *Lozekia* Hudec, 1970 and *Kovacsia* Nordsieck, 1993 (Mollusca, Gastropoda, Hygromiidae). *Zoosystematics and Evolution*, 85, 151–160. <https://doi.org/10.1002/zoos.200800021>
- Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.
- Forcart, L. (1946). Beiträge zur Kenntnis der Heliciden-Gattung *Perforatella* Schlüter und deren Untergattung *Monachoides* Gude & Woodward. *Verhandlungen der Naturforschende Gesellschaft in Basel*, 57, 55–61.
- Gheoca, V., Benedek, A. M., & Cameron, R. A. D. (2024). Geographical and environmental patterns of Carpathian land snail faunas in a region of high endemism. *Scientific Reports*, 14, 1392. <https://doi.org/10.1038/s41598-024-51870-6>
- Gittenberger, E. (1980). Three notes on Iberian terrestrial gastropods. *Zoologische Mededelingen*, 55, 201–213.
- Giusti, F., & Manganelli, G. (1987). Notulae malacologicae, XXXVI. On some Hygromiidae (Gastropoda: Helicoidea) living in Sardinia and in Corsica. (Studies on the Sardinian and Corsican malacofauna VI). *Bollettino Malacologico*, 23, 123–205.
- Grossu, A. V. (1979). Eine neue Gastropoden-Art: *Monachoides bacescui* sp. n. (Helicidae, Hygromiinae). *Travaux du Muséum d'Histoire Naturelle 'Grigore Antipa'*, 20, 21–25.
- Grossu, A. V. (1983). *Gastropoda Romania 4: Ordo Stylommatophora; Suprafam: Arionacea, Zonitacea, Ariophantacea si Helicacea*. Editura Litera.
- Gude, G. K., & Woodward, B. B. (1921a). On *Helicella*, Férussac. *Proceedings of the Malacological Society of London*, 14, 174–190. <https://doi.org/10.1093/oxfordjournals.mollus.a063749>
- Gude, G. K., & Woodward, B. B. (1921b). Some emendations to their recent paper "On *Helicella*, Férussac. *Annals and Magazine of Natural History, Ninth Series*, 8, 624–626. <https://doi.org/10.1080/00222932108632629>
- Häbllein, L. (1960). Weichtierfauna der Landschaften an der Pegnitz. Ein Beitrag zur Ökologie und Soziologie niederer Tiere. *Abhandlungen der Naturhistorischen Gesellschaft Nürnberg*, 29, 1–148.
- Hesse, P. (1921). Beiträge zur näheren Kenntnis der Subfamilie Fruticicolinae. *Archiv für Molluskenkunde*, 53, 55–83.
- Hesse, P. (1931). Zur Anatomie und Systematik palaearktischer Stylommatophoren. *Zoologica*, 31, 1–118.
- Hirc, D. (1881). Die Mollusken-Fauna des liburnischen Karstes. *Verhandlungen der Kaiserlich-königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 30, 519–530.
- Hofman, S., Cameron, R. A. D., Proćków, M., Sirbu, I., Osikowski, A., Jaszczynska, A., Sokół, M., & Falniowski, A. (2022). Two new pseudocryptic species in the medium-sized common European land snails, *Fruticicola* held, 1838; as a result of phylogeographic analysis of *Fruticicola fruticum* (O. F. Müller, 1774) (Gastropoda: Helicoidea: Camaenidae). *Molecular Phylogenetics and Evolution*, 168, 107402. <https://doi.org/10.1016/j.ympev.2022.107402>
- Hudec, V. (1963). Zur Definition der Unterscheidungsmerkmale am Geschlechtsorgan der Schneke *Perforatella dibothrion* (Kim.) und einiger verwandter Arten. *Biológia, Bratislava*, 18, 348–360.
- Hudec, V. (1970). Poznámky k anatomii některých plžů z Maďarska. (Bemerkungen zur Anatomie einiger Schneckenarten aus Ungarn). *Časopis Národního Musea, oddíl přírodovědný*, 137, 33–43.
- International Commission on Zoological Nomenclature. (1999). International code of zoological nomenclature. Fourth Edition. [Incorporating A. Declaration 45, Addition of Recommendations to Article 73 and of the term "specimen, preserved" to the Glossary, B. Declaration 44, amendments of Article 74.7.3, with effect from 31 December 1999, and C. the Amendment on e-publication, amendments to Articles 8, 9, 10, 21 and 78, with effect from 1 January 2012]. <https://www.iczn.org/the-code/the-code-online/>
- Jaekel, S. V., Klemm, W., & Meise, W. (1957). Die Land- und Süßwassermollusken der nördlichen Balkanhalbinsel. *Abhandlungen und Berichte aus dem Staatlichen Museum für Tierkunde in Dresden*, 23, 141–205.
- Juříčková, L., Horsák, M., Horáčková, J., Abraham, V., & Ložek, V. (2014). Patterns of land-snail succession in Central Europe

- over the last 15,000 years: Main changes along environmental, spatial and temporal gradients. *Quaternary Science Reviews*, 93, 155–166. <https://doi.org/10.1016/j.quascirev.2014.03.019>
- Kalyaanamoorthy, S., Minh, B., Wong, T., von Haeseler, A., & Jermin, L. S. (2017). ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14, 587–589. <https://doi.org/10.1038/nmeth.4285>
- Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, 30, 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kerney, M. P., Cameron, R. A. D., & Jungbluth, J. H. (1983). *Die Landschnecken Nord- und Mitteleuropas: Ein Bestimmungsbuch für Biologen und Naturfreunde*. Hamburg, Parey.
- Kneubühler, J., Baggenstos, M., & Neubert, E. (2022). On the verge of extinction—revision of a highly endangered swiss alpine snail with description of a new genus, *Raeticella* gen. nov. (Gastropoda, Eupulmonata, Hygromiidae). *ZooKeys*, 1104, 69–91. <https://doi.org/10.3897/zookeys.1104.82866>
- Kobelt, W. (1904). In E. A. Rossmässler & N. Fol (Eds.), *Iconographie der Land- & Süßwasser-Mollusken mit vorzüglicher Berücksichtigung der europäischen noch nicht abgebildeten Arten* Neue Folge, Elfter (Register) Band. Wiesbaden, C. W. Kreidel's Verlag.
- Koene, J. M., & Schulenburg, H. (2005). Shooting darts: co-evolution and counter-adaptation in hermaphroditic snails. *BMC Evolutionary Biology*, 5, 1–13. <https://doi.org/10.1186/1471-2148-5-25>
- Korábek, O., Adamcová, T., Pročków, M., Petrusek, A., Hausdorf, B., & Juříčková, L. (2023). In both directions: Expansions of European land snails to the north and south from glacial refugia. *Journal of Biogeography*, 50, 654–668. <https://doi.org/10.1111/jbi.14531>
- Korábek, O., Juříčková, J., & Petrusek, A. (2016). Splitting the Roman snail *Helix pomatia* Linnaeus, 1758 (Stylommatophora: Helicidae) into two: Redescription of the forgotten *Helix thesalica* Boettger, 1886. *Journal of Molluscan Studies*, 82, 11–22. <https://doi.org/10.1093/mollus/eyv048>
- Korábek, O., Juříčková, L., & Petrusek, A. (2022). Diversity of land snail tribe Helicini (Gastropoda: Stylommatophora: Helicidae): Where do we stand after 20 years of sequencing mitochondrial markers? *Diversity*, 14, 24. <https://doi.org/10.3390/d14010024>
- Kormos, T. (1907). Beiträge zur Molluskenfauna von Kroatien. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 39, 181–197.
- Kuźnik-Kowalska, E., & Roksela, A. (2009). Life cycle of *Perforatella bidentata* (Gmelin, 1791) (Gastropoda: Pulmonata: Helicidae). *Folia Malacologica*, 17, 199–214. <https://doi.org/10.2478/v10125-009-0016-x>
- Likharev, I. M., & Rammel'meyer, E. S. (1952). Nazemnye mol'yuski fauny SSSR. *Opredeliteli po Faune SSSR, Izdavaemye Zoologicheskim Institutom Akademii Nauk SSSR*, 43, 1–512.
- Lindholm, W. A. (1927). Zur Systematik und Nomenklatur einiger Heliciden und ihrer Verwandten. *Archiv für Molluskenkunde*, 59, 116–138.
- Locard, A. (1882). *Prodrome de la malacologie française. Catalogue général des mollusques vivants de France. Mollusques terrestres, des eaux douces et des eaux saumâtres*. Lyon, H. Georg. <https://doi.org/10.5962/bhl.title.10669>
- Ložek, V. (1964). Quartärmollusken der Tschechoslowakei. *Rozprawy Ústředního ústavu geologického*, 31, 1–37, pl. 1–32.
- Maassen, W. J. M. (1995). Die Verbreitung des Genus *Hiltrudia* Nordsieck 1993 im ehemaligen Jugoslawien (Gastropoda: Hygromiidae). *De Kreukel*, 31, 9–22.
- MolluscaBase (Eds.). (2023a). *MolluscaBase. Monachoides Gude & B. B. Woodward, 1921*. <https://www.molluscabase.org/aphia.php?p=taxdetails&id=996512>
- MolluscaBase (Eds.). (2023b). *MolluscaBase. Monachoides incarnatus* (O. F. Müller, 1774). <https://www.molluscabase.org/aphia.php?p=taxdetails&id=1003431>
- Neiber, M. T. (2019). On the phylogenetic relationships of *Elbasania* Schileyko et Fehér, 2017 (Pulmonata, Helicoidea, Hygromiidae). *Ruthenica, Russian Malacological Journal*, 29, 77–86. [https://doi.org/10.35885/ruthenica.2019.29\(2\).1](https://doi.org/10.35885/ruthenica.2019.29(2).1)
- Neiber, M. T., & Hausdorf, B. (2017). Molecular phylogeny and biogeography of the land snail genus *Monacha* (Gastropoda, Hygromiidae). *Zoologica Scripta*, 46, 308–321. <https://doi.org/10.1111/zsc.12218>
- Neiber, M. T., Razkin, O., & Hausdorf, B. (2017). Molecular phylogeny and biogeography of the land snail family Hygromiidae (Gastropoda: Helicoidea). *Molecular Phylogenetics and Evolution*, 111, 169–184. <https://doi.org/10.1016/j.ympev.2017.04.002>
- Neiber, M. T., Walther, F., & Hausdorf, B. (2018). Phylogeny and reclassification of the Caucasigenini radiation from the Caucasus region (Gastropoda, Hygromiidae). *Zoologica Scripta*, 47, 54–62. <https://doi.org/10.1111/zsc.12259>
- Nekola, J. C., Nováková, M., Horsák, M., & Adema, C. M. (2023). ELAV intron 8: A single-copy sequence marker for shallow to deep phylogeny in Eupulmonata Hasprunar & Huber, 1990 and Hygrophila Férussac, 1822 (Gastropoda: Mollusca). *Organisms Diversity & Evolution*, 23, 621–629. <https://doi.org/10.1007/s13127-022-00587-3>
- Neubauer, T. A., Xing, L., & Jochum, A. (2019). Land snail with periostacal hairs preserved in Burmese amber. *IScience*, 20, 567–574. <https://doi.org/10.1016/j.isci.2019.09.034>
- Nguyen, L. T., Schmidt, H. A., Von Haeseler, A., & Minh, B. Q. (2015). IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32, 268–274. <https://doi.org/10.1093/molbev/msu300>
- Nordsieck, H. (1987). Revision des systems der Helicoidea (Gastropoda: Stylommatophora). *Archiv für Molluskenkunde*, 118, 9–50.
- Nordsieck, H. (1993). Das system der paläarktischen Hygromiidae (Gastropoda: Stylommatophora: Helicoidea). *Archiv für Molluskenkunde*, 122, 1–23. <https://doi.org/10.1127/arch.moll/122/1993/1>
- Nordsieck, H. (2017). Higher classification of Helicoidea (Stylommatophora) and the molecular studies of their phylogeny. In H. Nordsieck (Ed.), *Pulmonata, Stylommatophora, Helicoidea: Systematics with comments* (pp. 30–40). Harxheim, ConchBooks.
- Palumbi, S. R., Martin, A., Romano, S., McMillan, W. O., Stice, L., & Grabowski, G. (1991). *The simple fool's guide to PCR, version 2.0*. Honolulu, University of Hawaii.
- Pawłowska-Banasiak, E. (2008). Shell, genital and colour variation in *Perforatella incarnata* (O. F. Müller, 1774) and *P. vicina* (Rossmässler, 1842) (Gastropoda: Pulmonata: Helicidae). *Folia Malacologica*, 16, 89–99. <https://doi.org/10.12657/folmal.016.013>

- Pfeiffer, L. (1848). *Monographia heliceorum viventium. Sistens descriptiones systematicas et criticas omnium huius familiae generum et specierum hodie cognitarum Vol 1*. Leipzig, Brockhaus. <https://doi.org/10.5962/bhl.title.10791>
- Pfenninger, M., Hrabáková, M., Steinke, D., & Dèpraz, A. (2005). Why do snails have hairs? A Bayesian inference of character evolution. *BMC Evolutionary Biology*, 5, 59. <https://doi.org/10.1186/1471-2148-5-59>
- Pieńkowska, J. R., Manganelli, G., Proćków, M., Gürelli, G., Kosicka, E., Giusti, F., & Lesicki, A. (2022). *Monacha samsunensis* (Pfeiffer, 1868): Another Anatolian species introduced to Western Europe, where it is known as *Monacha ataxis* Gittenberger & de Winter, 1985 (Gastropoda: Eupulmonata: Hygromiidae). *The European Zoological Journal*, 89, 966–990. <https://doi.org/10.1080/24750263.2022.2100932>
- Pinceel, J. A. N., Jordaens, K., Pfenninger, M., & Bäckeljau, T. (2005). Rangewide phylogeography of a terrestrial slug in Europe: Evidence for alpine refugia and rapid colonization after the Pleistocene glaciations. *Molecular Ecology*, 14, 1133–1150. <https://doi.org/10.1111/j.1365-294X.2005.02479.x>
- Pintér, L., & Suara, R. (2004). *Magyarországi puhatestűek katalógusa: hazai malakológusok gyűjtései alapján*. Budapest, Magyar Természettudományi Múzeum.
- Poje, M., & Rađa, T. (1975). Fosilna malakofauna pećine Veternice. *Speleolog*, 22/23, 6–8.
- Poliński, W. (1924). Anatomisch-systematische und zoogeographische Studien über die Heliciden Polens. *Bulletin International de l'Académie Polonaise des Sciences et des Lettres, Classe des Sciences Mathématiques et Naturelles, Série B: Sciences Naturelles*, 2, 131–279.
- Proćków, M., Duda, M., Kruckenhauser, L., Maassen, W. J., de Winter, A. J., & Mackiewicz, P. (2019). Redescription of the western Balkan species *Xerocampylaea waldemari* and its phylogenetic relationships to other Urticicolini (Gastropoda: Hygromiidae). *Systematics and Biodiversity*, 17, 367–384. <https://doi.org/10.1080/14772000.2019.1617365>
- Proćków, M., Mackiewicz, P., & Pieńkowska, J. R. (2013). Genetic and morphological studies of species status for poorly known endemic *Trochulus phorochaetius* (Bourguignat, 1864) (Gastropoda: Pulmonata: Hygromiidae), and its comparison with closely related taxa. *Zoological Journal of the Linnean Society*, 169, 124–143. <https://doi.org/10.1111/zoj.12048>
- Proćków, M., Proćków, J., Błażej, P., & Mackiewicz, P. (2018). The influence of habitat preferences on shell morphology in ecophenotypes of *Trochulus hispidus* complex. *Science of the Total Environment*, 630, 1036–1043. <https://doi.org/10.1016/j.scitotenv.2018.02.311>
- Ramos-Gonzalez, D., Saenko, S. V., & Davison, A. (2022). Deep structure, long-distance migration and admixture in the colour polymorphic land snail *Cepaea nemoralis*. *Journal of Evolutionary Biology*, 35, 1110–1125. <https://doi.org/10.1111/jeb.14060>
- Razkin, O., Gómez-Moliner, B. J., Prieto, C. E., Martínez-Ortí, A., Arrébola, J. R., Muñoz, B., Chueca, L. J., & Madeira, M. J. (2015). Molecular phylogeny of the western Palaearctic Helicoidea (Gastropoda, Stylommatophora). *Molecular Phylogenetics and Evolution*, 83, 99–117. <https://doi.org/10.1016/j.ympev.2014.11.014>
- Riedel, A. (1988). *Ślimaki lądowe (Gastropoda terrestria). Katalog Fauny Polski Cz. (XXXVI, t. 1)*. Warszawa, Państwowe wydawnictwo naukowe.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M. A., & Huelsenbeck, J. P. (2012). MrBayes 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>
- Schileyko, A. A. (1970). Ob'em, sistema i filogeniya gruppy *Perforatella-Zenobiella-Chilanodon* [scope, system and phylogeny of *Perforatella-Zenobiella-Chilanodon* group (Pulmonata, Helicidae)]. *Zoologicheskii Zhurnal*, 49, 1306–1321.
- Schileyko, A. A. (1972a). Taksonomicheskaya i geograficheskaya struktura triby Hygromiini Schileyko (Pulmonata, Helicidae) [Taxonomic and geographical structure of the tribe Hygromiini Schileyko (Pulmonata, Helicidae)]. *Zoologicheskii Zhurnal*, 51, 1129–1141.
- Schileyko, A. A. (1972b). Nekotorye aspekty izucheniya sovremennykh kontinental'nykh bryukhonogikh molluyuskov. [Some aspects of the study of recent continental gastropod molluscs]. In L. P. Poznanin (Ed.), *Itogi nauki i tekhniki. Zoologiya bespozvonochnykh. Vol. 1, Nazemnye i presnovodnye mollyuski* (pp. 7–188). Moskva, Akademiya Nauk SSSR.
- Schileyko, A. A. (1978). Nazemnye mollyuski nadsemeystva Helicoidea [Terrestrial molluscs of the superfamily Helicoidea]. In O. A. Skarlato (Ed.), *Fauna SSSR, Molluski, Tom III* (vyp. 6). Nauka.
- Schileyko, A. A. (1991). Taxonomic status, phylogenetic relations and system of the Helicoidea sensu lato (Pulmonata). *Archiv für Molluskenkunde*, 120, 187–236. <https://doi.org/10.1127/arch.moll/120/1991/187>
- Schileyko, A. A. (2006). Treatise on recent terrestrial pulmonate molluscs. Part 14. Helicodontidae, Ciliellidae, Hygromiidae. *Ruthenica, Russian Malacological Journal*, Supplement 2, 1907–2047.
- Schmidt, A. (1854). Malakologische Mittheilungen. *Malakozoologische Blätter*, 1, 1–25.
- Shvydka, Z., Kovalev, A., & Gorb, S. N. (2020). The frictional and adhesive properties of the shells of terrestrial hairy snails. *Journal of Zoology*, 310, 180–190. <https://doi.org/10.1111/jzo.12742>
- Soós, L. (1943). A Kárpát-medence Mollusca-faunája. In *Magyarország természetrajza, I. Állattani rész*. Budapest, Magyar Tudományos Akadémia.
- Štamol, V. (2010). A list of the land snails (Mollusca: Gastropoda) of Croatia, with recommendations for their Croatian names. *Natura Croatica*, 19, 1–76.
- Tamura, K., Stecher, G., & Kumar, S. (2021). MEGA11: Molecular evolutionary genetics analysis version 11. *Molecular Biology and Evolution*, 38, 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- von Ihering, H. (1892). Morphologie und Systematik des Genitalapparates von *Helix*. *Zeitschrift für wissenschaftliche Zoologie*, 54, 386–520. pl. 18–19.
- von Möllendorff, O. F. (1873). *Beiträge zur fauna Bosniens*. Görlitz, Hoffman & Reiber. <https://doi.org/10.5962/bhl.title.12899>
- Wade, C. M., & Mordan, P. B. (2000). Evolution within the gastropod molluscs; using the ribosomal RNA gene-cluster as an indicator of phylogenetic relationships. *Journal of Molluscan Studies*, 66, 565–569. <https://doi.org/10.1093/mollus/66.4.565>
- Wagner, A. J. (1915). Beiträge zur Anatomie und Systematik der Stylomatophoren aus dem Gebiete der Monarchie und der angrenzenden Balkanländer. *Denkschriften der Kaiserlichen Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse*, 91, 429–498, pl. 1–24. <https://doi.org/10.5962/bhl.title.46613>

- Watson, H. (1919). Notes on *Hygromia limbata* (Drap.). *Proceedings of the Malacological Society of London*, 13, 120–132.
- Welter-Schultes, F. (2012). *European non-marine molluscs, a guide for species identification. Bestimmungsbuch für europäische Land- und Süßwassermollusken*. Göttingen, Planet Poster Editions.
- Welter-Schultes, F., Audibert, C., & Bertrand, A. (2011). Liste des mollusques terrestres et dulcicoles de France continentale (excl. hydrobioïdes). *Folia Conchylologica*, 12, 4–44.
- Westerlund, C. A. (1902). Methodus dispositionis conchyliorum extramarinorum in Regione palaeartica viventium, familias, genera, subgenera, et stirpes sistens. *Rad Jugoslavenske Akademije Znanosti i Umjetnosti, Matematičko-Prirodoslovni Razred*, 151, 82–139.
- Wiktor, A. (2004). *Ślimaki lądowe Polski*. Olsztyn, Mantis.
- Wohlberedt, O. (1909). Zur Fauna des Sandschak Novipazar (Mollusken und Käfer). *Annalen des Naturhistorischen Museums in Wien*, 23, 237–262.
- Zilch, A. (1967). Geschichte der malakologischen Sektion. *Archiv für Molluskenkunde*, 97, 7–43.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Adamcová, T., Juříčková, L., Proćków, M., Neubert, E., Petrusek, A., & Korábek, O. (2024). Taxonomic revision and dissolution of the genus *Monachoides* (Gastropoda, Stylommatophora). *Zoologica Scripta*, 53, 419–437. <https://doi.org/10.1111/zsc.12658>