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Morphology and taxonomic assessment of eight genetic clades of *Mercuria* Boeters, 1971 (Caenogastropoda, Hydrobiidae), with the description of five new species

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Abstract. The freshwater snail genus *Mercuria* is widely distributed in lowland waters across Western Europe, Northern Africa and the Mediterranean islands. Approximately two-thirds of the currently recognised species are described based on their shell morphology, which may vary within species due to biotic and abiotic factors. Recent molecular phylogenies that included numerous previously documented populations recovered 14 species clades, nine of which correspond to nominal species and five, to undescribed taxa. Here, we formally describe the five undescribed taxa as new species and provide morphological descriptions of the shell and other anatomical structures for three of the other inferred clades and for the species *M. maceana* to elucidate their taxonomic status and assess the utility of morphological characters for species delimitation in *Mercuria*. Taken together, the morphological and molecular evidence suggest new identifications and synonymies, having implications on the known geographic range of the studied species, including the type species *M. similis*. Anatomical measurements and geometric morphometric analysis of shell shape revealed no clear differentiation among the species analysed, predicting the importance of molecular data in elucidating the species diversity of the genus.

Keywords. Taxonomy, phylogeny, freshwater gastropods, Mediterranean region, geometric morphometrics.

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Introduction

The Western Palaearctic freshwater snail genus *Mercuria* Boeters, 1971 comprises 30 currently recognised species (25 extant and 5 extinct; MolluscaBase 2022) that are primarily distributed in lowland localities in Mediterranean and Atlantic coastal regions (Glöer *et al.* 2015). Within the Mediterranean, this genus has been found in the Iberian and Italian peninsulas, southern France, some western Mediterranean islands and north-western Africa (Glöer *et al.* 2010, 2015; Boeters & Falkner 2017; Holyoak *et al.* 2017; Boulaassafer *et al.* 2018; Miller *et al.* 2022). On the Atlantic coast, confirmed records include the southern British Islands, northern continental Europe and Macaronesia (Kerney 1992, 1999). Members of the genus mainly inhabit springs, ditches, streams and even some river sections, all with permanent water and a slow flow, which help to clean and oxygenate the water. *Mercuria* snails have also been often found in environments associated with a high degree of salinity caused by the Keuper facies. These facies comprise Upper Triassic sediments that contain gypsiferous mudstones that change to alluvial fans and playa deposits (Sopeña *et al.* 1988).

Boeters & Falkner (2017) erected the subfamily Mercuriinae Boeters & Falkner, 2017 for this genus based on the unique set of morphological characters featured by the species of *Mercuria* and the molecular systematics findings of Wilke *et al.* (2001, 2013). The most diagnosable morphological character of the genus is the presence of a penial appendix at the distal end of the penis (Boeters 1971). Despite this, a low level of variability in this structure has been observed between closely related species, often leading to incorrect classifications (Boulaassafer *et al.* 2018). Moreover, a high level of intraspecific variation has been observed in the shell characters and the size of some species, due to parasites or seasonal variation in growth (e.g., *M. tensiftensis* Boulaassafer, Ghamizi & Delicado, 2018 in Boulaassafer *et al.* (2018); *M. tachoensis* (Frauenfeld, 1865) in Holyoak *et al.* (2017)). In other cases, some species are hardly distinguishable from one another and could be categorised as cryptic species (e.g., *M. tachoensis* and *M. bayonnensis* (Locard, 1894)). All these aspects, along with missing type material and unspecific descriptions of type localities in previous taxonomic studies, make it challenging to assign some populations to any single species of *Mercuria*.

The small size and simple shells of *Mercuria* snails, along with factors that increase intraspecific variability (e.g., colour of the periostracum and shell size and shape, among others), have led to some taxonomic confusion. Early authors assigned some species currently recognised as *Mercuria* to either the genus *Cyclostoma* Draparnaud, 1805; *Amnicola* Gould & Haldeman, 1840 or *Peringia* Paladilhe, 1874 on the basis of external features (e.g., Moquin-Tandon 1855; Paladilhe 1869; Bourguignat 1876; Letourneux & Bourguignat 1887). One example is represented by the type species *Amnicola confusa* Frauenfeld, 1863, which was erected by Frauenfeld (1863) based on the dubious conclusion of differences between the operculum of this species and that of *Cyclostoma simile* Draparnaud, 1805. The loss of type material and the imprecise descriptions of the type localities make it difficult to resolve some ongoing taxonomic questions, especially those involving the recognition and delimitation of widespread species. For these reasons, many authors have debated the discriminant value of shell characters to evaluate the diversity of *Mercuria* (e.g., Adam 1940; Boeters & Falkner 2000; Vinarski & Eschner 2016), leading to the conclusion that a taxonomy of the group based on only shell and external characters is complex and ineffective. To have a more robust taxonomy, new field surveys should be conducted to correctly identify extant populations of *Mercuria* using morphological, anatomical and taxonomic genetic markers.

Boulaassafer *et al.* (2018) reported the first DNA-based phylogeny for the genus based on fragments of the cytochrome *c* oxidase subunit I (COI) gene sequenced from 16 Moroccan populations. Based on the phylogenetic relationships among these populations and certain shell and anatomical features, the authors concluded that their dataset consists of five species. The recovered species exhibited low levels of intraspecific COI divergence (0%–1.3%), except *M. midarensis* Boulaassafer, Ghamizi & Delicado, 2018 (0%–3.4%), and a generally high degree of morphological variation within species (Boulaassafer *et al.* 2018). Recently, species delimitation methods conducted on a DNA-sequence dataset with dense geographic sampling detected 14 groups in *Mercuria*, of which five may represent new species (Miller *et al.* 2022). The proposed species classification for some of the populations, which was based on mitochondrial and nuclear sequences, contrasts with previous identifications made by other taxonomists using mostly shell characters. The anatomical data of these populations may be key for resolving their species identification.

The morphological characters of most of the populations studied and species proposed by Miller *et al.* (2022), and their degree of intraspecific variability, remain unknown. In fact, whether the species clades of *Mercuria* inferred in that study can even be distinguished based on morphological characters remains to be determined. In this study, our main goal is to fill this data gap by (*i*) describing the morphology of eight of the 14 putative species proposed by Miller *et al.* (2022), formally describing five of them here as new species, and the species *M. maceana* (Paladilhe, 1869), for which the shell and radula of a few museum specimens have also been examined, (*ii*) assessing their taxonomy and geographic distribution and (*iii*) quantifying shell shape variation among some of the species. The only putative species proposed by Miller *et al.* (2022) not included in the present study is *M. rolani* Glöer, Boeters & Walther, 2015, due to the lack of material. As a result of this study, we have a more accurate taxonomic assessment of the component populations of nine species of *Mercuria*, which will help clarify the overall geographic distribution of these taxa and their conservation status.

Material and methods

Studied specimens

Between 2016 and 2019, specimens from 129 populations of *Mercuria* were collected from across almost the entire known distribution range of the genus. Of these, 79 were sequenced and analysed in previous studies (Boulaassafer *et al.* 2018; Miller *et al.* 2022). For this study, specimens from 93 populations of the 129 populations sampled were morphologically examined (Supp. file 1: Table S1). These specimens were fixed using the methods described by Araujo *et al.* (1995) and Ramos *et al.* (2000) and stored in ethanol (80%) until dissected. The studied populations are distributed in Spain, France, Portugal, Italy and Tunisia (Fig. 1). All the collected material, after further study and proper labelling, will be housed in the Malacology Collection at the National Museum of Natural Science (MNCN-CSIC), Madrid, Spain and the University of Giessen Systematics and Biodiversity (UGSB) collection in Germany.

Morphological and anatomical descriptions

For the anatomical studies, the shells of the specimens selected (typically adults) were first removed using a decalcifying aqueous solution of 5% ethylenediaminetetraacetic acid (EDTA) prior to the dissection of the soft bodies (Ramos *et al.* 2000). Specimens were dissected in distilled water in a Petri dish containing a layer of paraffin, wax and charcoal.

To facilitate the dissection of the reproductive and digestive systems, the soft body parts lacking pigmentation (except the head) were first stained in an eosin solution (0.5 ml of distilled water + eosin until saturated at room temperature then diluted to 10%). To visualise and extract the nervous system and buccal bulb, the head was immersed in Bouin's solution (Galigher & Kozloff 1971) for one minute before being placed in a Petri dish with distilled water for dissection. All images were captured using a Leica MZ16 stereo microscope mounted with a Leica DFC550 camera.

To study the radular teeth of *M. similis* (Draparnaud, 1805), *M. balearica* (Paladilhe, 1869), *M. tachoensis*, *M. egarensis* Miller, García-Guerrero & Ramos sp. nov., *M. carrillorum* Miller, García-Guerrero & Ramos sp. nov. and *M. felixi* Miller, García-Guerrero & Ramos sp. nov., the buccal bulb was extracted to further dissolve its tissue with a 2.5% solution of sodium hypochlorite (NaClO). Once only the radula remained, it was transferred to a new Petri dish and rinsed with distilled water. To remove the periostracum, shells were immersed in the hypochlorite solution for 5–8 min and then placed in an ultrasonic cleaner for 3–5 s. Uncoated radulae and shells were mounted on stubs and imaged on a FEI INSPECT (FEI Company, Netherlands) environmental scanning electron microscope (ESEM) at low vacuum.

The radula of the individuals of *M. lupiaensis* Miller & Delicado sp. nov. and *M. veronicae* Miller, Khalloufi & Delicado sp. nov. were extracted from the buccal mass using the first step of a CTAB protocol for DNA isolation (Wilke *et al*. 2006). Then, after drying, radulae were mounted on metallic stubs and sputter-coated with gold (Balter Sputter Coater SCD004) for 50 s to finally be photographed with a field emission scanning electron microscope (FESEM) DSM982 Gemini (Carl Zeiss GmbH, Germany).

The shell and anatomical descriptions adopt the terminology of character states defined by Hershler & Ponder (1998). The terminology used to describe the nervous system structures follows that of Davis *et al.* (1976), which also provides an index to determine the degree of concentration of the ganglia and connectives in the dorsal nerve ring, or the RPG ratio: length of the pleuro-supraoesophageal connective divided by the sum of the lengths of the supraoesophageal ganglion, pleuro-supraoesophageal connective and right pleural ganglion. Accordingly, the dorsal nerve ring can be concentrated (RPG ≤ 0.29),

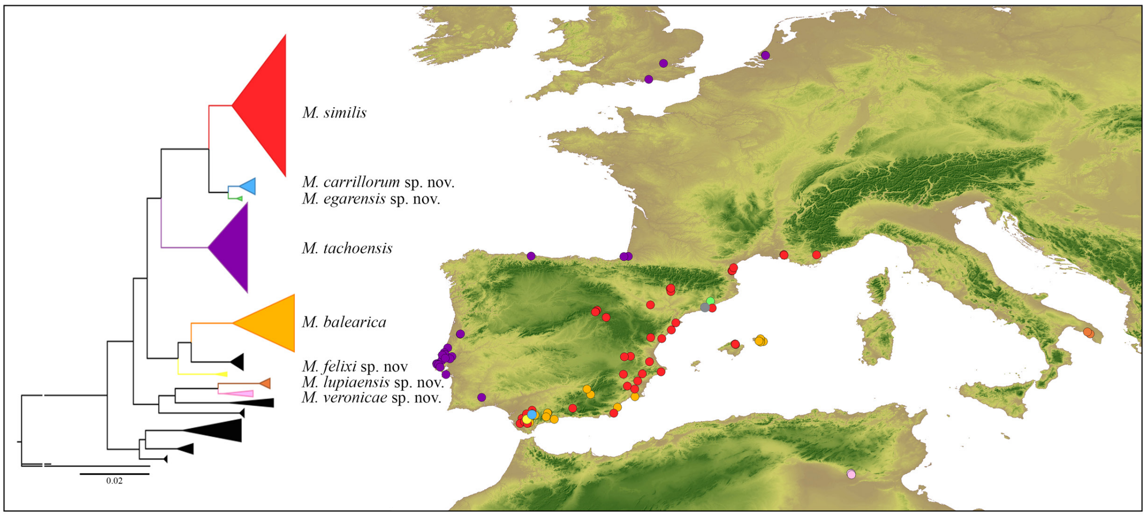

Fig. 1. Phylogenetic clustering and geographic location of the studied populations of *Mercuria* Boeters, 1971 throughout the western Palaearctic region. The tree topology on the left has been modified from Miller *et al.* (2022) to show the species clades (i.e., coloured clades) of the populations described here. One population (grey dot) represents the distribution of *M. maceana* (Paladilhe, 1869). Scale bar below topology: expected change per site.

moderately concentrated (0.30–0.49), elongated (0.50–0.67), or extremely elongated (≥ 0.68) (Davis & Pons da Silva 1984; Davis *et al.* 1986, 1992).

Morphometry

To study shell shape variation, a total of 1014 shell images of individuals from 35 populations of *Mercuria* (comprising eight species: *M. balearica*, *M. tachoensis*, *M. similis*, *M. targouasensis* Glöer, Boeters & Walther, 2015, *M. maceana*, *M. egarensis* sp. nov., *M. carrillorum* sp. nov. and *M. felixi* sp. nov.) were captured under a Leica MZ16 stereo microscope mounted with a Leica DFC550 camera. Images were taken in frontal view, with the spiral axis on the y-axis. To select homologous points, only specimens with a similar number of whorls were analysed, assuming that spire growth is a measure of maturity.

The shell variables, a total of nine landmarks and 12 semilandmarks per specimen (Fig. 2A), were scored using TPSdig ver. 2.31 (Rohlf 2018), which provides coordinate data for each point. Each of the image folders was compiled into a thin-plate spline (TPS) object in TPSUtil ver. 1.76 (Rohlf 2007b). To treat a small variation in position that may occur during the imaging process, all data were subjected to a Procrustes superposition analysis, which eliminates size differences and the potential impact of rotation, thus minimising errors. The consensus of each population and each species was obtained using TPSRelw ver. 1.45 (Rohlf 2007a). Landmarks were analysed at the two levels (i.e., population and species). Shell shape variation was characterised by a principal component analysis (PCA) of the landmark data (Jolliffe 2002) using the consensus of each population. To assess variation in shell shape between species, a warp analysis, as implemented in PAST ver. 4.10 (Hammer *et al.* 2022), was conducted to obtain a thin plate spline plot for each species using the species consensus.

Traditional morphological measurements of the shell (Fig. 2B–C) were also taken using the TPSdig ver. 2.31 software to provide a more complete characterisation of the species. These data included counts of the total number of whorls, following the method described by Ramos *et al.* (2000). Descriptive statistics on these data such as mean, standard deviation, and minimum and maximum values were used to summarise intra- and interspecific variation (Supp. file 2: Tables S2–S18).

Abbreviations

Shell measurements

AH = aperture height
AL = aperture length
AW = aperture width
LBW = length of body whorl
NPW = nucleus of protoconch width
NSW = number of spire whorls
PW = protoconch width
SL = shell length
SW = shell width
WAW = width of antepenultimate whorl
WBW = width of body whorl
WPW = width of penultimate whorl

Anatomy

Ag = albumen gland
Bc = bursa copulatrix
CC = cerebral commissure
Cg = capsule gland
Ct = ctenidium

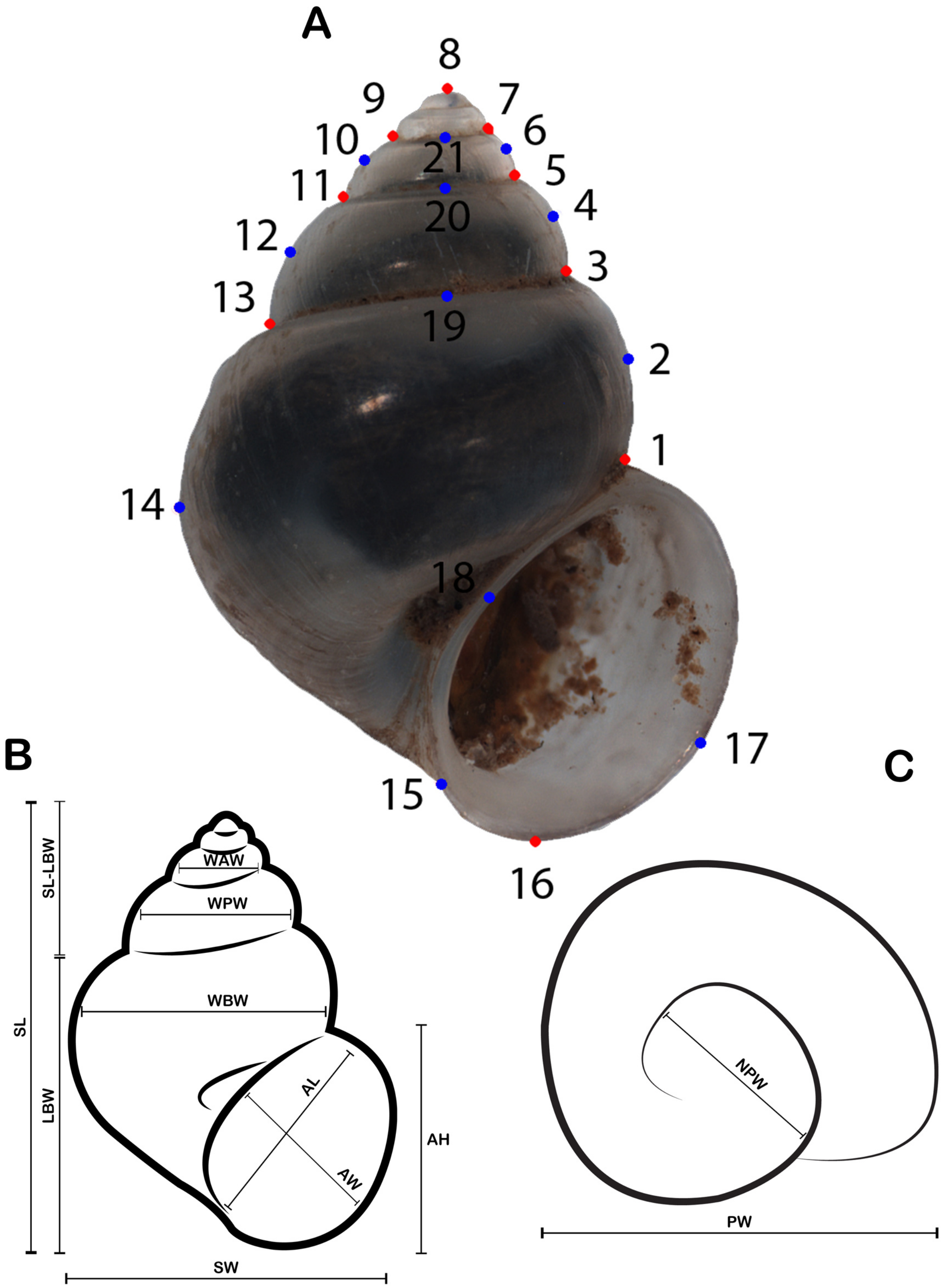

Fig. 2. Shell morphometric variables. **A**. Image of a specimen of *Mercuria similis* (Draparnaud, 1805) indicating the landmarks (red) and semilandmarks (blue) used for the geometric morphometric analysis (PCA). **B–C**. Drawings of shells of *Mercuria* Boeters, 1971, showing the linear measurements made on the shell and protoconch.

LCG = left cerebral ganglion
LPG = left pleural ganglion
Os = osphradium
P = distal end of penis
Pa = penial appendix
Pr = prostate gland
RCG = right cerebral ganglion
RPG = right pleural ganglion
SR = seminal receptacle
Ss = style sac
St = stomach
SubC = suboesophageal ganglion
SupG = supraoesophageal ganglion

Collections

JPM = Jonathan P. Miller's personal collection
MCP = Miguel Carrillo Pacheco personal collection
MNCN = Museo Nacional de Ciencias Naturales (CSIC), Madrid, Spain
MZB = Museu Zoologico Barcelona, Spain
NHMW = Naturhistorisches Museum Wien, Austria
RMNH = Naturalis Biodiversity Center, Leiden, The Netherlands
UM = Université de Montpellier, France
UGSB = University of Giessen Systematics and Biodiversity Collection, Germany

Results

Geometric morphometrics of shell shape

In the PCA of the consensus of each of the analysed populations, the first two components accounted for 75.3% of the variation in shell shape; the inclusion of the third component explained 81.5% of the variation (Fig. 3). Although the first two components differentiated the species, similar shell shape patterns were observed for the species pairs formed by *M. balearica* and *M. egarensis* sp. nov., and *M. tachoensis* and *M. carrillorum* sp. nov. The populations of *M. similis* and *M. maceana* formed distinct clusters and could easily be distinguished from the rest of the species. In general, three clear shell shape patterns were observed according to the components. The first component described variation in the body whorl and aperture against variation in the apex. In this sense, species vary from having a slender to sub-globose shape with a wider aperture and a compact body whorl to being more elongated towards the apex and with a narrower aperture (compare specimens on the left versus right side of Fig. 3). The second component also described variables that represent variations in the body whorl and aperture against the apex: specimens at the top of the plot have a wider body whorl and aperture and a shorter apex than those at the bottom of the plot.

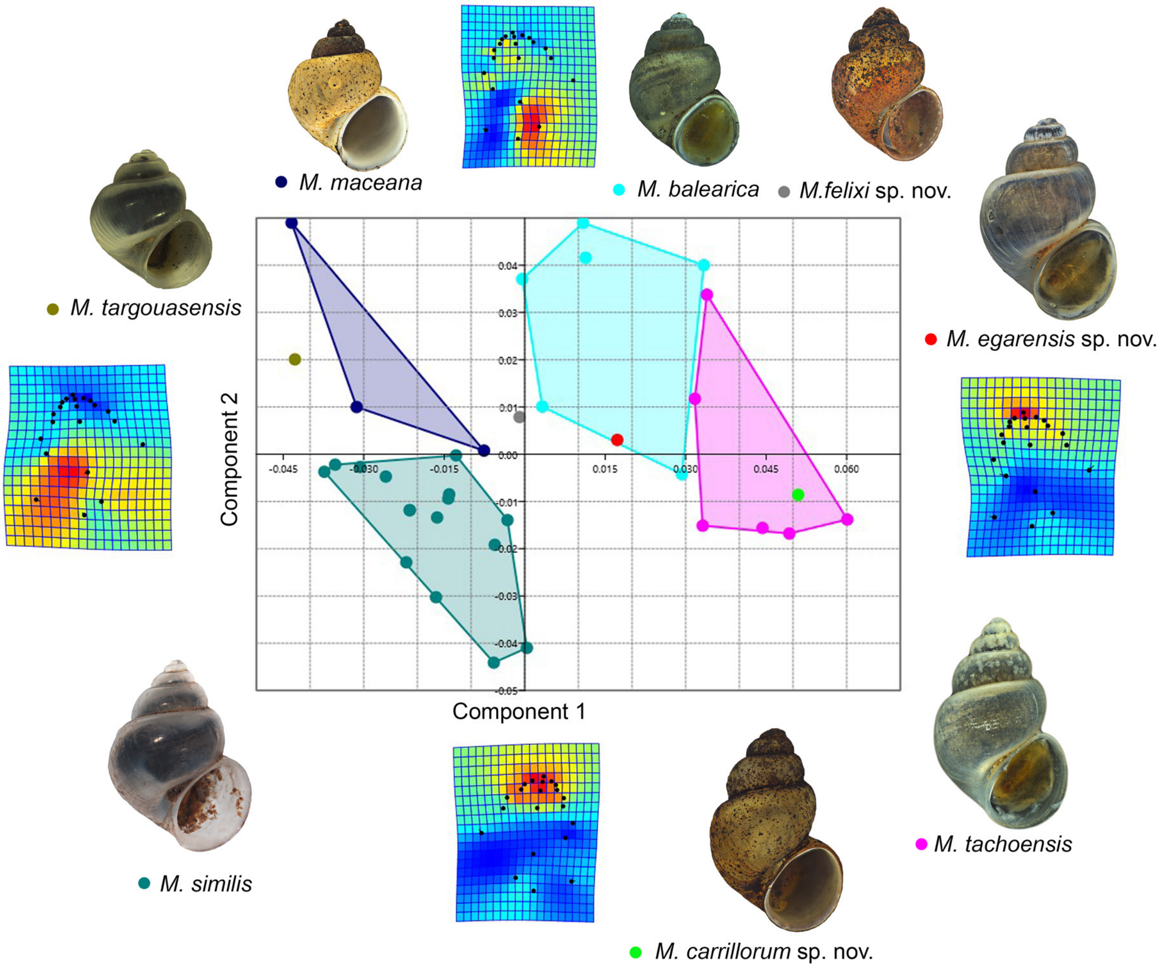

Fig. 3. Principal components analysis plot for species of *Mercuria* Boeters, 1971 based on 21 coordinates (9 landmarks and 12 semilandmarks). Each dot on the plot represents the consensus of the shape of each of the sampled populations. Warp grid deformations (TPS) show expansion (in red colour) and contraction (in blue) of the shell shape.

Taxonomic account

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Order Littorinimorpha Golikov & Starobogatov, 1975
Family Hydrobiidae W. Stimpson, 1865
Subfamily Mercuriinae Boeters & Falkner, 2017
Genus *Mercuria* Boeters, 1971

Mercuria similis (Draparnaud, 1805)

Figs 4–7; Supp. file 2: Tables S2–S5

Cyclostoma simile Draparnaud, 1805: 34, pl. 1 fig 15.
Bythinia meridionalis Risso, 1826: 100.
Amnicola confusa Frauenfeld, 1863: 1029.
Amnicola emiliana Paladilhe, 1869: 229, pl. 19 figs 22–23; 106, pl. 5.

Amnicola compacta Paladilhe, 1869: 110, pl. 19 figs 14–15.
Paludina cerulea Massot, 1872: 128.
Amnicola roigiana Salvañá, 1887: 141.
Amnicola monjoi Chia, 1887: 14.
Amnicola vallensana Almera & Bofill, 1898: 83; pl. III fig. 23.

Paludina similis – Turton & Gray 1840.
Hydrobia similis – Dupuy 1851: 553.
Pseudamnicola confusa – Adam 1940: 1–7, figs 1–2.
Mercuria confusa – Boeters 1971: 178–179, fig. 10.
Pseudamnicola similis – Gasull 1971: 45; pl. II fig. 8.
Mercuria emiliana – Boeters 1988: 208, figs 92–93; 210, figs 118, 125; 211, pl. 3 fig. 34.

non *Mercuria meridionalis* (Risso, 1826) – Girardi 2003: 83.
non *Pseudamnicola emilianus* (Paladilhe, 1869) – Boeters & Falkner 2017: 251, fig 11i–j.

Revised diagnosis

Shell ovate-conic; aperture obliquely broad ovate; periostracum whitish to grey; protoconch microsculpture granulated; central radular tooth formula (2)3-C-3(2)/1-1; female genitalia with bursa copulatrix pyriform to elongate, ca 3 times as long as wide; seminal receptacle elongate with a short duct; penis darkly pigmented, gradually tapering; penial appendix triangular, variable in length (equal to or shorter/longer than the distal end of the penis), strongly pigmented at the junction with the penis; distal end of the penis triangular; nervous system pigmented, elongate (mean RPG ratio = 0.63); cerebral ganglia approximately equal in size.

Type material (not examined)

Neotype

FRANCE • sex unknown; “Gallia meridionalis” [South France]; NHMW-MO 92596; designated by Boeters & Falkner (2000).

Type locality

According to original description: “Gallia meridionalis”.

Material examined

FRANCE – **Languedoc-Roussillon** • 30 specs; Salses-le-Château, Font Dame Spring; MNCN 15.05/94776 • 30 specs; Salses-le-Château, Font d‘Estramar Spring; MNCN 15.05/94777 • 30 specs; pond in La Palme; MNCN 15.05/94778. – **Provence-Alpes-Côte d’Azur** • 30 specs; Étang de Berre, stream near La Suriane; MNCN 15.05/94789 • 30 specs; Étang de Berre, Arc River near Les Cabanes; MNCN 15.05/94790 • 30 specs; Var, La Foux-de-Draguignan Spring; MNCN 15.05/94791.

SPAIN – **Granada Prov.** • 30 specs; La Malahá Spring; MNCN 15.05/94758 • La Pucha Spring; MNCN 15.05/94759. – **Cádiz** • 30 specs; Prado del Rey, Pilar de los Playeros Spring; MNCN 15.05/94760 • 30 specs; Villamartín, La Zarza Spring; MNCN 15.05/94761 • 30 specs; Medina-Sidonia, El Berrueco Spring; MNCN 15.05/94803 • 30 specs; Arcos de la Frontera, Platero Spring; MNCN 15.05/94795 • 30 specs; Puerto Serrano, Pozo Amargo Spring; MNCN 15.05/94796 • 30 specs; spring in Alcalá de los Gazules; MNCN 15.05/94797 • 30 specs; Algodonales, El Algarrobo Spring; MNCN 15.05/94799 • 30 specs; Medina-Sidonia, La Salá Spring; MNCN 15.05/94800-2546; 30 specs; Alcalá de los Gazules, Las Presillas Spring; MNCN 15.05/94802. – **Guadalajara** • 30 specs; saltings of Riba de Santiuste; MNCN 15.05/94762 • 30 specs; Alcolea Stream, tributary of Salado River, road from Imón to Santamera;

MNCN 15.05/94763 • 30 specs; Salado River at Santamera; MNCN 15.05/94764, 15.05/94765 • 30 specs; La Vega Stream at Saelices de la Sal; MNCN 15.05/94766. – **Almería** • 30 specs; Las Negras ravine; MNCN 15.05/94767. – **Albacete** • 30 specs; Cordovilla saltings; MNCN 15.05/94768 • 30 specs; Casas de Ves, La Salaboreja Spring; MNCN 15.05/94769 • 30 specs; Casas de Ves, La Cañada Stream near La Salaboreja Spring; MNCN 15.05/94770 • 30 specs; Fuentealbilla, stream feeding Galayo's Pond; MNCN 15.05/94771. – **Zaragoza** • 30 specs; Gelsa, stream in Barranco del Agua Salada; MNCN 15.05/94772. – **Huesca** • 30 specs; saltwater stream near Aguinaliu; MNCN 15.05/94773 • 30 specs; stream crossing the town of Peralta de la Sal; MNCN 15.05/94774 • 30 specs; Torres del Obispo Spring; MNCN 15.05/94794. – **Tarragona** • 30 specs; Amposta, Ullals de Baltasar; MNCN 15.05/94780. – **Murcia** • 30 specs; Chícamo Stream near La Umbría; MNCN 15.05/94781 • 30 specs; La Mula River; MNCN 15.05/94782 • 30 specs; river in Sierra de la Muela; MNCN 15.05/94742 • 30 specs; Puerto de la Cadena; MNCN 15.05/94793. – **Castellón** • 30 specs; Fuente Amarga Spring; MNCN 15.05/94783 • 30 specs; marsh at Peñíscola; MNCN 15.05/94786 • 30 specs; irrigation ditch in Moli de la Font; MNCN 15.05/94787 • 30 specs; irrigation ditch in Cirat; MNCN 15.05/94788. – **Valencia** • 30 specs; Sax, Vinalopó River; MNCN 15.05/94784. – **Alicante** • 30 specs; Braña's Ravine, near L'Olla Beach; MNCN 15.05/94785. – **Islas Baleares** • 30 specs; Majorca, Albufera of Majorca, Siquia de Son Senyor; MNCN 15.05/94805 • 30 specs; Majorca, Albufera of Majorca, Siquia d'en Moix; MNCN 15.05/94806 • 30 specs; Majorca, Muro, Font de Son Sant Joan; MNCN 15.05/94804. – **Barcelona** • 30 specs; El Prat de Llobregat, Estany de la Ricarda Pond; MNCN 15.05/94779.

Additional locality information provided in Supp. file 1: Table S1.

Description

SHELL. Ovate-conic, whorls 4–5, height 3.5–5.7 mm, width 1.5–3.3 mm (Fig. 4 A–O; Supp. file 2: Table S2); periostracum whitish to grey; protoconch of 1.5 whorls, ca 400 µm wide, nucleus ca 200 µm wide (Fig. 5A–B); protoconch microsculpture granulated (Fig. 5C); teleoconch whorls very convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin straight, inner lip touching the shell wall; umbilicus narrow, not covered by the inner lip.

OPERCULUM. As for the genus, orange to brown, sometimes yellowish, about two whorls; muscle attachment oval, located near the nucleus (Fig. 4P–Q).

RADULA. Length intermediate, ca 800 µm long (35% of total shell length), containing about 65 rows of teeth. Central tooth formula (2)3-C-3(2)/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 5D–F). Lateral tooth formula (3)2-C-2(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 11–15 cusps (Fig. 5E); outer marginal teeth with 12–25 cusps (Fig. 5F). Radular data were collected from the following specimens: MNCN 15.05/94760 – Spring Pilar de los Playeros, Prado del Rey, Cádiz, Spain; MNCN 15.05/94767 – Las Negras ravine, Almería, Spain; MNCN 15.05/94768 – Cordovilla Saltings, Albacete, Spain; MNCN 15.05/94776 – Fonte Dame Spring, Salses-le-Château, Aude, France; MNCN 15.05/94777 – Estramar Spring, Salses-le-Château, Aude, France; MNCN 15.05/94778 – pond in La Palme, Aude, France; MNCN 15.05/94791 – La Foux-de-Draguignan Spring, France and 15.05/94804 – Font de Son Sant Joan, Muro, Majorca, Spain.

PIGMENTATION AND ANATOMY. Animal darkly pigmented, although unpigmented specimens were also found (Fig. 4E); head and tentacles black, pigmentation lighter on eye lobes, snout and neck; snout about as long as wide, approximately parallel-sided, with medium distal lobation (Fig. 7F). Ctenidium occupying almost the total length of the pallial cavity; 22–27 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 6E). Pallial tentacle present. Osphradium elongate, more than 3 times as long as wide (Supp. file 2: Table S3), positioned opposite middle of ctenidium. Stomach

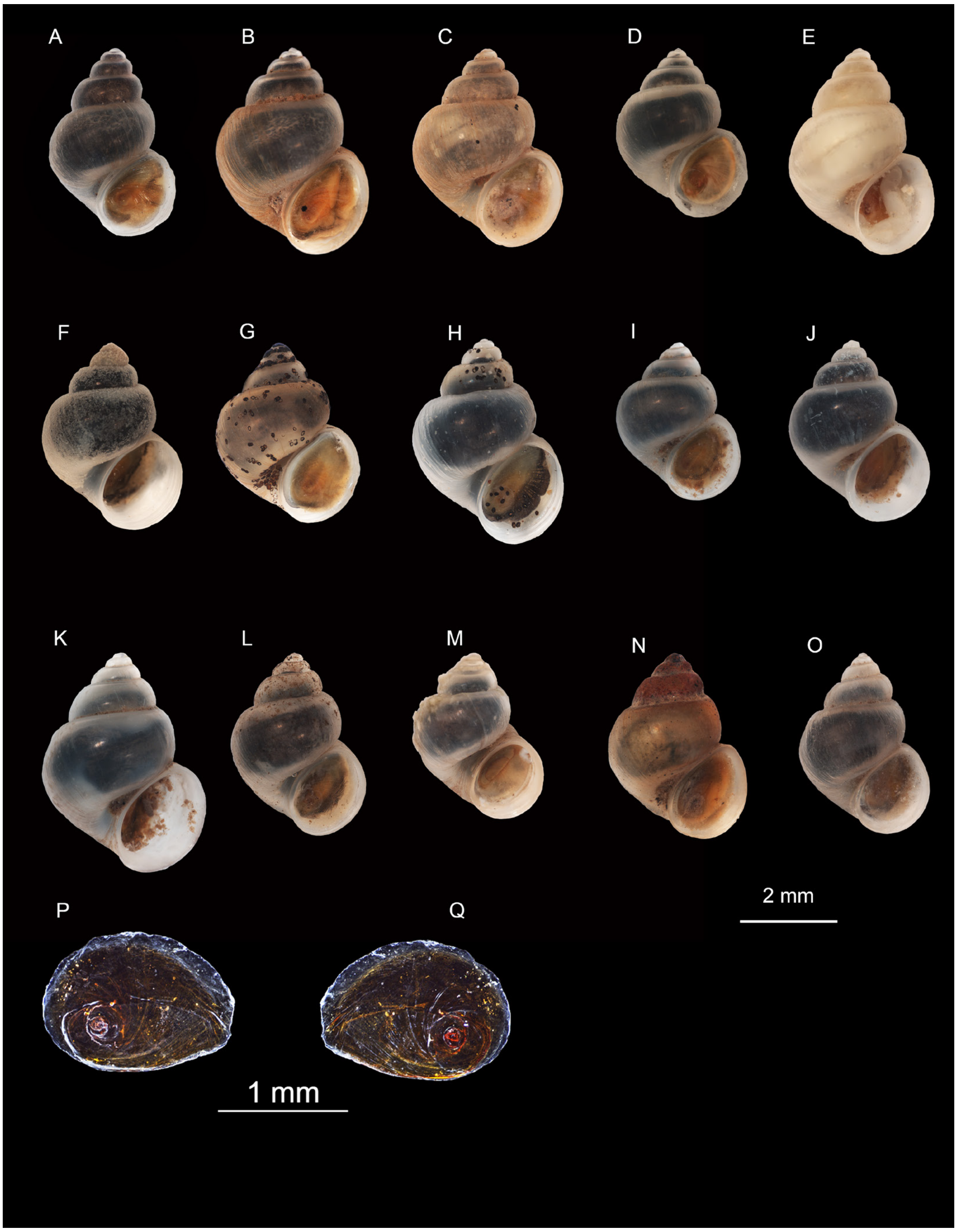

Fig. 4. Intraspecific variation of the shell shape and colour of *Mercuria similis* (Draparnaud, 1805). **A**. Salaboreja Spring, Casa de Ves, Albacete, Spain. **B**. Salado Stream, Casa de Ves, Albacete, Spain. **C**. Galayo´s Pond, Fuentalbilla, Albacete, Spain. **D**. Stream in Barranco del Agua Salada, Gelsa, Zaragoza, Spain (pigmented animal). **E**. Stream in Barranco del Agua Salada, Gelsa, Zaragoza, Spain (unpigmented animal). **F**. Saltwater gully in Aguinaliu, Huesca, Spain. **G**. Stream in Peralta de la Sal, Huesca, Spain. **H**. Sosa River at Peralta de la Sal, Huesca, Spain. **I**. Fonte Dame, Salses-le-Château, Aude, France. **J**. Font d´Estramar, Salses-le-Château, Aude, France. **K**. Pond at La Palme, Aude, France. **L**. Estany de la Ricarda, El Prat de Llobregat, Barcelona, Spain. **M**. Ullals de Baltasar, Amposta, Tarragona, Spain. **N**. Arc River near Les Cabanes, Bouches-du-Rhône, France. **O**. La Foux-de-Draguignan, France. **P–Q**. Arc River near Les Cabanes, Bouches-du-Rhône, France. **P**. Operculum, inner side. **Q**. Operculum, outer side.

almost as long as wide with two chambers almost equal in size; style sac longer than wide (Supp. file 2: Table S3), with the unpigmented intestine surrounding its distal end before continuing on as a straight rectum (Fig. 6F).

Female genitalia. Glandular oviduct 2.5 times as long as wide; albumen gland longer than capsule gland (Fig. 6A–D; Supp. file 2: Table S4); bursa copulatrix pyriform to elongate, ca 3 times as long as wide; bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal receptacle elongate, with a short duct, positioned at the distal end of the renal oviduct just above the junction with the bursal duct (Fig. 6A–D).

Male genitalia. Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix longer (Fig. 7A–C) or shorter (Fig. 7D–F) than the distal end of the penis, triangular, strongly pigmented at the junction with the penis, pigmentation gradually weakens from the junction to the middle of the penial appendix where it is very weak. Penial appendix base narrow, medially positioned on the inner edge of the penis. Prostate gland bean-shaped, about 2 times as long as wide, connected by the posterior vas deferens to a convoluted seminal vesicle and the testis (Fig. 7G–H; Supp. file 2: Table S5).

Nervous system. Pigmented, elongate (mean RPG ratio = 0.63; Supp. file 2: Table S15); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 9 times as long as pleuro-suboesophageal one (Fig. 6G).

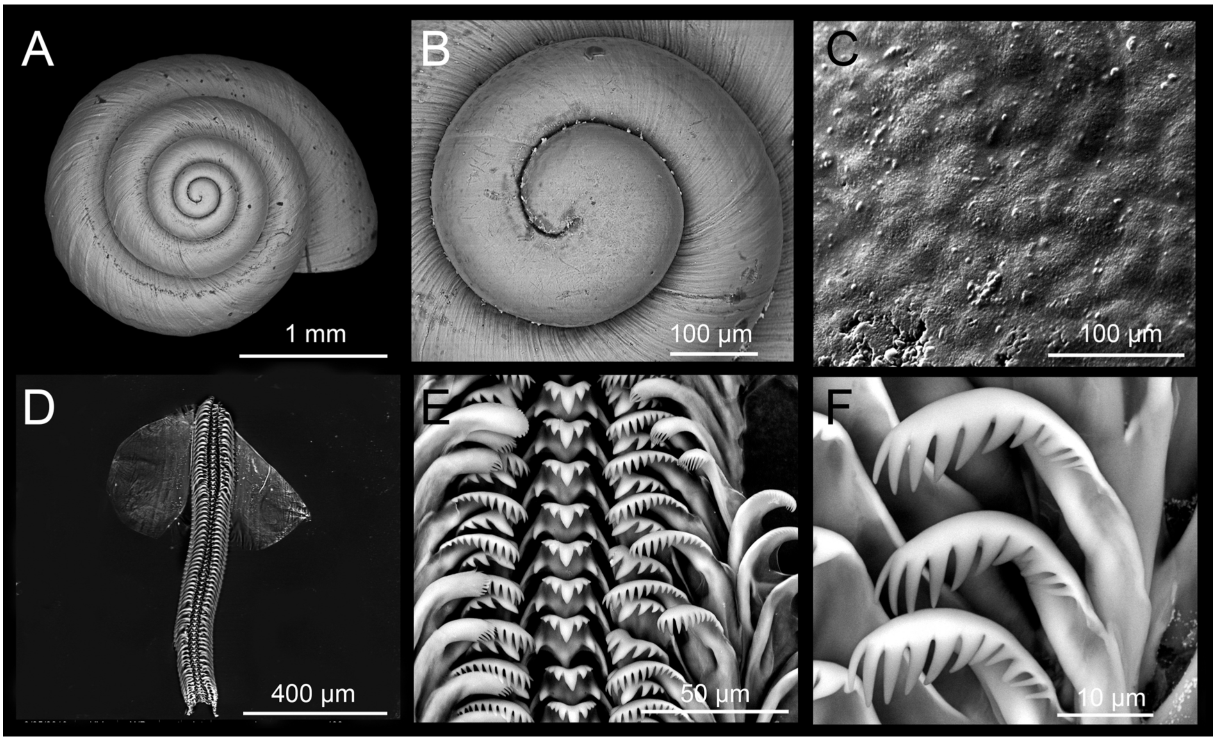

Fig. 5. Shell and radula of *Mercuria similis* (Draparnaud, 1805) from Étang de Berre, Bouches-du-Rhône, France. **A**. Apical view of the shell. **B**. Details of the protoconch. **C**. Protoconch microsculpture. **D**. General view of the radular ribbon. **E**. Central, lateral, inner marginal and outer marginal teeth. **F**. Detailed view of the inner marginal teeth.

Ecology and distribution

Most of the examined specimens were found in waters with very high conductivities (592–28 900 µS/cm, average 6364 µS/cm). These localities are affected by the Keuper facies, Mesozoic evaporitic deposits that contain high levels of NaCl and $CaSO_4$, among others, that dissolve into the superficial waters inhabited by the species. Specimens were most often found in the mud among the lower parts of the shoreline vegetation. Co-occurring gastropod species are *Melanopsis* spp., *Theodoxus* spp., *Belgrandia gibba* (Draparnaud, 1805), *Hydrobia acuta* (Draparnaud, 1805), *Pseudamnicola subproductus* (Paladilhe, 1869), *Diegus gasulli* (Boeters, 1981) and *Potamopyrgus antipodarum* (Gray, 1843).

The species is distributed in springs, streams, small rivers, coastal lakes (étangs) and ditches near the Mediterranean coast of southern France, the Iberian Peninsula and North Africa (Boulaassafer *et al.* 2018) and on the island of Majorca (Fig. 1). It has also been reported near the Atlantic coast of the Iberian Peninsula, northern France, Apennine peninsula, Great Britain and various Atlantic islands (Wollaston 1878; Kerney 1999; Bodon *et al.* 2005; Kadolsky 2011). We were unable to confirm previous records of the species for Great Britain (Baker *et al.* 1999; Abrehart & Forster 2012), the Azores islands (Wollaston 1878) and North Africa (Taybi *et al.* 2017). Some of these citations may have been incorrectly attributed to *M. similis* instead of *M. tachoensis*, which is found in, at least, Great Britain (see below).

Remarks

The material here referred to as *M. similis* from southern France (Fig. 4I–K, N–O) closely conforms to the neotype of this species in terms of shell shape, size and colouration (for comparison with the

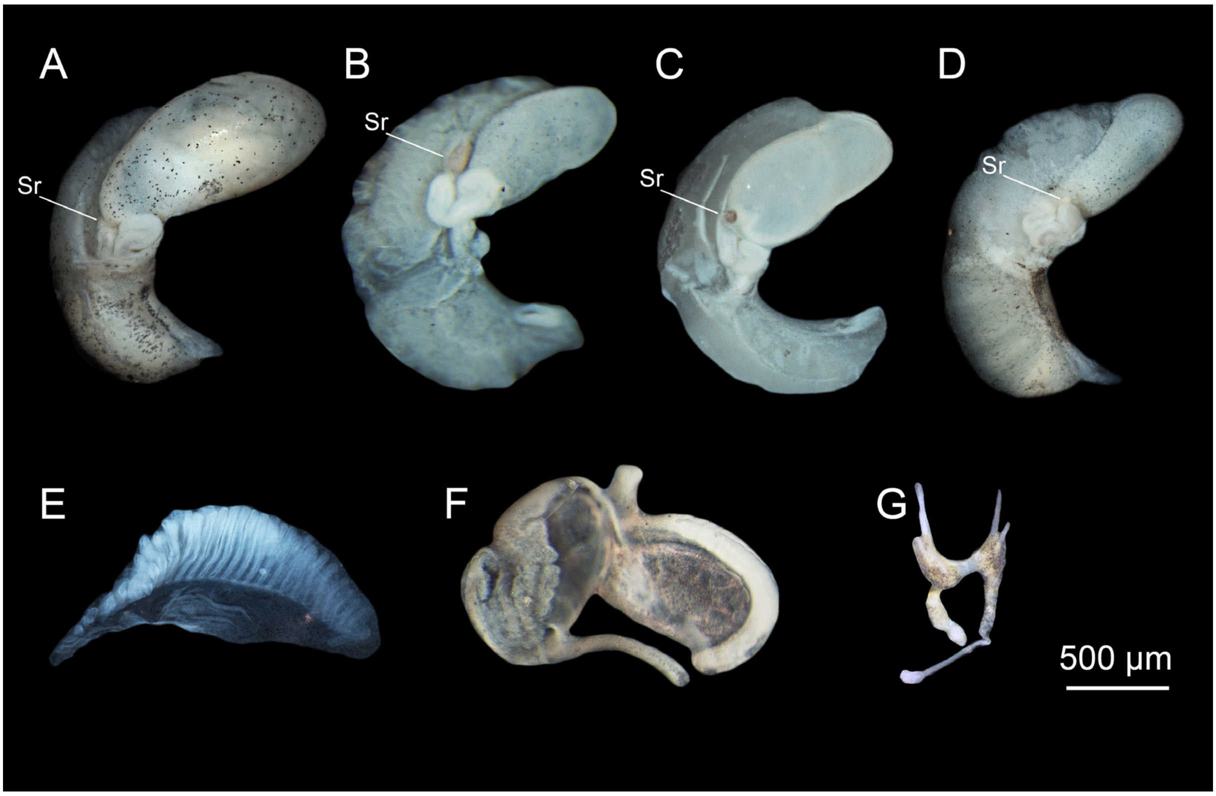

Fig. 6. Anatomy of *Mercuria similis* (Draparnaud, 1805). **A**–**D**. Female genitalia. **A**. Font Dame Spring, Salses-le-Château, Languedoc-Roussillon, France. **B**–**C**. Galayo´s Pond, Fuentalbilla, Albacete, Spain. **D**. Pond in La Palme, Languedoc-Roussillon, France. **E**–**G**. Arc River near Les Cabanes, Bouches-du-Rhône, France. **E**. Ctenidium and osphradium. **F**. Stomach. **G**. Perioesophageal ring.

type material, see Boeters & Falkner (2017: fig. 9) or Eschner *et al.* (2020: fig. 1t)). Based on our morphological and previous phylogenetic results (Miller *et al.* 2022), we suggest that several populations previously assigned to other species of *Mercuria* should now be considered as members of *M. similis* (see discussion), which increases the known geographic range and intraspecific variation of this species.

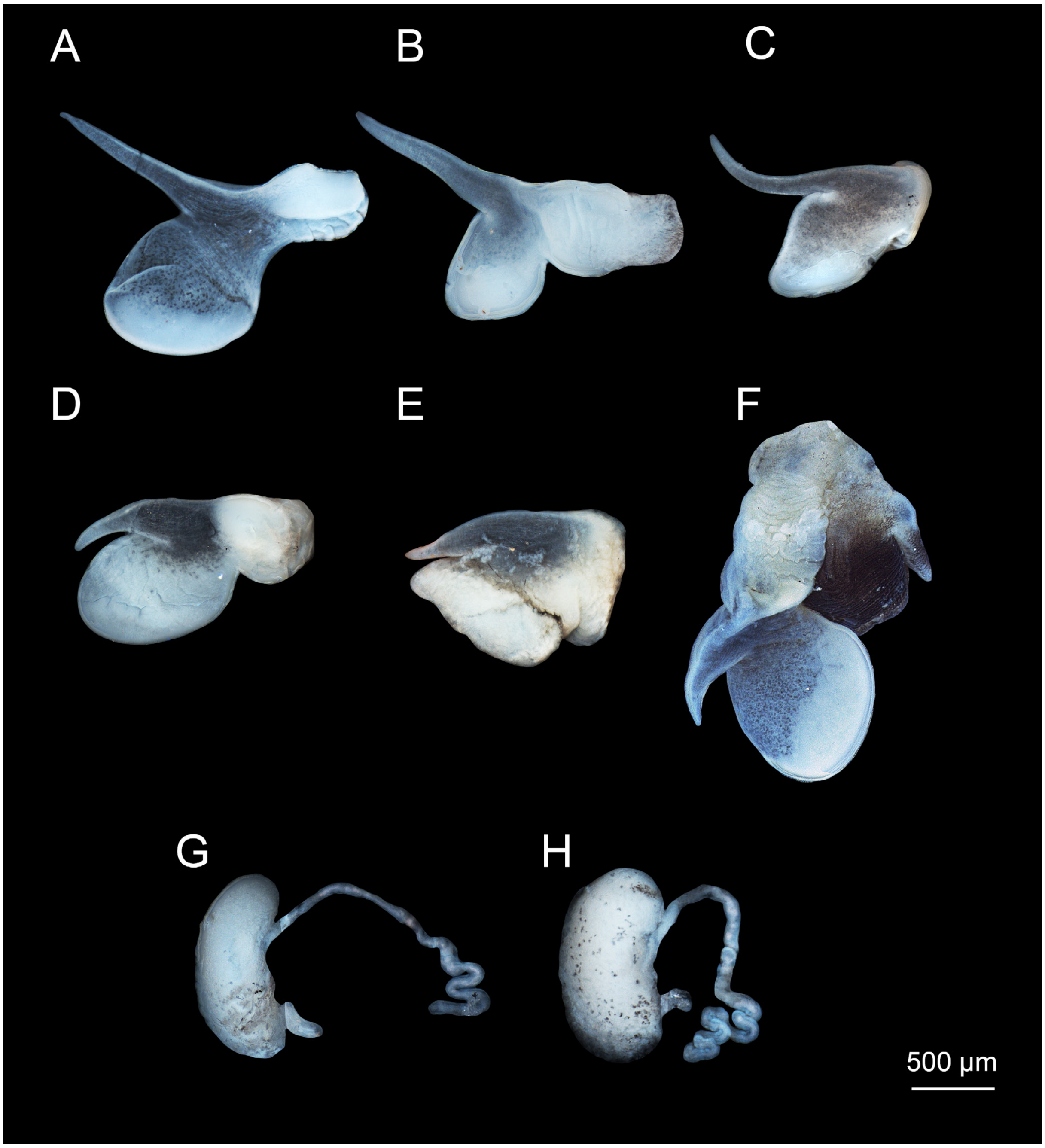

Fig. 7. Male genitalia of *Mercuria similis* (Draparnaud, 1805). **A**–**E**. Penis. **F**. Penis and head. **G**–**H**. Prostate gland. **A**. La Cañada Stream. **B**. Font d´Estramar Spring. **C**. Fonte Dame Spring. **D**. Pond in La Palme. **E**. Barranco de las Negras. **F**. Stream crossing the town of Peralta de la Sal. **G**. Saltings of Riba de Santiuste, Guadalajara. **H**. Font d´Estramar Spring.

The species' moderate shell variation can be observed across its geographic range (Figs 1, 4). However, the PCA displayed all populations identified as *M. similis* in proximity, suggesting a low level of intraspecific variation in shell shape. Most of the variation is attributed to differences in colour pattern and shell size. Although some individuals are orangish-brown [e.g., those from the La Cañada Stream (MNCN 15.05/94770), stream feeding Galayo's Pond (MNCN 15.05/94771), the stream in Peralta de la Sal (MNCN 15.05/94774) and the Arc River near Les Cabanes (MNCN 15.05/94790), Fig. 4B–C, G, N] the majority of the specimens have a whitish-grey periostracum. Another character that affects the perception of shell colour is the colouration of the epithelium. Most specimens have a darkly pigmented epithelium, though a few have an unpigmented epithelium [e.g., individuals from Barranco del Agua Salada (MNCN 15.05/94772), Fig. 4E]. Unpigmented individuals were found cohabiting with pigmented ones in MNCN 15.05/94772. Additionally, the species presents moderate variability in shell size both within and among populations (Supp. file 2: Table S2), varying from 3.00–4.84 mm, although larger specimens (5.4–5.7 mm) were found in the saltings in Riba de Santiuste, Guadalajara (MNCN 15.05/94762). This variability is likely influenced by environmental factors, such as flow rate and turbidity (Verhaegen *et al.* 2018), and by the relative age of the animal. Hydrobiids are generally univoltine (i.e., have one generation per year) and semelparous (i.e., breed only once in a lifetime). In the case of the population from Riba de Santiuste, we found animals from a previous generation living together with adults from the current one. The older specimens (i.e., those with a greater number of whorls) collected from this population were indeed the larger-sized adults.

Major anatomical differences are observed in penis features, with three penis morphotypes found in the populations examined: 1-distal end of the penis longer than the penial appendix (Fig. 7A–B), 2-distal end of the penis and penial appendix about the same length (Fig. 7C), 3-distal end of the penis shorter than the penial appendix (Fig. 7E–F). This variation was observed within individual populations and thus does not correspond with any geographic distribution pattern. Holyoak *et al.* (2017) described the same phenomenon for *M. tachoensis*. These authors attributed the variation to allometric changes in the sexual maturity of the animals that occur during the reproductive season. Boulaassafer *et al.* (2018) found high variability of penis features in parasitized specimens of *M. tensiftensis*. Nevertheless, in our case, none of the specimens of *M. similis* dissected were parasitized.

Mercuria similis can be distinguished from the phylogenetically closest species *M. egarensis* sp. nov. and *M. carrillorum* sp. nov. by its larger, more globose shell (Fig. 3). It can be distinguished from the geographically closest species *M. balearica* by its larger, more globose shell and also its slightly smaller, often pigmented, penial appendix and from *M. tachoensis* by its distant geographic distribution (*M. tachoensis* lives in Atlantic coastal zones, whereas *M. similis* inhabits Mediterranean areas), granulated protoconch microsculpture and radula, which present one cusp less on the central and lateral teeth.

Mercuria tachoensis (Frauenfeld, 1865)

Figs 8–10; Supp. file 2: Tables S6–S9

Amnicola tachoensis Frauenfeld, 1865: 529.
Mercuria edmundi Boeters, 1986: 126, fig 4–7. pl. 18a fig. 2.

Mercuria edmundi – Boeters 1988: 209, figs 96–98. — Holyoak *et al.* 2017: 208, fig. 2.
Mercuria tachoensis – Boeters 1988: 207, figs 99–103.

non *M. bayonnensis* (Locard, 1894) – Boeters & Falkner 2017 [in part]: 230, fig. 6p.
non *M. anatina* (Poiret, 1801) – Boeters & Falkner 2017 [in part]: 239, fig. 2.

Revised diagnosis

Shell ovate-conic; aperture obliquely and broadly ovate; protoconch microsculpture pitted; periostracum whitish to pale grey; central radular tooth formula (3)4-C-4(3)/1-1; female genitalia with bursa copulatrix elongate, ca 4 times as long as wide; seminal receptacle pyriform; penis darkly pigmented; penial appendix longer than the distal end of the penis, strongly pigmented at the junction with the penis, pigmentation gradually weakens from the junction until two-thirds of the appendix where it is weak; penial appendix base narrow, distally positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.61); cerebral ganglia approximately equal in size.

Type material (not examined)

Syntypes

PORTUGAL • 2 specs (sex unknown); NHMW 113526 to 113531.

Type locality

According to the original description, the type locality is a spring close to the Tagus River [Quellen des Tajo bei Ajuda] near Ajuda, Lisbon, Portugal.

Material examined

PORTUGAL • 30 specs; Mataçaes, Fonte dos passarinhos Spring; MNCN 15.05/94807 • 30 specs; Coimbra, Fonte dos Amores Spring; MNCN 15.05/94809 • 30 specs; Coimbra, spring in Jardim da Sereia; MNCN 15.05/94810 • 30 specs; Leiria, Alpedriz Spring, Nascente do Senhor Jordão; MNCN 15.05/94811 • 30 specs; Leiria, Alpedriz, Das Mouras Spring; MNCN 15.05/94812 • 30 specs; Leiria, spring in Salir de Matos; MNCN 15.05/94813 • 30 specs; Leiria, São Gregório da Fanadia, Padre Antonio Spring; MNCN 15.05/94814 • 30 specs; Santarém, spring along road N114 near the crossing to Moçarria and Vila Nova da Babeca; MNCN 15.05/94815 • 30 specs; Santarém, Ereira, spring in Rua da Fonte; MNCN 15.05/94816 • 30 specs; Leiria, spring in São Mamede; MNCN 15.05/94817 • 30 specs; Lisbon, pond in Pragança; MNCN 15.05/94818 • 30 specs; Lisbon, Ericeira, Fonte do Cabo Spring; MNCN 15.05/94819 • 30 specs; Lisbon, Mafra, Fonte dos Tritôes Spring; MNCN 15.05/94820 • 30 specs; Lisbon, Carvoeira, spring in Valbom; MNCN 15.05/94821 • 30 specs; Mafra, Ribiera da Maciel Forro, Fonte da Ribera Spring; MNCN 15.05/94822 • 30 specs; Lisbon, Almargem do Bispo, spring in Vale de Lobos; MNCN 15.05/94823 • 30 specs; Setúbal, Oleiros, Fonte de Oleiros Spring; MNCN 15.05/94824 • 30 specs; Baixo Alentejo near Pomarão, Guadiana River; MNCN 15.05/94825.

UNITED KINGDOM • 1 spec.; Arundel, stream outflowing from Swanbourne Lake; UGSB 14156 • 280 specs; Barking, Cuckold's Haven Wetland, reed belt of Hand Trough Creek; UGSB 14157 • 30 specs; West Sussex, Burpham, Arun Banks; MNCN 15.05/94828.

SPAIN • 30 specs; Asturias, Camoca, Fuente Tebia Spring; MNCN 15.05/94808.

FRANCE • 30 specs; Mouguerre, stream near Chemin d'Elizaberry; MNCN 15.05/94826 • 30 specs; stream near the beach in Bidart; MNCN 15.05/94827.

THE NETHERLANDS • 8 specs; Hoogvliet, small stream; UGSB 23178 • 8 specs; Hoogvliet, junction of the running surface in the tidal area; UGSB 23179 • 3 specs; Hoogvliet, Ruigeplaatbosch Park, Oude Maas River; ; wet reed land; UGSB 23177.

Additional locality information is provided in Supp. file 1: Table S1.

Description

SHELL. Ovate to ovate-conic, whorls 4–5, height 2–4 mm, width 2–3 mm (Fig. 8A–G; Supp. file 2: Table S6); periostracum yellowish to pale grey, occasionally dark brown; protoconch of 1.5 whorls, ca 350 µm wide, nucleus ca 180 µm wide (Fig. 9A–B); protoconch microsculpture pitted (Fig. 9C); teleoconch whorls convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of

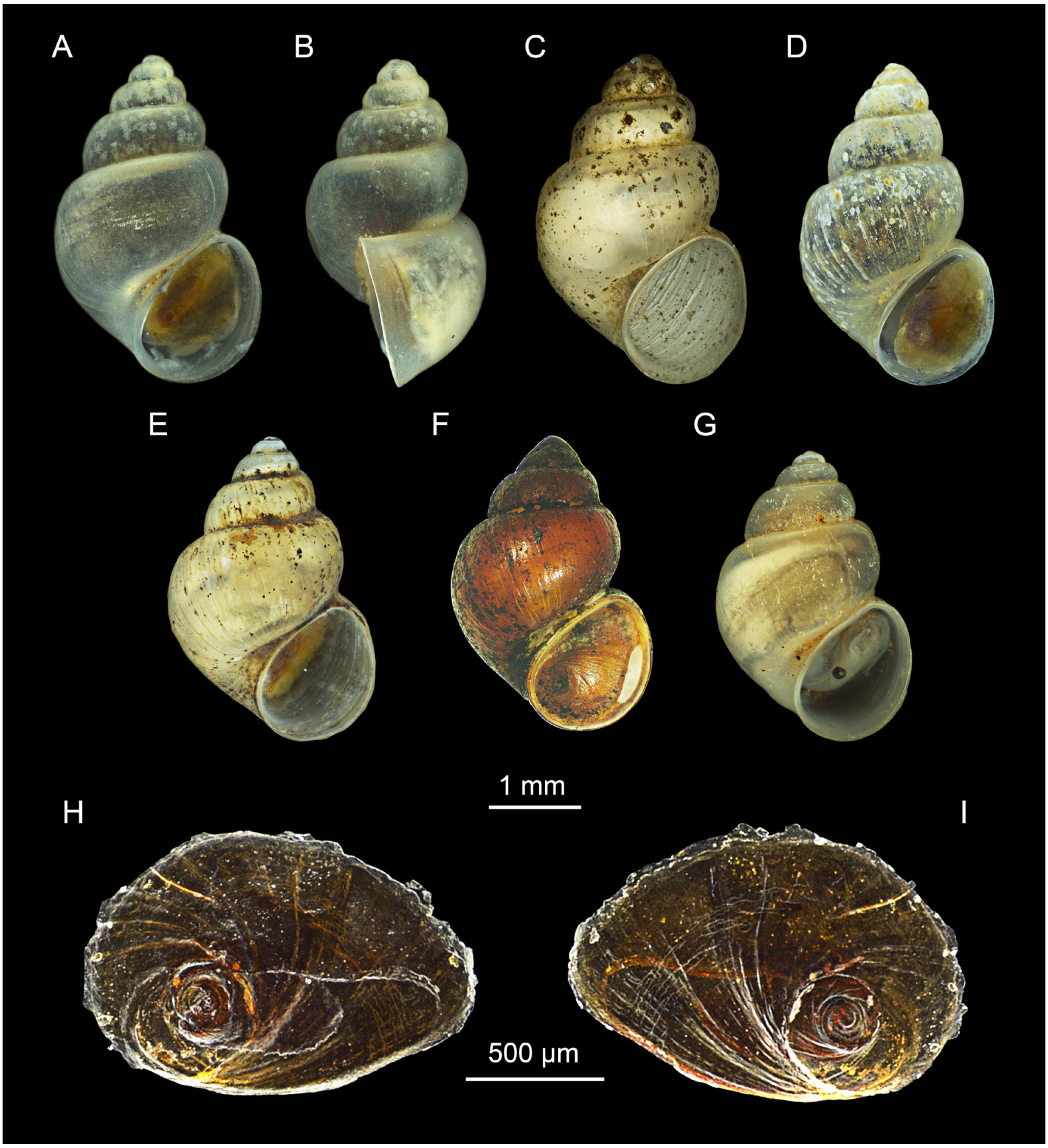

Fig. 8. Shells and operculum of *Mercuria tachoensis* (Frauenfeld, 1865). **A–B**. Spring at Saô Mamede, Leiria, Portugal. **C**. Oude Maas at Hoogvliet, Netherlands. **D**. Das Mouras Spring, Alpedriz, Leiria, Portugal. **E**. Arun Banks, Burpham, West Sussex, United Kingdom. **F**. Spring at Vale de Lobos, Almargem do Bispo, Lisboa, Portugal. **G–I**. Spring at Jardim da Sereia, Coimbra, Portugal. **H**. Operculum, inner side. **I**. Operculum, outer side.

the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin slightly reflexed; inner lip attached to the body whorl; umbilicus narrow, not covered by the inner lip (Fig. 8A, C–G).

Operculum. As for the genus, orange to brown, sometimes yellowish, about two whorls; muscle attachment oval, located near the nucleus (Fig. 8H–I).

Radula. Length intermediate, ca 800 µm long (35% of total shell length), containing about 65 rows of teeth. Central tooth formula (4)3-C-3(4)/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 9D). Lateral tooth formula (3)4-C-4(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 12–17 cusps; outer marginal teeth with 17–27 cusps (Fig. 9E–F). Radular data were collected from the following specimens: MNCN 15.05/94808 – Fuente Tebia Spring, Camoca, Asturias, Spain; MNCN 15.05/94820 – Dos Tritôes Spring, Mafra, Lisbon, Portugal; MNCN 15.05/94821 – spring in Valbom, Carvoeira, Lisbon, Portugal; MNCN 15.05/94824 – Fonte de Oleiros Spring, Oleiros, Setúbal, Portugal; MNCN 15.05/94826 – stream near Chemin d'Elizaberry, Mouguerre, France; MNCN 15.05/94827 – stream near the beach in Bidart, France; MNCN 15.05/94828 – Arun Banks, Burpham, West Sussex, United Kingdom.

Pigmentation and anatomy. Animal usually darkly pigmented, head and tentacles black to brown, pigmentation lighter on eye lobes and snout; snout about as long as wide, approximately parallel-sided, with medium distal lobation (Fig. 10B). Ctenidium occupying almost the total length of the pallial cavity; 20–26 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 10D). Pallial tentacle present. Osphradium elongate, more than 3 times as long as broad, positioned opposite middle

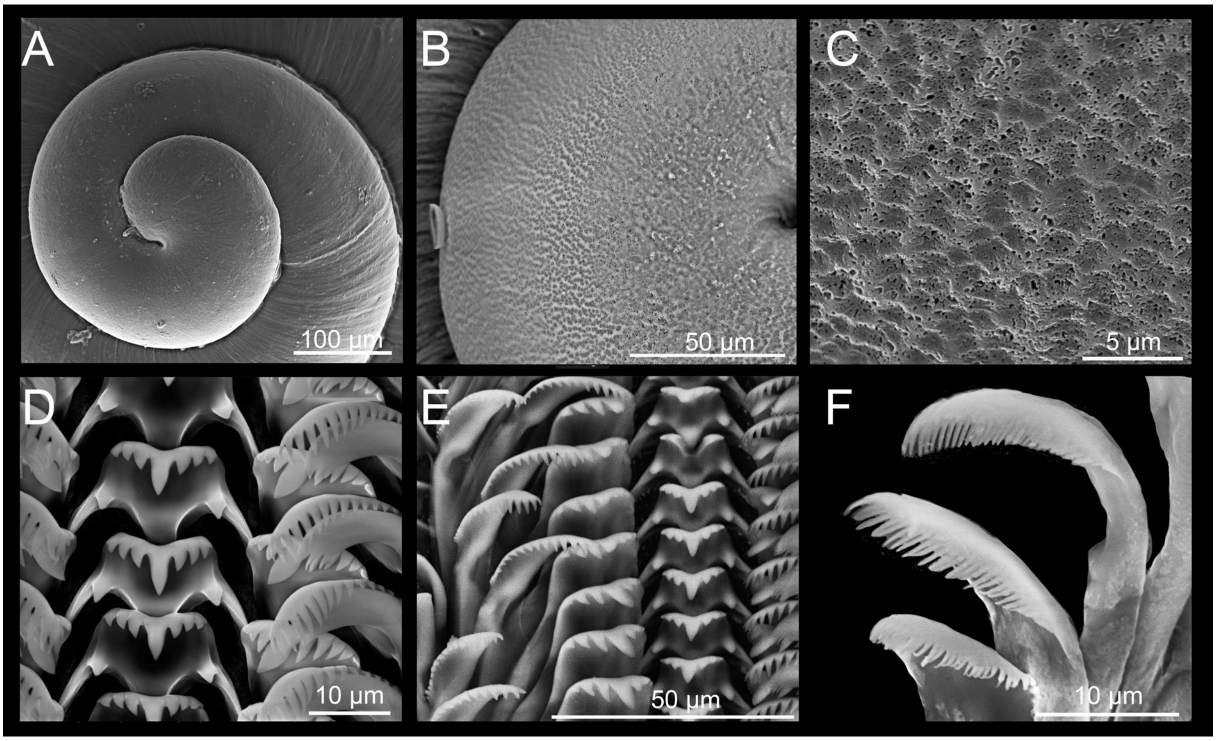

Fig. 9. Protoconch and radula of *Mercuria tachoensis* (Frauenfeld, 1865). **A–C**. Fonte dos Amores Spring, Coimbra, Portugal. **A**. Protoconch. **B**. Details of the protoconch. **C**. Protoconch microsculpture. **D–E**. Stream near the beach in Bidart, France. **D**. Detailed view of the central and lateral teeth. **E**. Detailed view of the outer marginal teeth. **F**. Spring at Jardim da Sereia, Coimbra, Portugal.

of ctenidium. Stomach almost as long as wide with two chambers almost equal in size (Supp. file 2: Table S7); style sac longer than wide, with the unpigmented intestine surrounding its distal end before continuing on as a straight rectum (Fig. 10E).

Male genitalia. Prostate gland bean-shaped, about 2 times as long as wide (Supp. file 2: Table S9), connected by the posterior vas deferens to a convoluted seminal vesicle and the testis. Pallial vas deferens emerge near both the anterior end of the prostate gland and the external margin of the penis (Fig. 10C). Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix longer than the distal end of the penis, strongly pigmented at the junction with the penis, pigmentation gradually weakens from the junction until two-thirds of the appendix where it is weak. Penial appendix base narrow, distally positioned on the inner edge of the penis (Fig. 10B).

Female genitalia. Glandular oviduct 2.5 times as long as wide; albumen gland and capsule gland about the same length (Fig. 10A); bursa copulatrix elongate, ca 4 times as long as wide (Supp. file 2: Table S8); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal receptacle pyriform, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct (Fig. 10A).

Nervous system. Slightly pigmented, elongate (mean RPG ratio = 0.61; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 7 times as long as pleuro-suboesophageal one (Fig. 10F).

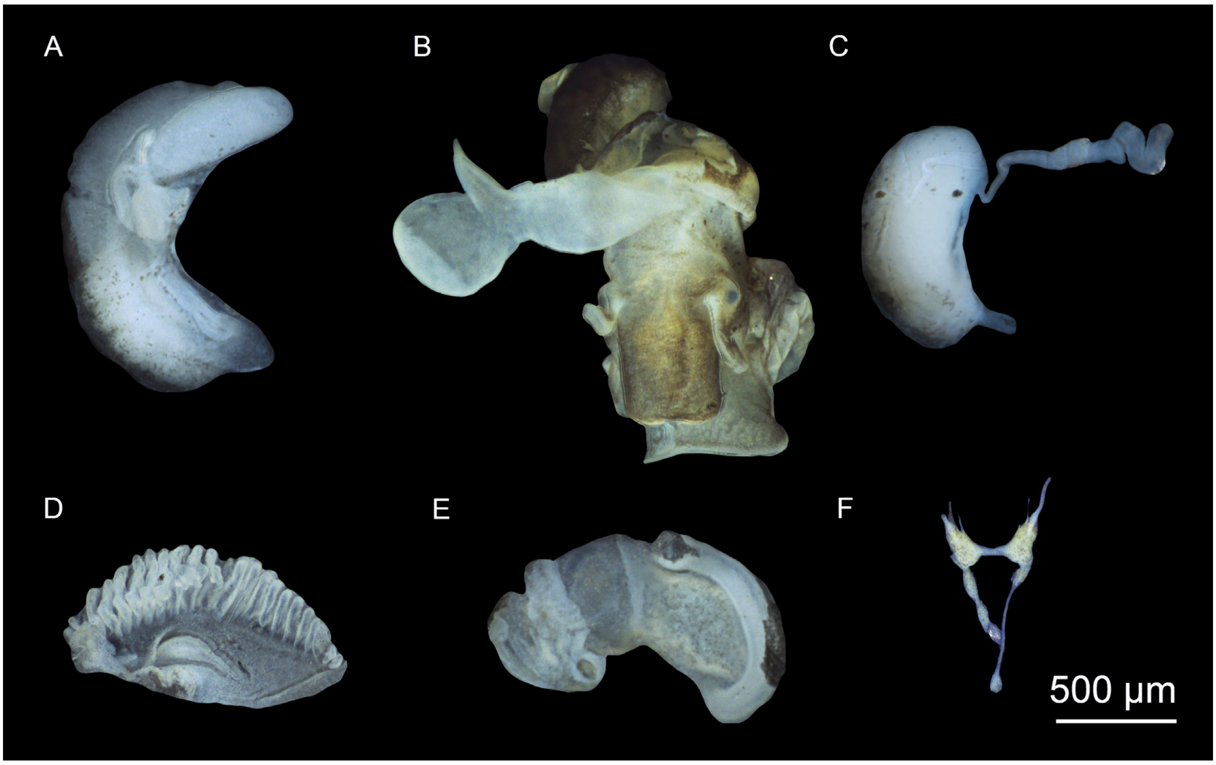

Fig. 10. Anatomy of *Mercuria tachoensis* (Frauenfeld, 1865) from Nascente do Senhor Jordão Spring, Alpedriz, Leiria, Portugal. **A**. Female genitalia. **B**. Animal and penis. **C**. Prostate gland. **D**. Ctenidium and osphradium. **E**. Stomach. **F**. Perioesophageal ring.

Ecology and distribution

Mercuria tachoensis has a lower conductivity tolerance than *M. similis*. The analysed populations of this species from Spain, Portugal and France inhabit springs, streams and ponds with conductivities from 359 to 1805 µS/cm. Water parameters of the localities in the UK and the Netherlands were not available. Specimens were usually found inside the water. Amphibious behaviour has not been commonly observed in this species, except for populations located on the tide banks of the Guadiana River (David Holyoak pers. com.) and those of the Arun River (Martin Willing pers. com.). The species occurs sympatrically with the gastropod species *Theodoxus* aff. *fluviatilis* (Linnaeus, 1758), *Belgrandia lusitanica* (Paladilhe, 1867), and *Potamopyrgus antipodarum.*

This species was previously recorded from springs and streams in Portugal. In this study, we report new records, extending its distribution to include northern Spain, northern France, the UK and the Netherlands (Fig. 1). At these localities, the species was found in the tidal mud of small rivers near the river mouth. According to this extended distribution, *M. tachoensis* inhabits water bodies that have an Atlantic drainage. The type locality of the species has likely disappeared due to the extensive growth of the city of Lisbon, intensive exploitation of local aquifers and pollution. Recent surveys around Ajuda, Lisbon, did not yield any new records (Rui da Costa Mendes pers. com.).

Remarks

Based on our morphological observations and previous phylogenetic results (Miller *et al*. 2022), we suggest several synonymization of several previously described species of *Mercuria* to *M. tachoensis* (see Discussion), which increases the previously known geographic range and intraspecific variation of this species.

The species' moderate shell variation can be observed across its geographic range (Figs 1, 8). Also, the PCA (Fig. 3) showed near the all populations identified by Miller *et al.* (2022) as *M. tachoensis*, (although it is closely related in shape to *M. balearica*), suggesting a low level of intraspecific variation in shell shape. This variability is due to differences in overall shell shape and colour pattern. Regarding shell shape, we found populations with only elongated ovate-conic shells [e.g., Fonte dos Amores Spring (MNCN 15.05/94809), spring in Jardim da Sereia (MNCN 15.05/94810), spring in Rua da Fonte, Ereira (MNCN 15.05/94816), Arun Banks (MNCN 15.05/94828)] or only ovate-conic shells [e.g., spring in Salir de Matos (MNCN 15.05/94813), Fonte dos Tritôes Spring (MNCN 15.05/94820)]. We also observed populations with both shell morphotypes [e.g., Fonte dos Passarinhos Spring (MNCN 15.05/94807), spring in Vale de Lobos (MNCN 15.05/94823), Fonte de Oleiros Spring (MNCN 15.05/94824)]. Colour pattern does not show high intraspecific variation: only the specimens from the spring in Vale de Lobos (MNCN 15.05/94823) are remarkable for being particularly darkly coloured with a dark brown thick periostracum (Fig. 8F) compared with the rest of the specimens, which have yellowish-brown periostracum.

Anatomically, the bursa copulatrix is about the same size in all of the dissected specimens of the species, except for those from the spring in Jardim da Sereia (MNCN 15.05/94810) and Nascente do Senhor Jordão (MNCN 15.05/94811), which are considerably smaller (Supp. file 2: Table S8). Males from the stream near Chemin d'Elizaberry (MNCN 15.05/94826) and Nascente do Senhor Jordão, Alpedriz (MNCN 15.05/94811) have the smallest prostate glands and penises. Despite this, all males present the same penis characteristics: a rounded, pigmented penial appendix that is longer than the distal end of the penis. However, Boeters (1988) described the penis as longer than the penial appendix. Based on this discrepancy in the size and shape of the male genitalia, Holyoak *et al*. (2017) proposed *M. edmundi* as a junior synonym of *M. tachoensis* and described an allometric growth of the male genitalia related to the sexual maturity of the animals. Miller *et al*. (2022) confirmed with taxonomic multilocus data that only one species occurs in the localities where both species have been cited.

Mercuria tachoensis differs from all the Iberian congeners by its pitted protoconch microsculpture (which is granulated in the rest of the species; visible only with electronic microscopy). In addition to this character, it differs from the phylogenetically closely related species *M. similis* and *M. egarensis* sp. nov. by often having one more cusp in the central radular teeth and a longer bursa copulatrix (ca 4 times as long as wide). Although our PCA (Fig. 3) was unable to differentiate *M. tachoensis* and *M. carrillorum* sp. nov. by shell shape, both species can be distinguished by differences in the radula (smaller in *M. carrillorum* and often with one cusp less in the lateral teeth), the bursa copulatrix (smaller in *M. carrillorum*) and the male genitalia (the distal end of the penis is longer than the penial appendix, which is flattened, ovate and less pigmented in *M. carrillorum*).

Mercuria balearica (Paladilhe, 1869)
Figs 11–14; Supp. file 2: Tables S10–S13

Amnicola balearica Paladilhe, 1869: 113.

Mercuria balearica – Boeters 1988: 207, figs 106–107.
Pseudamnicola balearica – Quintana 2019: 19, fig 1a.

Revised diagnosis

Shell ovate-conic; aperture obliquely broad ovate; protoconch microsculpture granulated; central radular tooth formula (4)3-C-3(4)/1-1; glandular oviduct 2.5 times as long as wide; albumen gland longer than capsule gland; bursa copulatrix pyriform to elongate; seminal receptacle elongate, with a short duct; penis darkly pigmented, as long as the penial appendix; penial appendix unpigmented or slightly pigmented at the junction with the penis, rounded, small, base narrow, medially positioned on the inner edge of the penis; nervous system pigmented, elongated (mean RPG ratio = 0.53).

Type material (not examined)

Syntype
FRANCE • 1 spec. (sex unknown); UM.PLD.005 (Breure & Audibert 2017).

Type locality

According to the original description (Paladilhe 1869), the type locality is Port Mahon, Minorca, Balearic Islands [Port-Mahon (Illes Balears)].

Material examined

SPAIN – **Islas Baleares** • 30 specs; Minorca, Colarsega River in Port Mahon; MNCN 15.05/94744 • 30 specs; Minorca, stream near Sant Joan de Carbonell; MNCN 15.05/94745 • 30 specs; Minorca, Cala en Porter; MNCN 15.05/94746 • 30 specs; Minorca, Son Bou, Barranc de Bec; MNCN 15.05/94747. – **Málaga** • 30 specs; Ardales, El Chorro Spring; MNCN 15.05/94732 • 30 specs; spring in Montecorto; MNCN 15.05/94731, MNCN 15.05/94737 • 30 specs; trough in Churriana; MNCN 15.05/94733 • 30 specs; Venta El Pilar Spring; MNCN 15.05/94734, MNCN 15.05/94738 • 30 specs; trough in Los Granados; MNCN 15.05/94735 • 30 specs; stream in Montecorto; MNCN 15.05/94736. – **Cádiz** • 30 specs; Alozaina, Valentín Spring; MNCN 15.05/94739. – **Jaén** • 30 specs; Fontanar, stream in Caño de la Rambla; MNCN 15.05/94740 • 30 specs; Peal de Becerro, Cinco Caños Spring; MNCN 15.05/94743. – **Granada** • 30 specs; Mojácar, Arabic Spring; MNCN 15.05/94741). – **Murcia** • 30 specs; spring in Sierra de la Muela; MNCN 15.05/94742.

Additional locality information is provided in Supp. file 1: Table S1.

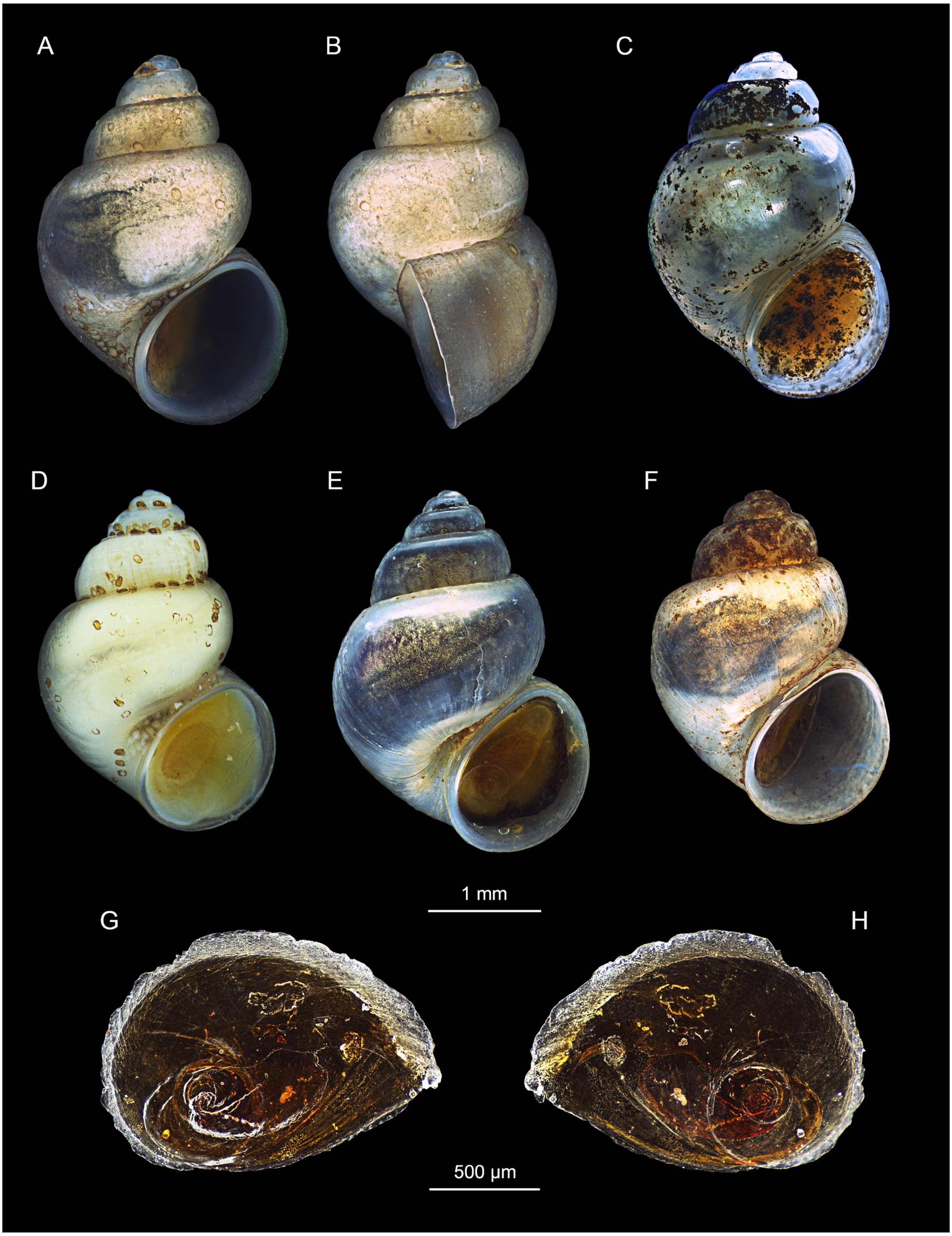

Fig. 11. Shells and operculum of *Mercuria balearica* (Paladilhe, 1869). **A–B, G–H**. Stream at Sant Joan de Carbonell, Minorca, Spain. **C**. Colarsega River, near the Port of Mahon (type locality). **D**. Fuente Árabe Spring, Mojácar, Granada, Spain (unpigmented specimen). **E**. Venta El Pilar Spring, Málaga, Spain. **F**. Spring, Alozaina, Cádiz, Spain. **G**. Operculum, inner side. **H**. Operculum, outer side.

Description

Shell. Ovate-conic, whorls 4–5, height 2–3.5 mm, width 1.4–2.6 mm (Fig. 11A–F; Supp. file 2: Table S10); periostracum yellowish to brown; protoconch with 1.5 whorls, ca 350 µm wide, nucleus less than 200 µm wide; protoconch microsculpture granulated (Fig. 12A–C); teleoconch whorls convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin straight, inner lip touching the shell wall; umbilicus narrow, not covered by the inner lip (Fig. 11A–F).

Operculum. As for the genus, orange to brown, sometimes yellowish, about two whorls; muscle attachment oval, located near the nucleus (Fig. 11G–H).

Radula. Length intermediate, ca 800 µm long (35% of total shell length), containing about 65 rows of teeth. Central tooth formula (4)3-C-3(4)/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 12D). Lateral tooth formula (3)4-C-4(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 14–18 cusps; outer marginal teeth with 15–17 cusps (Fig. 12E–F). Radular data were collected from the following specimens: MNCN 15.05/94745 – stream near Sant Joan de Carbonell, Minorca; MNCN 15.05/94747 – Barranc de Bec, Son Bou, Minorca; MNCN 15.05/94738 – Venta El Pilar Spring, Málaga; MNCN 15.05/94741 – Arabic Spring, Mojácar, Granada; MNCN 15.05/94743 – Fuente de los Cinco Caños Spring, Peal de Becerro, Jaén.

Pigmentation and anatomy. Animal slightly darkly pigmented, although unpigmented specimens were also found (Fig. 11D); head and tentacles black, pigmentation lighter on eye lobes, snout and neck; snout about as long as wide, approximately parallel-sided, with medium distal lobation. Ctenidium

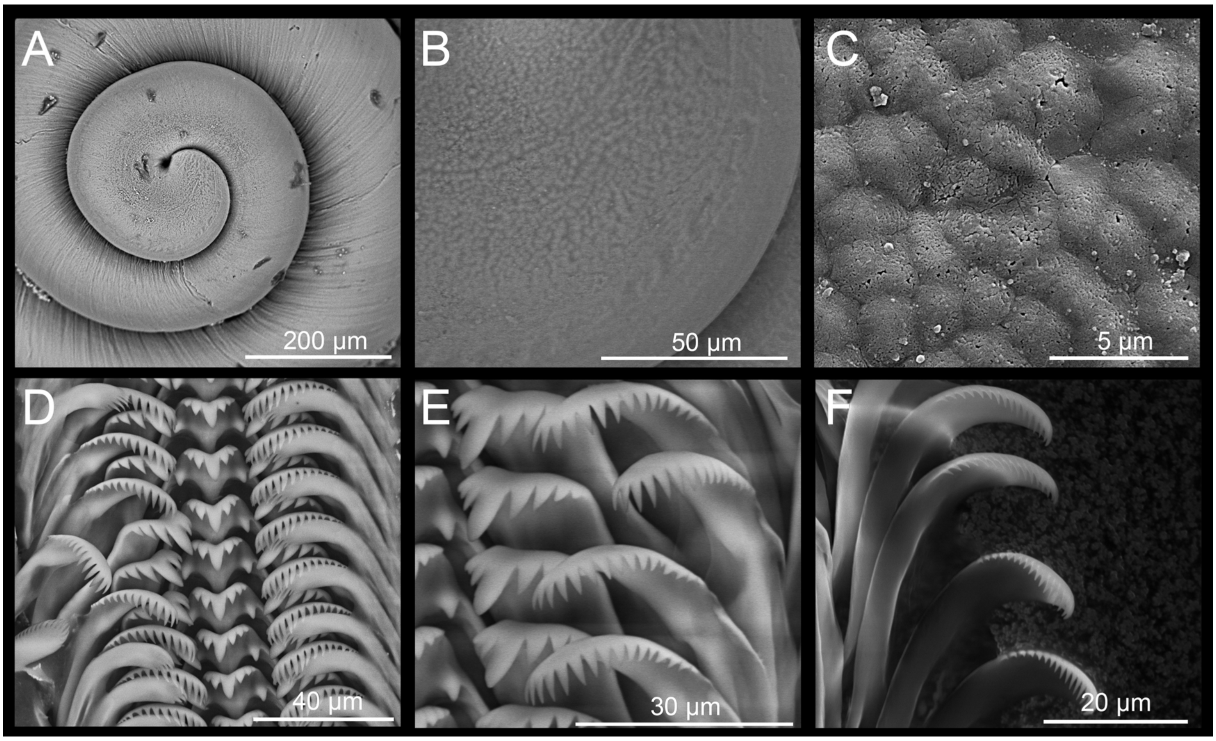

Fig. 12. Protoconch and radula of *Mercuria balearica* (Paladilhe, 1869). **A**–**C**. Venta El Pilar Spring, Málaga, Spain. **A**. Details of the protoconch. **B**. Details of the protoconch nucleus. **C**. Protoconch microsculpture. **D**–**F**. Stream at Sant Joan de Carbonell, Minorca. **D**. Overview of radular teeth rows. **E**. Rows of lateral and inner marginal radular teeth. **F**. Detailed view of the outer marginal teeth.

occupying almost the total length of the pallial cavity; 21–27 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 13D). Osphradium elongate, more than 3 times as long as broad, positioned opposite to the middle of the ctenidium. Stomach almost as long as wide with two nearly equally sized chambers (Supp. file 2: Table S11); style sac longer than wide, with the unpigmented intestine surrounding its distal part before continuing on as a straight rectum (Fig. 13E).

MALE GENITALIA. Prostate gland bean-shaped, about 2 times as long as wide (Supp. file 2: Table S13), connected by the posterior vas deferens to a convoluted seminal vesicle and the testis (Fig. 13C). Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix and distal end of the penis nearly equal in size; penial appendix unpigmented or slightly pigmented at the junction with the penis, rounded, small, base narrow, medially positioned on the inner edge of the penis (Fig. 13B).

FEMALE GENITALIA. Glandular oviduct 2.5 times as long as wide; albumen gland longer than capsule gland (Fig. 13A); bursa copulatrix pyriform (Fig. 14B–D) to elongate (Fig. 14A), ca 2 times as long as wide (Supp. file 2: Table S12), lying against the albumen gland; bursal duct shorter than bursa length; renal oviduct unpigmented, coiled, with three loops; coils can be wide open (Fig. 14E) or highly coiled (Fig. 14F–G); seminal receptacle elongate, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct (Fig. 14E–G).

NERVOUS SYSTEM. Pigmented, elongated (mean RPG ratio = 0.53; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 9 times as long as pleuro-suboesophageal one (Fig. 13F).

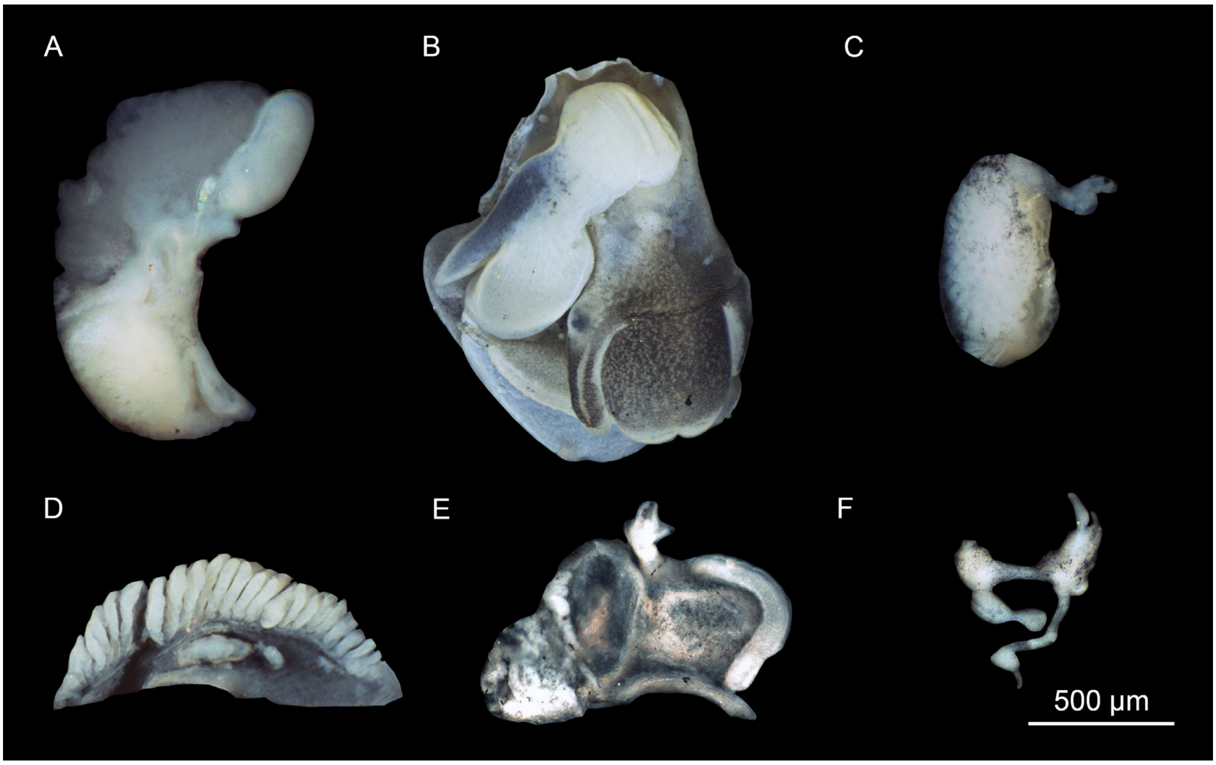

Fig. 13. Anatomy of *Mercuria balearica* (Paladilhe, 1869). **A**, **D**, **F**. Stream at Sant Joan de Carbonell, Minorca, Spain. **B**, **C**, **E**. Venta El Pilar Spring, Málaga, Spain. **A**. Female genitalia. **B**. Penis and head. **C**. Prostate gland. **D**. Ctenidium and osphradium. **E**. Stomach. **F**. Perioesophageal ring.

Ecology and distribution

Mercuria balearica presents broad ecological plasticity, inhabiting springs, streams and ponds with conductivities ranging from 179 to 2750 µS/cm. Population densities were low. During our field surveys, we found evidence of local extinctions in the regions of Andalusia and Minorca (e.g., extirpated populations in the towns of Zuheros, Arriate, Alozaina, Gaucín, Ferreries), suggesting that the species was more abundant in the late twentieth century. This species occurs sympatrically with *Pseudamnicola meloussensis* Altaba, 2007, *Theodoxus* aff. *fluviatilis*, *Melanopsis* spp. and *Potamopyrgus antipodarum.*

The species was previously cited from springs, streams, small rivers and ditches in the southern Iberian Peninsula and on the Balearic Islands of Ibiza and Minorca (Boeters 1988; Glöer *et al.* 2015). We confirmed the species in Minorca (Ibiza was not included as a field site) and in several other springs and streams in south-eastern Iberia (Fig. 1).

Remarks

The taxonomy of the species has undergone several revisions, with the most recent change occurring in 2019, when Quintana (2019) placed the species in the genus *Pseudamnicola* Paulucci, 1878. He had found an abundant population living in Colarsega River at Port-Mahon (Minorca Island), which is the type locality of *M. balearica*. He sent a subsample to the MNCN in Madrid so that we could review the classification. We confirmed that all the specimens received belong to *Pseudamnicola meloussensis* and communicated to Quintana that more exhaustive sampling would be necessary to find specimens of *M. balearica*. However, he thought that if all the specimens found in this locality are *Pseudamnicola*,

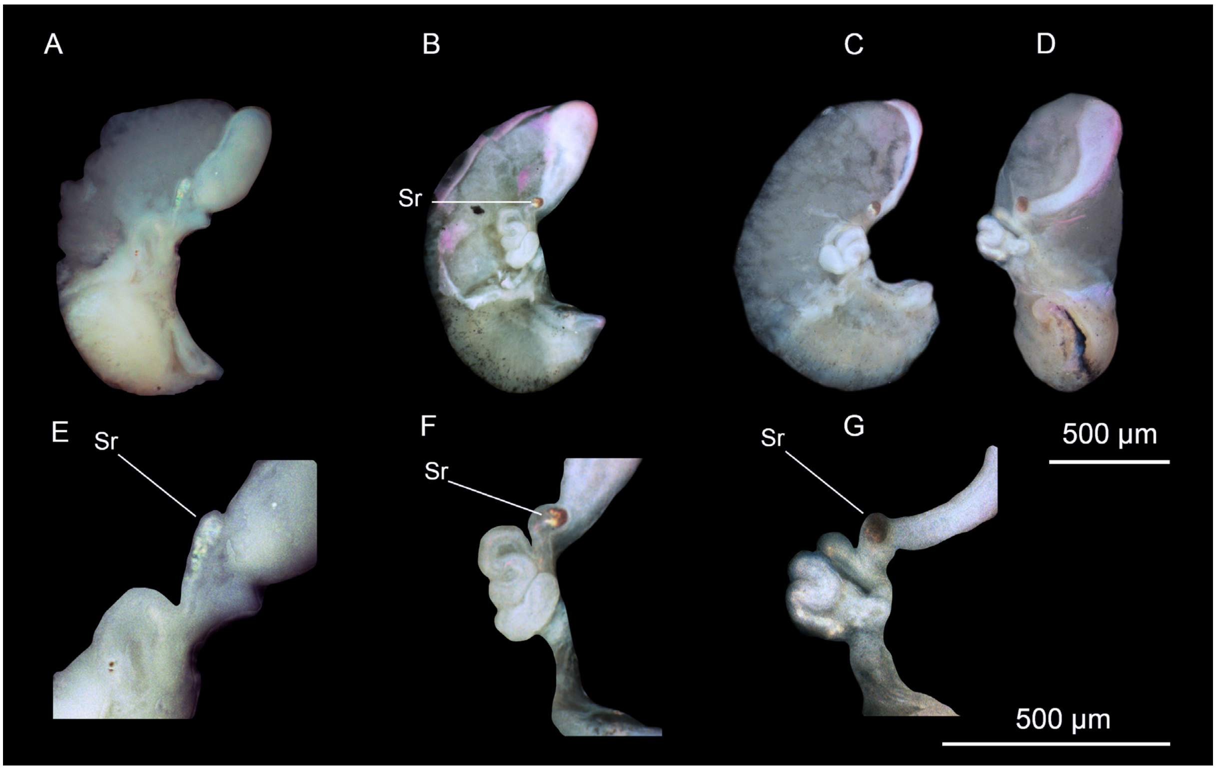

Fig. 14. Variation of the bursa copulatrix of *Mercuria balearica* (Paladilhe, 1869). **A**. Elongate, stream at Sant Joan de Carbonell, Minorca, Spain. **B**. Pyriform, Venta El Pilar Spring, Málaga, Spain. **C–D**. Pyriform, Fuente Valentín Spring, Alozaina, Cádiz, Spain. **E–G**. Detailed views of the seminal receptacle (Sr) and renal oviduct loops.

then *M. balearica* and *P. meloussensis* are probably the same species and they should be renamed as *Pseudamnicola balearica*, the species described by Paladilhe (1869) (as *Amnicola balearica*), with *P. meloussensis* consequently being a junior synonym of *P. balearica*. However, during a more detailed sampling of this population in 2018, we were able to collect a few specimens of *M. balearica* living together with *P. meloussensis*. The DNA-based sequences (Miller *et al.* 2022) and shell morphology (Fig. 11C) of these specimens correspond to those of a member of *Mercuria*, confirming their placement in this genus (and their continued presence at the type locality).

Our morphological observations (this study) and DNA results (Miller *et al.* 2022) confirm the previous assignments of other Iberian populations to *M. balearica* (Boeters 1988; Glöer *et al.* 2015). Populations from the stream near Sant Joan de Carbonell, Minorca (MNCN 15.05/94745), Venta El Pilar Spring, Málaga (MNCN 15.05/94738) and Fuente Valentin Spring, Cádiz (MNCN 15.05/94739) accounted for most of the morphological variation observed between Minorcan and Iberian populations. Sequence divergence of COI among these populations was low (< 1.2%) (Miller *et al.* 2022).

Intraspecific morphological differences for this species are observed mainly in shell, penis and female genitalia features. Specimens from Minorca are generally larger in size and present globose to high-spired shells, whereas the Iberian specimens have only globose shells (Supp. file 2: Table S10). The specimens from Los Granados Trough in Málaga (MNCN 15.05/94735) have the smallest shells. All the specimens have a pigmented epithelium, though some specimens from Arabic Spring in Mojácar (MNCN 15.05/94741) are unpigmented. Variation in the male reproductive organs is as previously described for the genus: the penis is either slightly longer or shorter than the appendix, and the appendix is usually rounded and unpigmented (only the population in Peal del Becerro, Jaén presents a slightly pigmented appendix). The bursa copulatrix varies from pyriform in most of the populations to elongate in the specimens from Venta El Pilar Spring, Málaga (MNCN 15.05/94734). Populations from Minorca have both morphotypes. Females from Venta El Pilar Spring (MNCN 15.05/94734), the stream in Montecorto (MNCN 15.05/94736), Fuente Valentín Spring (MNCN 15.05/94739) and Arabic Spring (MNCN 15.05/94741) have a bursa copulatrix that surrounds the albumen gland, which is located beneath it (see Fig. 14C) rather than parallel to it (the typical orientation in other members of the genus).

Mercuria balearica can be distinguished from *M. similis* by its smaller, less globose shell, less convex body whorl, shorter tapering triangular penis with a rounded unpigmented penial appendix that is slightly larger than or equal in size to the penis, pyriform bursa copulatrix and higher number of cusps on the central and lateral teeth of the radula. *Mercuria balearica* resembles *M. carrillorum* sp. nov. and *M. felixi* sp. nov. in shell shape (ovate-conic) and colour but differs from these congeners by having a shorter, more pigmented penis with a larger rounded penial appendix. Also, their distribution areas do not overlap. Sequence divergences for COI indicated that *M. balearica* is most closely related to *M. tensiftensis* and *M. felixi* (5.2% mean divergence with both species) and most distantly to *M. midarensis* and *M. melitensis* (Paladilhe, 1869) (8.6% mean divergence with both species) (Miller *et al.* 2022).

Mercuria maceana (Paladilhe, 1869)

Figs 15–16

Amnicola maceana Paladilhe, 1869: 103.

Mercuria maceana – Bank & Neubert 2017: 16.

Revised diagnosis

Shell ovate-conic; aperture obliquely broad ovate; periostracum yellowish to pale grey; protoconch microsculpture granulated; central radular tooth formula 3-C-3/1-1.

Type material (not examined)

Syntypes

SPAIN • 1 spec. (sex unknown); Barcelona, C’an Tunis; MHNG-MOLL-105438/2 • 1 spec. (sex unknown); same collection data as for preceding; MHNL 45013950 • 1 spec. (sex unknown); same collection data as for preceding; UM.PDL.006 (Breure & Audibert 2017).

Type locality

C’an Tunis, Barcelona, Spain. The type locality of this species in the original description “récoltée à Antunez, près de Barcelone” refers to a series of local geographic names for a private property: C’an

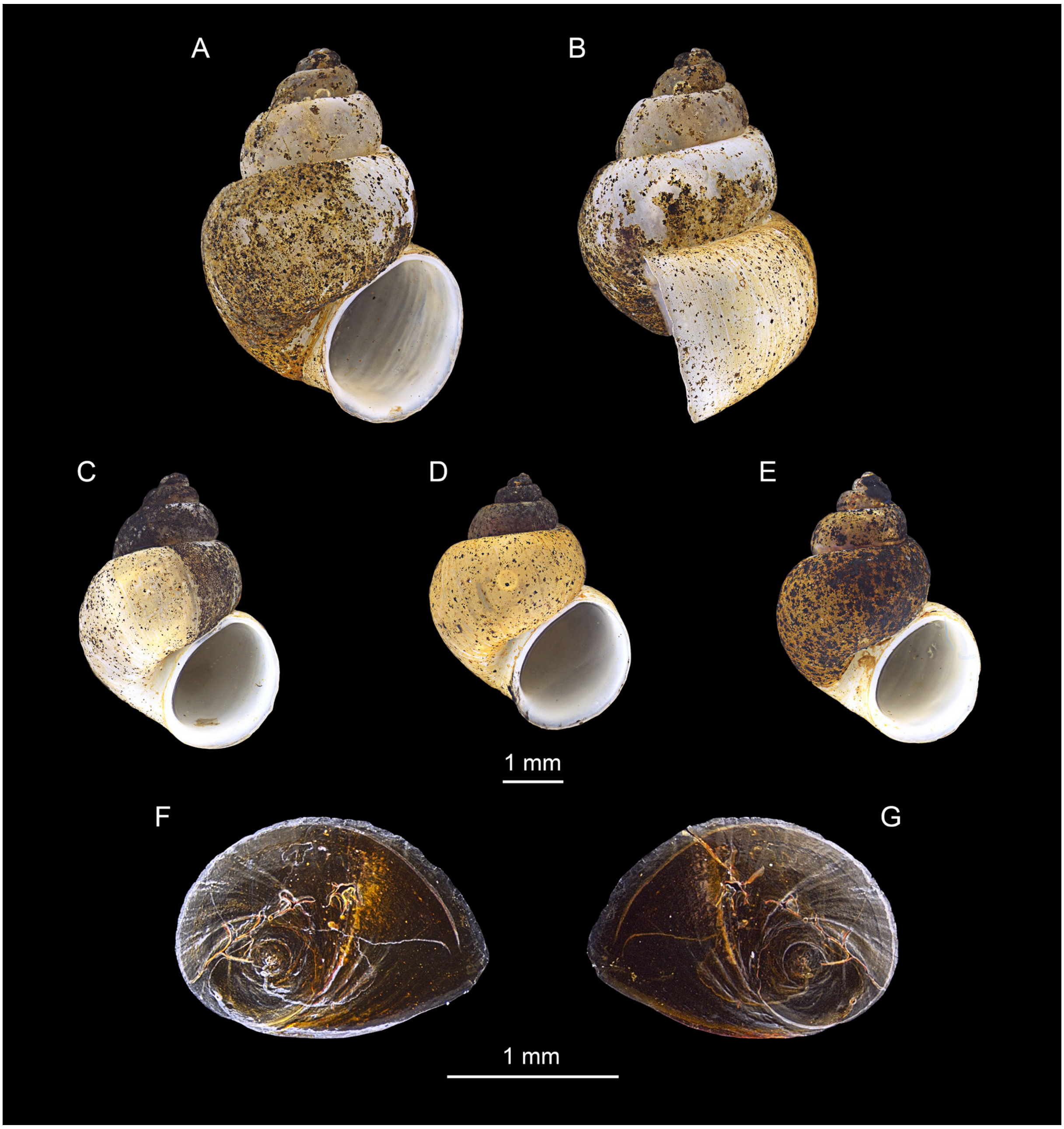

Fig. 15. Shells and operculum of *Mercuria maceana* (Paladilhe, 1869) from C’an Tunis, Barcelona, Spain. **A**–**E**. Shells. **F**. Operculum, inner side. **G**. Operculum, outer side.

Tunis, Casa Antúnez, Camp de la Bota, Llano del Llobregat. These names have been written either conserving the original language, Catalan, sometimes using the Spanish form, or even using other local names for the same place.

Material examined

SPAIN • 30 specs; Barcelona, C'an Tunis; MNCN 15.05/7009 • 30 specs; same collection data as for preceding; MZB 77-8445, MZB 77-8107.

Description

Shell. Ovate-conic, whorls 4–5, height 3.9–5.2 mm, width 3–3.8 mm (Fig. 15A–E); periostracum yellowish to pale grey; protoconch of 1.5 whorls, ca 350 µm wide, nucleus ca 200 µm wide (Fig. 16A); protoconch microsculpture granulated (Fig. 16B–C); teleoconch whorls convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin slightly reflexed; umbilicus narrow, not covered by the inner lip (Fig. 15A–E).

Radula. Length intermediate, ca 800 µm long (35% of total shell length), containing about 63 rows of teeth. Central tooth formula 3-C-3/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 16D). Lateral tooth formula (3)4-C-4(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 12–14 cusps; outer marginal teeth with 12–14 cusps (Fig. 16E–F). Radular data were compiled from a dry specimen (MZB 77-8445) collected from the type locality.

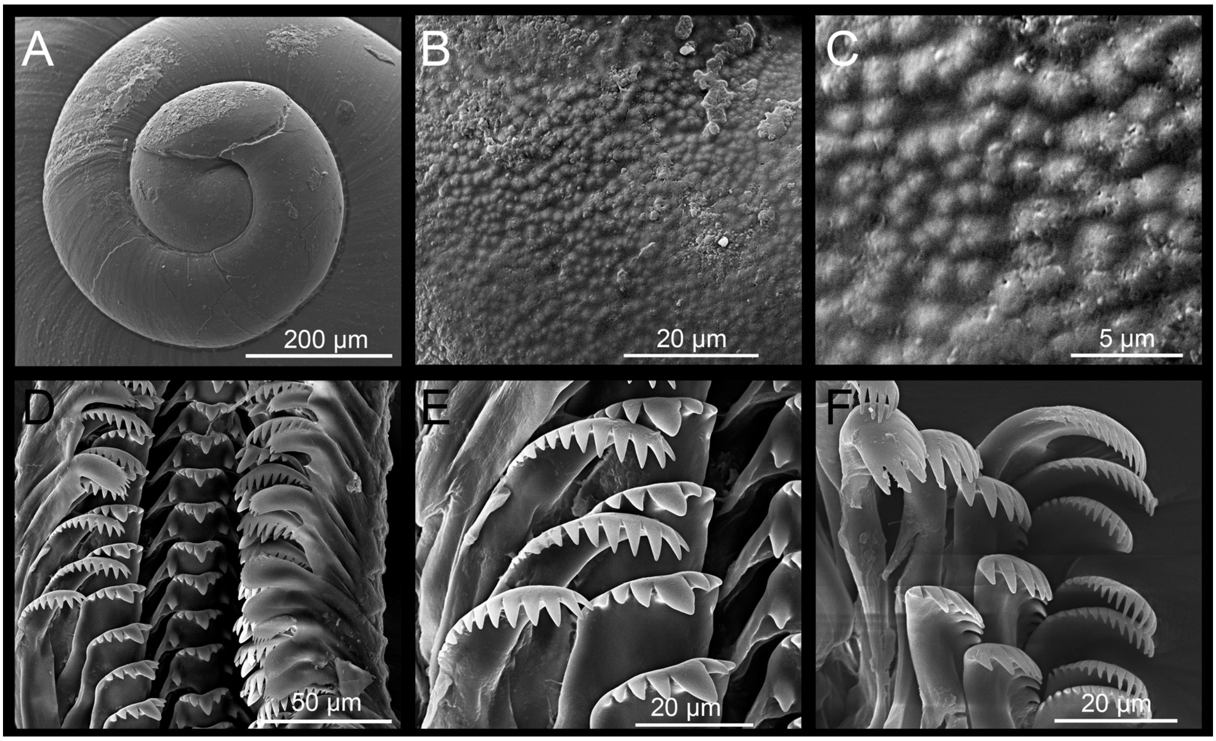

Fig. 16. Protoconch (A–C) and radula (D–F) of *Mercuria maceana* (Paladilhe, 1869) from C'an Tunis, Barcelona, Spain. **A**. Protoconch nucleus. **B**. Details of the protoconch. **C**. Protoconch microsculpture. **D**. Overview of radular teeth rows. **E–F**. Detailed view of the lateral and inner teeth.

Ecology and distribution

This species is only known from the type locality, C'an Tunis (Casa Antúnez), Catalonia, Spain. The type locality has likely disappeared due to extensive alterations (e.g., construction, pollution) of the area as a result of port works conducted in the Barcelona harbour and the industrial zone in the 1980s and the construction work carried out for the 1992 Olympic Games (Jordi Corbella and Francesc Uribe pers. com.). Recent surveys conducted around Barcelona did not yield live specimens.

Remarks

Mercuria maceana is only known from its type locality, which has been destroyed over the past few decades. Specimens of this species have not been found in the nearby areas, suggesting that the species is extinct (IUCN category EX). The shells and dry specimens of *M. maceana* deposited in the Zoological Museum of Barcelona were examined to delineate the morphological variation presented by the species and to support its recognition. Our PCA based on shell shape differentiated this species (Fig. 3). Accordingly, *M. maceana* differs from *M. egarensis* sp. nov. by its shorter and more globose or subglobose shell and is more similar to the Moroccan species *M. targouasensis*. Based on the characters observed on the radulae, *M. maceana* cannot be distinguished from *M. similis* or *M. egarensis*. We were unable to study other anatomical features due to the lack of ethanol-preserved material.

Mercuria egarensis Miller, García-Guerrero & Ramos sp. nov.

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Figs 17–19; Supp. file 2: Tables S14–S18

Diagnosis

Shell ovate-conic; aperture obliquely ovate; protoconch microsculpture granulated; periostracum whitish to pale grey; central radular tooth formula (2)3-C-3(2)/1-1; female genitalia with bursa copulatrix pyriform to elongate, ca 2.5–3 times as long as wide; seminal receptacle elongate with short peduncle; penis darkly pigmented, gradually tapering; penial appendix unpigmented, ovate, about equal in length or slightly shorter than the distal end of the penis and medially positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.57); cerebral ganglia approximately equal in size.

Etymology

The name '*egarensis*' refers to the ancient Roman city of Egara, present-day Terrassa, Catalonia, where the species occurs.

Type material

Holotype

SPAIN • sex unknown (dry preserved); Barcelona, Font de les Canyes; MNCN 15.05/200174H.

Paratypes

SPAIN • 38 specs (preserved in ethanol 80%, 10 dissected and 3 processed for DNA sequencing); same collection data as for holotype; MNCN 15.05/94752 • 13 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/94753 • 25 specs (preserved in ethanol 80%); same collection data as for holotype; MZB 2021-2798 • 1 spec. (dry preserved); same collection data as for holotype; NHMW 113529 • 2 specs (dry preserved); same collection data as for holotype; RMNH. MOL.507925 • 1 spec. (dry preserved); same collection data as for holotype; JPM-586 • 1 spec. (dry preserved); same collection data as for holotype; MCP • 1 spec. (dry preserved); same collection data as for holotype; MCP.

Type locality

Font de les Canyes, Catalonia, Spain 41.586217° N, 2.038500° E, 340 m a.s.l.

Description

Measurements. Holotype: SL = 3.32 mm, SW = 2.53 mm, SL/SW = 1.31, AH = 1.51 mm, SL-LBW = 0.86 mm, WBW = 2.05 mm, AL = 1.61 mm, AW= 1.23 mm, WPW = 1.22 mm, WAW = 0.70 mm.

Shell. Ovate-conic, whorls 4–5, height 3–4.3 mm, width 1.7–2.8 mm (Fig. 17A–E; Supp. file 2: Table S14); periostracum whitish to pale grey; protoconch of 1.5 whorls, ca 350 µm wide, nucleus ca 150 µm wide (Fig. 18A); protoconch microsculpture granulated (Fig. 18B–C). Teleoconch whorls slightly convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin straight; umbilicus narrow, not covered by the inner lip (Fig. 17A–E).

Operculum. As for the genus, orange to brown, sometimes yellowish, about two whorls; muscle attachment oval, located near the nucleus (Fig. 17F–G).

Radula. Length intermediate, ca 800 µm long (35% of total shell length), containing about 55 rows of teeth. Central tooth formula (2)3-C-3(2)/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 18D). Lateral tooth formula (3)2-C-2(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 11–15 cusps; outer marginal teeth with 15–17 cusps (Fig. 18E–F). Radular data were obtained from specimens from the type locality.

Pigmentation and anatomy. Animal slightly brownish to darkly pigmented (Fig. 19C); head and tentacles dark brown, pigmentation lighter on eye lobes, snout and neck; snout about as long as wide, approximately parallel-sided, with medium distal lobation. Ctenidium occupying almost the total length of the pallial cavity; 19–23 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 19D). Osphradium elongate, more than 3 times as long as broad, positioned opposite middle of ctenidium. Stomach almost as long as wide with two chambers almost equal in size (Supp. file 2: Table S16); style sac longer than wide, protruding anteriorly into the intestinal loop (Fig. 19E). Intestine unpigmented, continuing on as a straight rectum.

Male genitalia. Prostate gland bean-shaped, about 2 times as long as wide (Supp. file 2: Table S18), connected by the posterior vas deferens to a convoluted seminal vesicle and the testis. Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix unpigmented, ovate, about equal in length or slightly shorter than the distal end of the penis and medially positioned on the inner edge of the penis (Fig. 19F).

Female genitalia. Glandular oviduct 2.5 times as long as wide; albumen gland longer than capsule gland (Fig. 19A); bursa copulatrix pyriform to elongate (Fig. 19A–B), ca 2.5–3 times as long as wide (Supp. file 2: Table S17); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal receptacle elongate, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct (Fig. 19B).

Nervous system. Pigmented, elongate (mean RPG ratio = 0.57; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size and have small black dots of pigment; pleuro-supraoesophageal connective ca 7 times as long as pleuro-suboesophageal one (Fig. 19G).

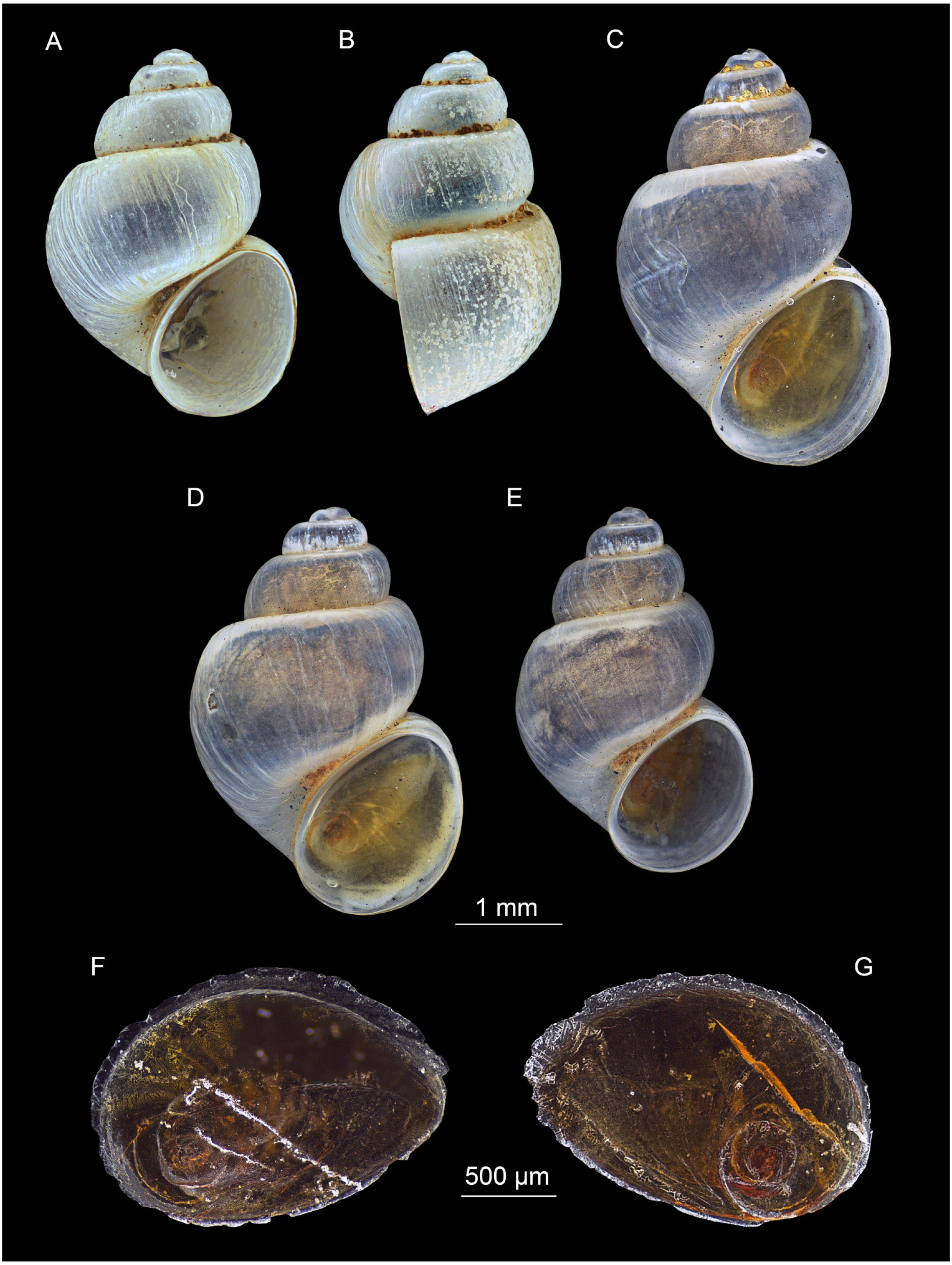


Fig. 17. Shells and operculum of *Mercuria egarensis* Miller, García-Guerrero & Ramos sp. nov. **A–B**. Holotype (MNCN 15.05/200174H), frontal and lateral views. **C–G**. Paratypes (MNCN 15.05/94753). **F**. Operculum, inner side. **G**. Operculum, outer side.

Ecology and distribution

The species is endemic to the Font de les Canyes Spring, alongside the Besós River. The conductivity of this spring is relatively high (1412 µS/cm). The species was collected from the rocky bottom of the spring at a low abundance. No other snail species were found in the spring. The water is used for human consumption, which may have had an impact on this and other snail populations.

A series of sampling campaigns of this and nearby areas were carried out between 2016 and 2018 and the species was not found elsewhere. The spring, located in a small zone in the eastern part of the municipality of Terrassa, discharges to the Besós River basin. Watercourses from the western part of the municipality drain into the Llobregat River basin (Jordi Corbella pers. com.). Bofill & Haas (1920) cited *M. similis* from Terrassa; however, as the drainage of this spring is associated with another hydrological basin, it is unlikely that Bofill & Haas (1920) citation for *M. similis* corresponds to Font de les Canyes.

Remarks

Mercuria egarensis sp. nov. differs from the closely related species *M. carrillorum* sp. nov. by having a slightly shorter penis, a larger penial appendix, a longer radular ribbon, a larger number of cusps on the central radular tooth [(2)3–C–3(2)/1–1 vs (3)4–C–4(3)/1–1], a more concentrated perioesophageal ring, a pyriform SR1 positioned on the renal oviduct just above the junction with the bursal duct (in *M. carrillorum*, it is positioned at the junction) and the absence of a pallial tentacle. Regarding their ecology, the two species differ in their conductivity preferences, with *M. egarensis* occurring in waters with higher conductivity.

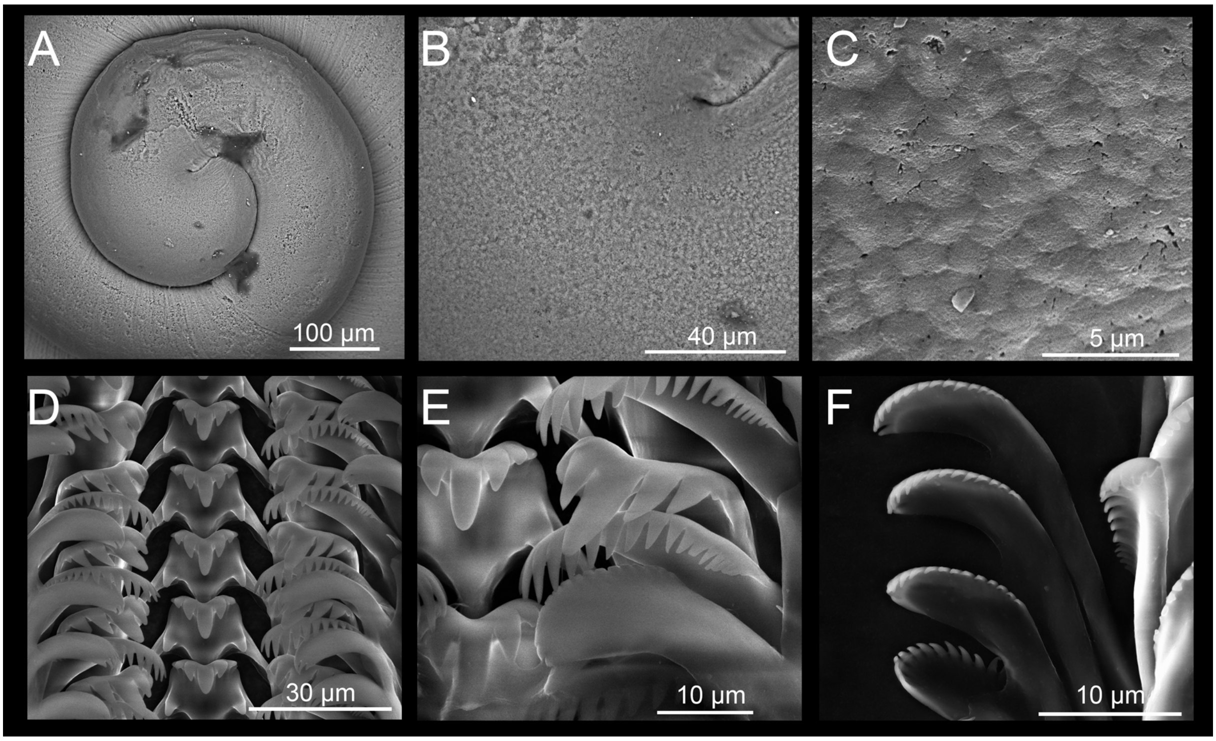


Fig. 18. Protoconch and radula of *Mercuria egarensis* Miller, García-Guerrero & Ramos sp. nov. from Font de les Canyes, Barcelona, Spain. **A**. Details of the protoconch. **B**. Protoconch nucleus. **C**. Protoconch microsculpture. **D**. Overview of radular teeth rows. **E**–**F**. Detailed view of the inner and outer marginal teeth, respectively.

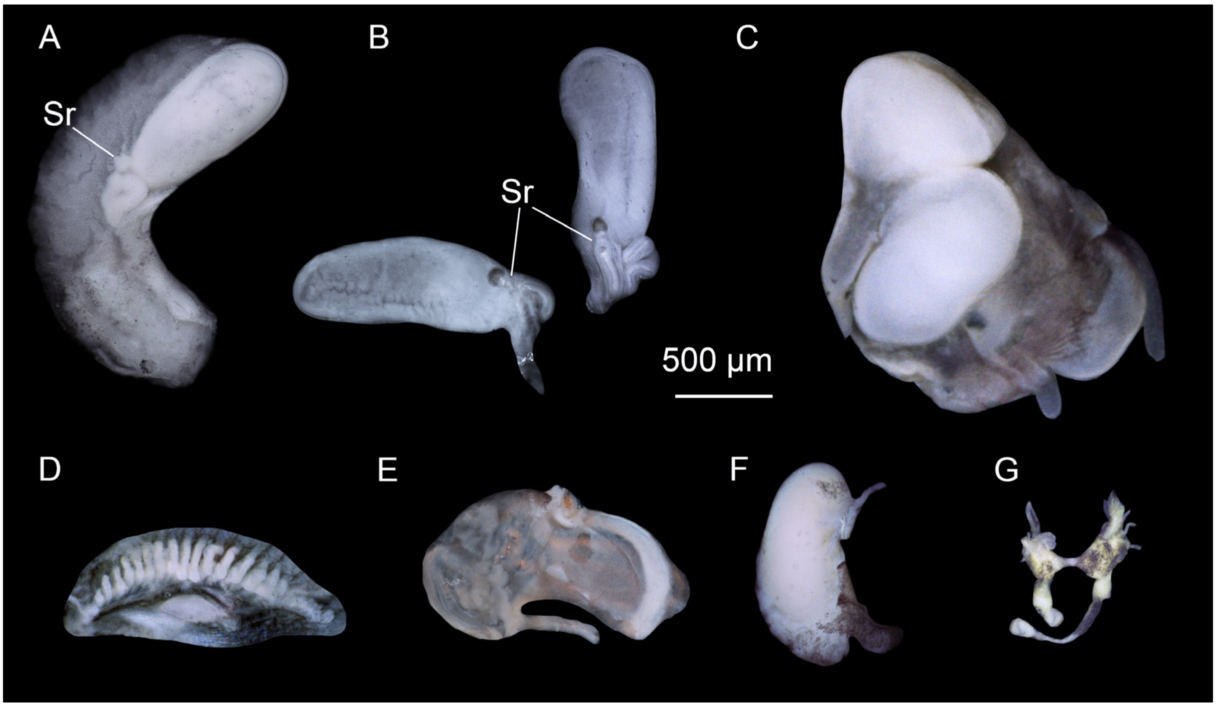


Fig. 19. Anatomy of *Mercuria egarensis* Miller, García-Guerrero & Ramos sp. nov. from Font de les Canyes, Barcelona, Spain. **A**. Female genitalia. **B**. Detailed view of the bursa copulatrix and seminal receptacle. **C**. Head and penis. **D**. Ctenidium and osphradium. **E**. Stomach. **F**. Prostate gland. **G**. Perioesophageal ring.

Mercuria egarensis sp. nov. does not resemble any of the congeners found in the Catalonia region. However, according to our PCA results, *M. egarensis* and *M. balearica* have overlapping shell shape variation (Fig. 3), though the latter presents a more globose shell with a wider aperture (Fig. 11). Although *M. egarensis* also resembles *M. tachoensis* and *M. similis* in terms of shell shape, its granulated protoconch microsculpture discriminates it from the pitted one in *M. tachoensis*. The shape and colouration of the penial appendix differentiate *M. egarensis* from *M. similis*: it is highly ovate and unpigmented in the former species and triangular and pigmented in the latter.

The sequence divergence of COI indicated that *M. egarensis* sp. nov. is closely related to *M. carrillorum* sp. nov. with a divergence of only 1.3%. *Mercuria egarensis* diverges 3.7% with *M. similis* and 8.1% with *M. balearica.* The species is most distantly related to *M. tensiftensis* and *M. melitensis*, diverging with both at around 9% (Miller *et al.* 2022).

Mercuria carrillorum Miller, García-Guerrero & Ramos sp. nov.

urn:lsid:zoobank.org:act:E9ED5EC6-E8DC-42ED-8EDC-2D2322296196
Figs 20–22; Supp. file 2: Tables S14–S18

Diagnosis

Shell ovate-conic; periostracum dark brown to blackish; protoconch microsculpture granulated; aperture obliquely ovate; central radular tooth formula (3)4-C-4(3)/1-1; female genitalia with bursa copulatrix elongate, ca 3 times as long as wide; seminal receptacle elongate; distal end of the penis ca 1.5 times as long as penial appendix, darkly pigmented; penial appendix ovate, pigmented to the distal part, medially positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.63); cerebral ganglia approximately equal in size.

Etymology

Named after the family of Miguel Carrillo Pacheco who instilled his scientific curiosity and passion for malacology and in recognition for his help with the fieldwork conducted across Spain, France and Portugal.

Type material

Holotype

SPAIN • sex unknown (dry preserved); Cádiz, Jerez de la Frontera, Canuto de la Gallina, Montes de Propios; MNCN 15.05/200175H.

Paratypes

SPAIN • 33 specs (preserved in ethanol 80%, 10 dissected and 4 processed for DNA sequencing); same collection data as for holotype; MNCN 15.05/94748 • 16 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/94750 • 17 specs (preserved in ethanol 80%); same collection data as for holotype; MZB 2021-2796 • 2 specs (dry preserved); same collection data as for holotype; NHMW 113527 • 2 specs (dry preserved); same collection data as for holotype; RMNH. MOL.507924 • 1 spec. (dry preserved); same collection data as for holotype; JPM-586 • 2 specs (dry preserved); same collection data as for holotype; MCP • 2 specs (dry preserved); same collection data as for holotype; MCP.

Additional material examined

SPAIN – **Cádiz** • 30 specs; Jerez de la Frontera, Montes de Propios, stream in Canuto de las Palas; MNCN 15.05/94751 • 3 specs; same collection data as for preceding; MNCN 15.05/94749. – **Málaga** • 3 specs; Manantial de los Doce PIlares spring; MNCN-ADN 110673 to 110675.

Additional locality information provided in Supp. file 1: Table S1.

Type locality

Stream in Canuto de la Gallina, Montes de Propios, Jerez de la Frontera, Cádiz, Spain. 36.587509° N, 5.574243° W; 379.72 m a.s.l.

Description

Measurements. Holotype: SL = 3.04 mm, SW = 2.26 mm, SL/SW = 1.34, AH = 1.43 mm, SL-LBW = 0.73 mm, WBW = 1.78 mm, AL = 1.44 mm, AW = 1.07 mm, WPW = 1.03 mm, WAW = 0.52 mm.

Shell. Ovate-conic, whorls 4–5, height 2.4–3.8 mm, width 1.8–2.7 mm (Fig. 20A–F; Supp. file 2: Table S14); periostracum dark brown to blackish; protoconch of 1.5 whorls, ca 350 µm wide, nucleus ca 150 µm wide (Fig. 21A–B); protoconch microsculpture granulated (Fig. 21C). Teleoconch whorls slightly convex, separated by a deep suture; body whorl large and convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip slightly thicker than outer lip; aperture margin straight; outer lip slightly sinuated; umbilicus narrow, not covered by the inner lip (Fig. 20A, C–F).

Operculum. As for the genus, orangish to brown, about 2 whorls; muscle attachment oval, located near the nucleus (Fig. 20G–H).

Radula. Length intermediate, ca 600 µm long (20% of total shell length), containing about 70 rows of teeth. Central tooth formula (3)4-C-4(3)/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 21D–E). Lateral tooth formula (4)3-C-3(4), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 12–16 cusps; outer marginal teeth with 25–27 cusps

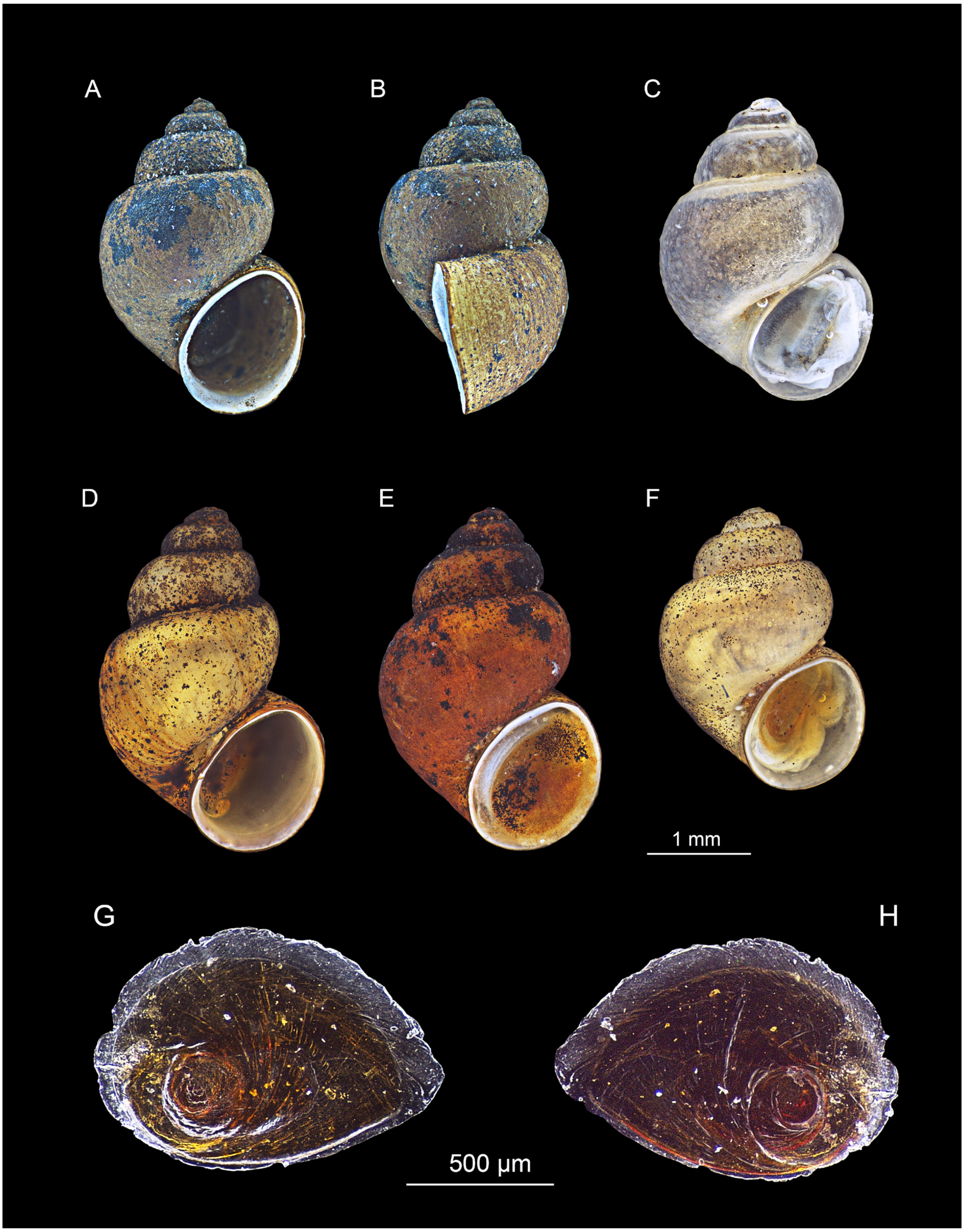


Fig. 20. Shells and operculum of *Mercuria carrillorum* Miller, García-Guerrero & Ramos sp. nov. **A**–**B**. Holotype (MNCN 15.05/200175H), frontal and lateral views. **D, G**–**H**. Paratypes (MNCN 15.05/94748). **C**. Manantial de los Doce Pilares Spring, Málaga, Spain. **D**. Stream in Canuto de la Gallina, Montes de Propios, Jerez de la Frontera, Cádiz, Spain. **E**–**F**. Stream in Canuto de las Palas, Montes de Propios, Jerez de la Frontera, Cádiz, Spain (MNCN 15.05/94751). **G**–**H**. Stream in Canuto de la Gallina, Montes de Propios, Jerez de la Frontera, Cádiz, Spain. **G**. Operculum, inner side. **H**. Operculum, outer side.

(Fig. 21F). Radular data were collected from the following specimens: MNCN 15.05/94748 and MNCN 15.05/94750 from Canuto de la Gallina, Cádiz and MNCN 15.05/94749 and MNCN 15.05/94751 from Canuto de las Palas, Cádiz.

Pigmentation and anatomy. Animal brownish to pale brown (Fig. 22E); head and tentacles brown, eye lobes unpigmented; snout and neck weakly pigmented; snout longer than wide, approximately parallel-sided, with medium distal lobation. Pallial tentacle present. Ctenidium occupying almost the total length of the pallial cavity; 22–26 gill filaments, broad, triangular, and fused at the base by an epithelium (Fig. 22G). Osphradium elongate, more than 3 times as long as wide, positioned opposite to the middle of the ctenidium. Stomach almost as long as wide with two chambers about equal in size (Supp. file 2: Table S16); style sac longer than wide, with the unpigmented intestine surrounding its distal part before continuing on as a straight rectum (Fig. 22H).

Male genitalia. Prostate gland small, bean-shaped, about 2 times as long as wide, connected by the posterior vas deferens to a convoluted seminal vesicle and the testis (Fig. 22F). The distal end of the penis ca 1.5 times as long as penial appendix (Supp. file 2: Table S18), darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix ovate, pigmented on the distal part, medially positioned on the inner edge of the penis (Fig. 22C–E).

Female genitalia. Glandular oviduct 2.5 times as long as wide; albumen gland longer than capsule gland (Fig. 22A); bursa copulatrix elongate, ca 3 times as long as wide (Supp. file 2: Table S17); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal

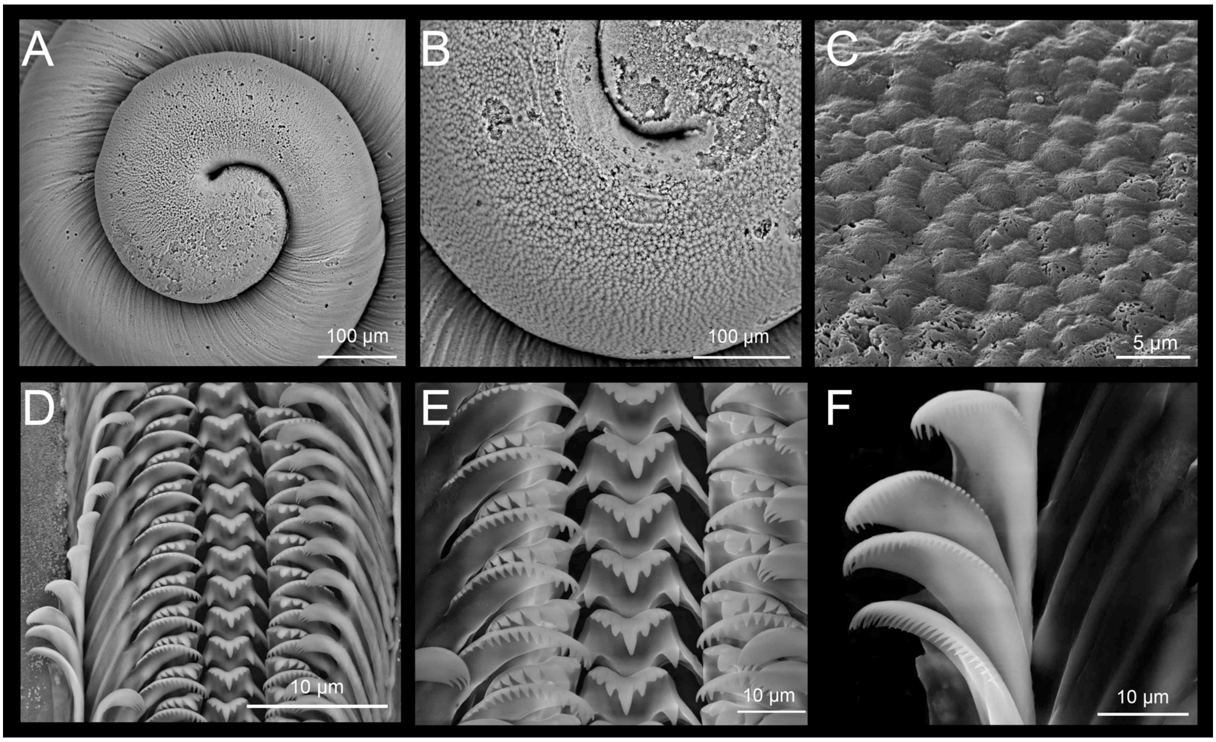


Fig. 21. Protoconch and radula of *Mercuria carrillorum* Miller, García-Guerrero & Ramos sp. nov. from the stream in Canuto de las Palas, Montes de Propios, Jerez de la Frontera, Cádiz, Spain. **A**. Details of the protoconch. **B**. Protoconch nucleus. **C**. Protoconch microsculpture. **D**. Overview of radular teeth rows. **E–F**. Detailed view of the central and outer marginal teeth, respectively.

receptacle elongate, with a short duct, positioned on the distal part of the renal oviduct at the junction with the bursal duct (Fig. 22B).

NERVOUS SYSTEM. Pigmented, elongate (mean RPG ratio = 0.63; Supp. file 2: Table S15); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 9 times as long as pleuro-suboesophageal one (Fig. 22I).

Ecology and distribution

Restricted, as the species has been found at only three localities, all in Cádiz and Málaga, Spain. Very small specimens (probably juveniles) of the species were collected for the first time at Manantial de los Doce Pilares Spring, Málaga in 2015. However, we were unable to find any specimens at this locality during a subsequent sampling trip in 2017.

Contrary to other species of *Mercuria*, *M. carrillorum* sp. nov. lives in streams with very low conductivities, ranging from 80–179 µS/cm. Co-occurring species, though at low abundances, are *Ancylus fluviatilis* O.F. Müller, 1774 and *Galba truncatula* (O.F. Müller, 1774), except the stream in Canuto de la Gallina in which only *M. carrillorum* is found (Félix Ríos Jiménez pers. com.).

Remarks

Mercuria carrillorum sp. nov. differs from the phylogenetically closely related species *M. egarensis* sp. nov. by having a more ovate than a high-spired shell, a smaller and more pigmented penial appendix, an elongated bursa copulatrix (from pyriform to elongate in *M. egarensis*), a smaller radular ribbon, a larger number of cusps on the central radular tooth and the presence of a pallial tentacle.

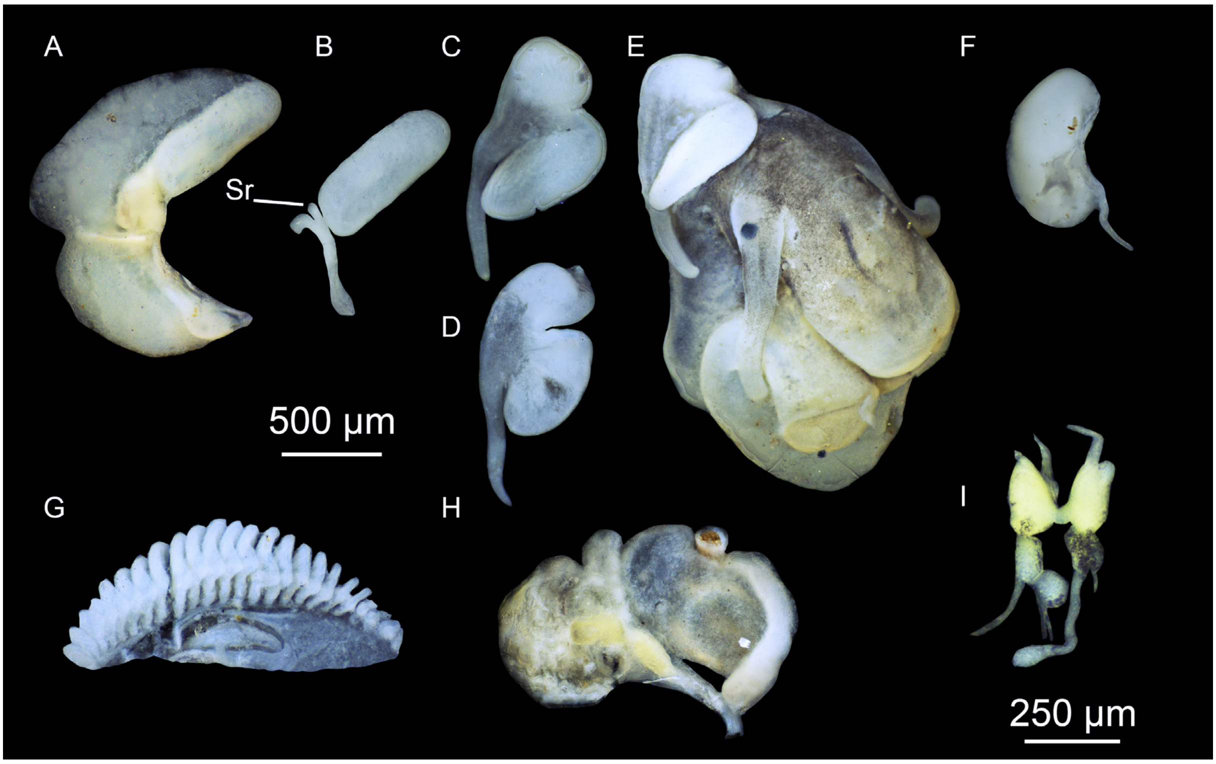


Fig. 22. Anatomy of *Mercuria carrillorum* Miller, García-Guerrero & Ramos sp. nov. from the stream in Canuto de las Palas, Cádiz, Spain. **A**–**B**. Female genitalia. **C**–**D**. Penis. **E**. Penis and head. **F**. Prostate gland. **G**. Ctenidium and osphradium. **H**. Stomach. **I**. Perioesophageal ring.

Mercuria carrillorum sp. nov. resembles *M. felixi* sp. nov. and *M. balearica* in terms of shell shape (Fig. 3) but differs from them in other features. The new species has an ovate, pigmented penial appendix that is shorter than the distal end of the penis, whereas in *M. felixi*, the distal end of the penis and appendix are about equal in length. In *M. balearica*, the penial appendix is longer than the distal end of the penis, which is triangular and extremely pigmented. These species also differ in the lengths of the bursa copulatrix (longer in *Mercuria carrillorum* than in *M. balearica*) and the pleuro-supraoesophageal connective (longer in *M. felixi*). The major difference in the radula is the number of cusps on the outer marginal teeth: *M. carrillorum* has considerably more cusps (25–27) than *M. balearica* and *M. felixi*.

The sequence divergence of COI for *Mercuria carrillorum* sp. nov. and the other Iberian congeners ranged between 1.3% (with *M. egarensis* sp. nov.) and 8% (with *M. felixi* sp. nov.). With a divergence of 8.9%, the most distantly related species was the Tunisian *M. saharica* Letourneux & Bourguignat, 1887 (Miller *et al.* 2022)

Mercuria felixi Miller, García-Guerrero & Ramos sp. nov.

urn:lsid:zoobank.org:act:798D1589-DD36-4893-9FEB-8BF7026FF008
Figs 23–25; Supp. file 2: Tables S14–18

Diagnosis

Shell ovate-conic; aperture obliquely ovate; protoconch microsculpture granulated; periostracum dark brown to blackish; central radular tooth formula 3(4)-C-(4)3/1-1; female genitalia with bursa copulatrix pyriform to elongate, ca 3 times as long as wide; seminal receptacle elongate; penis darkly pigmented; penial appendix ovate, darkly pigmented at the junction with the penis, about the same length or slightly shorter than the distal end of the penis and medially positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.60). Cerebral ganglia are approximately equal in size.

Etymology

Named after Félix Ríos Jiménez, who provided us with valuable samples of the new species.

Type material

Holotype

SPAIN • sex unknown (dry preserved); Cádiz, stream in Canuto de la Tala; MNCN 15.05/200176H.

Paratypes

SPAIN – **Cádiz** • 27 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/94754 • 22 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/94756 • 1 spec. (dry preserved); same collection data as for holotype; MZB 2021-2798 • 2 specs (dry preserved); same collection data as for holotype; NHMW 113528 • 1 spec. (dry preserved); same collection data as for holotype; RMNH.MOL.507926 • 2 specs (dry preserved); same collection data as for holotype; JPM-586 • 1 spec. (dry preserved); same collection data as for holotype; MCP.

Additional material examined

SPAIN – **Cádiz** • 30 specs; stream in Canuto del Zapato; MNCN 15.05/94755, MNCN 15.05/94757.

Additional locality information provided in Supp. file 1: Table S1.

Type locality

Stream in Canuto de la Tala, Cádiz, Spain. 36.477025° N, 5.592611° W, 673.97 m a.s.l.

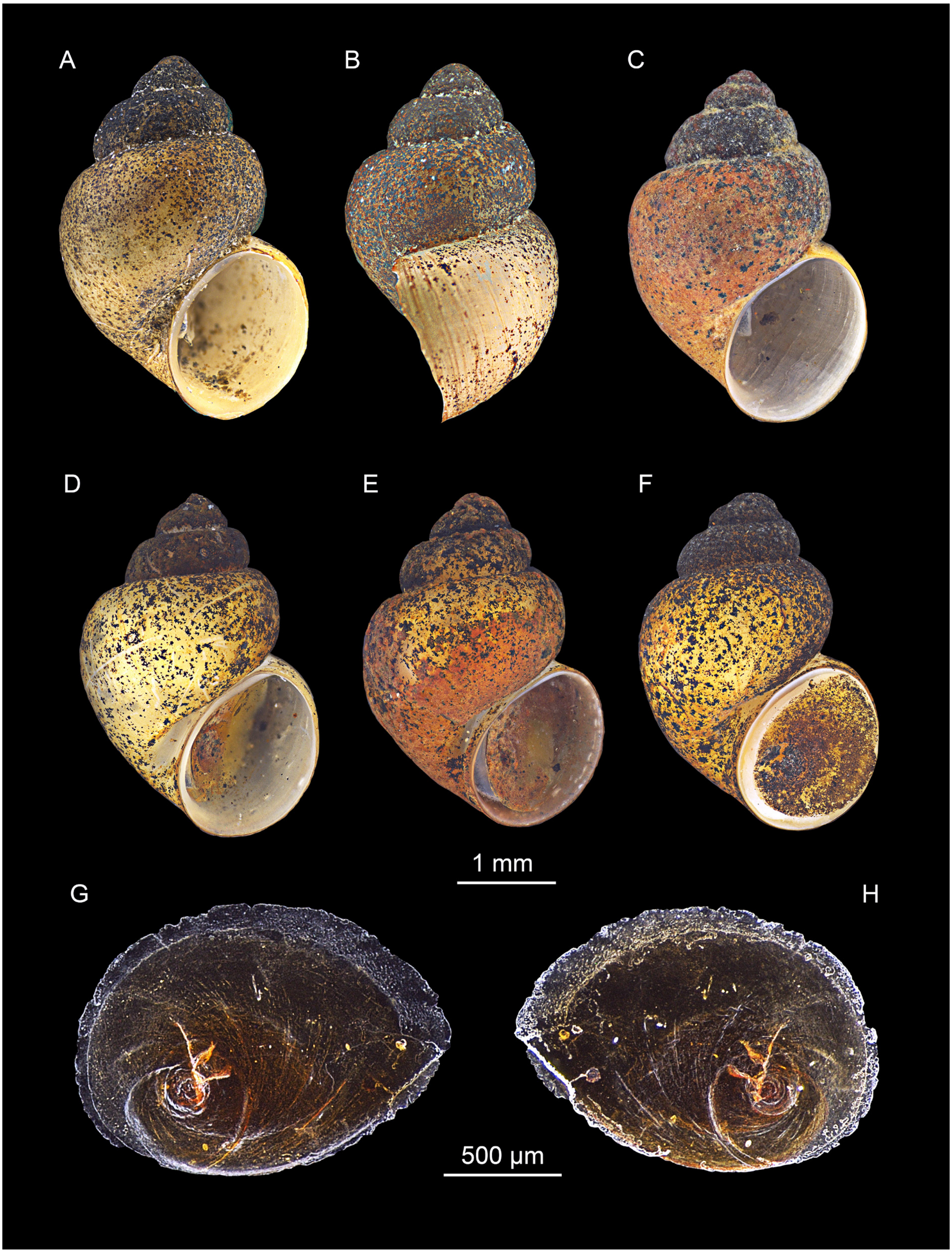


Fig. 23. Shells and operculum of *Mercuria felixi* Miller, García-Guerrero & Ramos sp. nov. from the stream in Camuto de la Tala, Cádiz, Spain. **A**–**B**. Holotype (MNCN 15.05/200176H), frontal and lateral views. **C**–**H**. Paratypes (MNCN 15.05/94754). **G**. Operculum, inner side. **H**. Operculum, outer side.

Description

Measurements. Holotype: SL = 3.78 mm, SW = 2.87 mm, SL/SW = 1.31, AH = 1.77 mm, SL-LBW = 0.90 mm, WBW = 2.25 mm, AL = 1.75 mm, AW = 1.36 mm, WPW = 1.33 mm, WAW = 0.60 mm.

Shell. Ovate-conic, whorls 4–5, height 2.4–3.8 mm, width 2–2.9 mm (Fig. 23A–F; Supp. file 2: Table S14); periostracum dark brown to blackish; protoconch of 1.5 whorls, ca 270 µm wide, nucleus ca 125 µm wide (Fig. 24A); protoconch microsculpture granulated (Fig. 24B–C). Teleoconch whorls slightly convex, separated by a deep suture; body whorl large, convex, occupying more than two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; outer margin straight, inner lip touching the body whorl; umbilicus narrow, not covered by the inner lip (Fig. 23A, C–F).

Operculum. As for the genus, orange to brown, sometimes yellowish, with about two whorls; muscle attachment oval, located near the nucleus (Fig. 23G–H).

Radula. Length intermediate, ca 700 µm long (35% of total shell length), containing about 60 rows of teeth. Central tooth formula 3(4)-C-(4)3/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 24D). Lateral tooth formula 3-C-3, central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 15–18 cusps; outer marginal teeth with 23–27 cusps (Fig. 24E–F). Radular data were collected from specimens from the type locality.

Pigmentation and anatomy. Animal weakly pigmented (Fig. 25E); head and tentacles unpigmented to weakly pigmented; eye lobe unpigmented; snout and neck weakly pigmented; snout longer than wide,

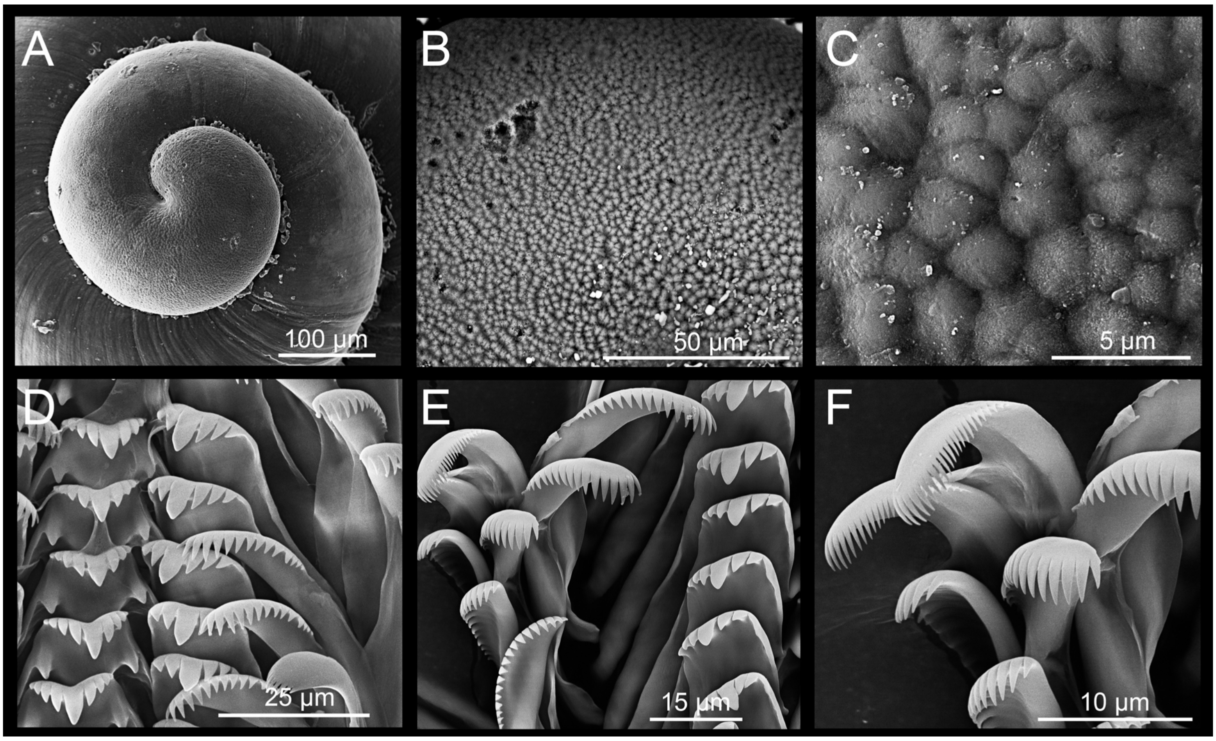


Fig. 24. Protoconch and radula of *Mercuria felixi* Miller, García-Guerrero & Ramos sp. nov. from the stream in Canuto de la Tala, Cádiz, Spain. **A**. Protoconch. **B**. Details of the protoconch. **C**. Protoconch microsculpture. **D**. Overview of radular teeth rows. **E**–**F**. Detailed view of the inner and outer marginal teeth, respectively.

approximately parallel-sided, with medium distal lobation. Ctenidium occupying almost the total length of the pallial cavity; 21–25 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 25F). Osphradium elongate, more than 3 times as long as wide, positioned opposite middle of ctenidium. Stomach almost as long as wide with two chambers almost equal in size (Supp. file 2: Table S16); style sac longer than wide, with the unpigmented intestine surrounding its distal part and then continuing on as a straight rectum (Fig. 25G).

Male genitalia. Prostate gland bean-shaped, about 3 times as long as wide (Supp. file 2: Table S18), connected by the posterior vas deferens to a convoluted seminal vesicle and the testis (Fig. 25C). Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye; penial appendix ovate, darkly pigmented at the junction with the penis, about the same length or slightly shorter than the distal end of the penis and medially positioned on the inner edge of the penis (Fig. 25D–E).

Female genitalia. Glandular oviduct 3 times as long as wide; albumen gland ca 2 times as long as capsule gland; bursa copulatrix pyriform to elongate, ca 3 times as long as wide (Fig. 25A–B; Supp. file 2: Table S17); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with

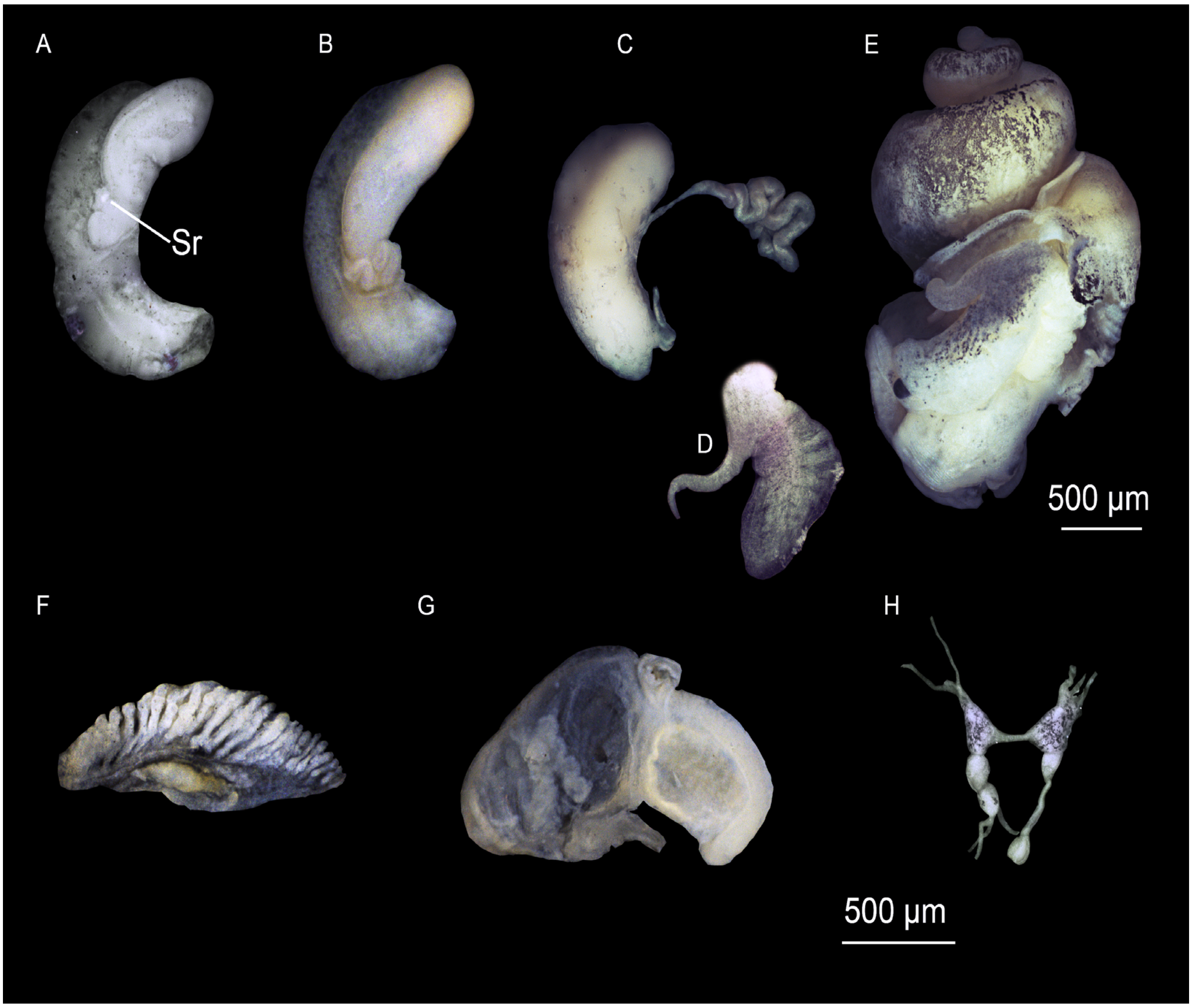


Fig. 25. Anatomy of *Mercuria felixi* Miller, García-Guerrero & Ramos sp. nov. from the stream in Canuto de la Tala, Cádiz, Spain. **A**–**B**. Female genitalia. **C**. Prostate gland. **D**. Penis. **E**. Animal and penis. **F**. Ctenidium and osphradium. **G**. Stomach. **H**. Perioesophageal ring.

three loops; seminal receptacle elongate, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct (position SR1).

NERVOUS SYSTEM. Pigmented, elongate (mean RPG ratio = 0.60; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size, pleuro-supraoesophageal connective ca 11 times as long as pleuro-suboesophageal one (Fig. 25H).

Ecology and distribution

This species was collected from two streams in southern Spain: the stream in Canuto de la Tala (type locality) and the stream in Canuto del Zapato. The ecology of the species is not well known. The species inhabits streams of very clear running waters with relatively low conductivities (75–292 mS/cm^2). The specimens collected from the stream in Canuto del Zapato were found in very low abundance. Co-occurring species are *Ancylus fluviatilis* and *Galba truncatula* in low abundance and *Pisidium* sp. in high abundance (Félix Ríos Jiménez pers. com.).

Remarks

Mercuria felixi sp. nov. differs from the phylogenetically closely related species *M. tensiftensis* and *M. balearica* by having a narrower aperture (wider in *M. balearica*); a more globose shell (high-spired in *M. tensiftensis)*; a granulated protoconch microsculpture (grooved in *M. tensiftensis*); an ovate, pigmented penial appendix that is about the same length or slightly shorter than the distal end of the penis (rounded, unpigmented and shorter than the distal end of the penis in *M. balearica* and darkly pigmented and shorter than the distal end of the penis in *M. tensiftensis*); a thin, filiform, pigmented distal end of the penis (broad, triangular, and strongly and darkly pigmented in *M. balearica,* and triangular and pigmented in *M. tensiftensis*); a prostate gland that is 3 times as long as wide (2 times as long as wide in *M. tensiftensis* and *M. balearica*) and a smaller radular ribbon. The species also has one more cusp on the central teeth than in *M. tensiftensis.*

The shell shape of *M. felixi* sp. nov. resembles that of *M. carrillorum* sp. nov. and *M. tachoensis*; however, our PCA (Fig. 3) showed that *M. felixi* can be differentiated from the rest of the *Mercuria* species. The penile morphology of *M. felixi* further differentiates it from the Iberian congeners: it has a very thin, pigmented penial appendix and a long, filiform and pigmented distal penis.

According to DNA-sequence analyses (Miller *et al.* 2022), this species forms a clade with *M. balearica* (5.3% of mean COI divergence) and *M. tensiftensis* (5.1% of mean COI divergence). It is most distantly related to *M. midarensis* and *M. saharica*, diverging from these species by 8% and 8.6%, respectively.

Mercuria lupiaensis Miller & Delicado sp. nov.

urn:lsid:zoobank.org:act:A3B189DF-8A84-46B5-82BD-A083F46F8CF9
Figs 26–28; Supp. file 2: Tables S14–S18

Diagnosis

Shell ovate-conic; aperture obliquely ovate; periostracum whitish to pale grey; central radular tooth formula 3-C-3/1-1; female genitalia with bursa copulatrix pyriform to elongate, ca 2 times as long as wide; seminal receptacle pyriform; penis darkly pigmented; penial appendix unpigmented, ovate, smaller than the distal end of the penis and medially positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.53); cerebral ganglia approximately equal in size, with small black spots.

Etymology

The specific epithet '*lupiaensis*' refers to Lupia, the name of the city of Lecce during the time of the ancient Roman empire.

Type material

Holotype

ITALY • sex unknown (preserved in ethanol 80%); Lecce, Frigole, Giammateo Creek; MNCN 15.05/200123H.

Paratypes

ITALY • 4 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/200123P • 13 specs (preserved in ethanol 80%, 7 dissected and 2 processed for DNA sequencing); same collection data as for holotype; UGSB 8015.

Additional material examined

ITALY • 9 specs; Apulia, Nardò, San Isidoro, Palude del Capitano Pond; UGSB 16236 • 7 specs; Apulia, Porto Cesareo, Ionian Coast, spring in Torre Castiglione; UGSB 16237.

Additional locality information provided in Supp. file 1: Table S1.

Type locality

Giammateo Creek, Frigole, Lecce, Italy. 44.9436° N, 12.0213° E.

Description

MEASUREMENTS. Holotype: SL = 3.73 mm, SW = 2.95 mm, SL/SW = 1.26, AH = 1.92 mm, SL-LBW = 0.94 mm, WBW = 2.27 mm, AL = 1.96 mm, AW = 1.32 mm, WPW = 1.29 mm, WAW = 0.63 mm.

SHELL. Ovate-conic, whorls 4–5, height 3.10–3.75 mm, width 2.50–3.00 mm (Fig. 26A–F; Supp. file 2: Table S14); periostracum whitish to pale grey; protoconch of 1.5 whorls, ca 300 µm wide, nucleus ca 150 µm wide; teleoconch whorls slightly convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin straight, inner lip attached to the body whorl; umbilicus narrow, not covered by the inner lip (Fig. 26A, C–F).

OPERCULUM. As for the genus, orange to brown, about two whorls; muscle attachment oval, located near the nucleus (Fig. 26G–H).

RADULA. Length intermediate, ca 800 µm long (35% of total shell length), containing about 60 rows of teeth (Fig 27A). Central tooth formula 3-C-3/1-1, central cusp V shaped, cutting edge slightly concave (Fig. 27B). Lateral tooth formula 3-C-3, central cusp V shaped and slightly longer than the central tooth one (Fig. 27C). Inner marginal teeth with 14–17 cusps; outer marginal teeth with 22–25 cusps (Fig. 27D). Radular data were collected from specimens from Giammateo Creek, Frigole, Lecce (UGSB 8015); Palude del Capitano Pond, San Isidoro, Ionian coast, Nardó, Apulia (UGSB 16236) and a spring in Torre Castiglione, Ionian Coast, Porto Cesareo, Apulia (UGSB 16237).

PIGMENTATION AND ANATOMY. Animal darkly pigmented (Fig. 28E, I); head and tentacles black pigmented, pigmentation lighter on eye lobes, snout and neck; snout about as long as wide, approximately parallel-sided, with medium distal lobation. Ctenidium occupying almost the total length of the pallial cavity; 23–27 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 28G). Stomach almost as long as wide with two chambers almost equal in size (Supp. file 2: Table S16); style sac longer

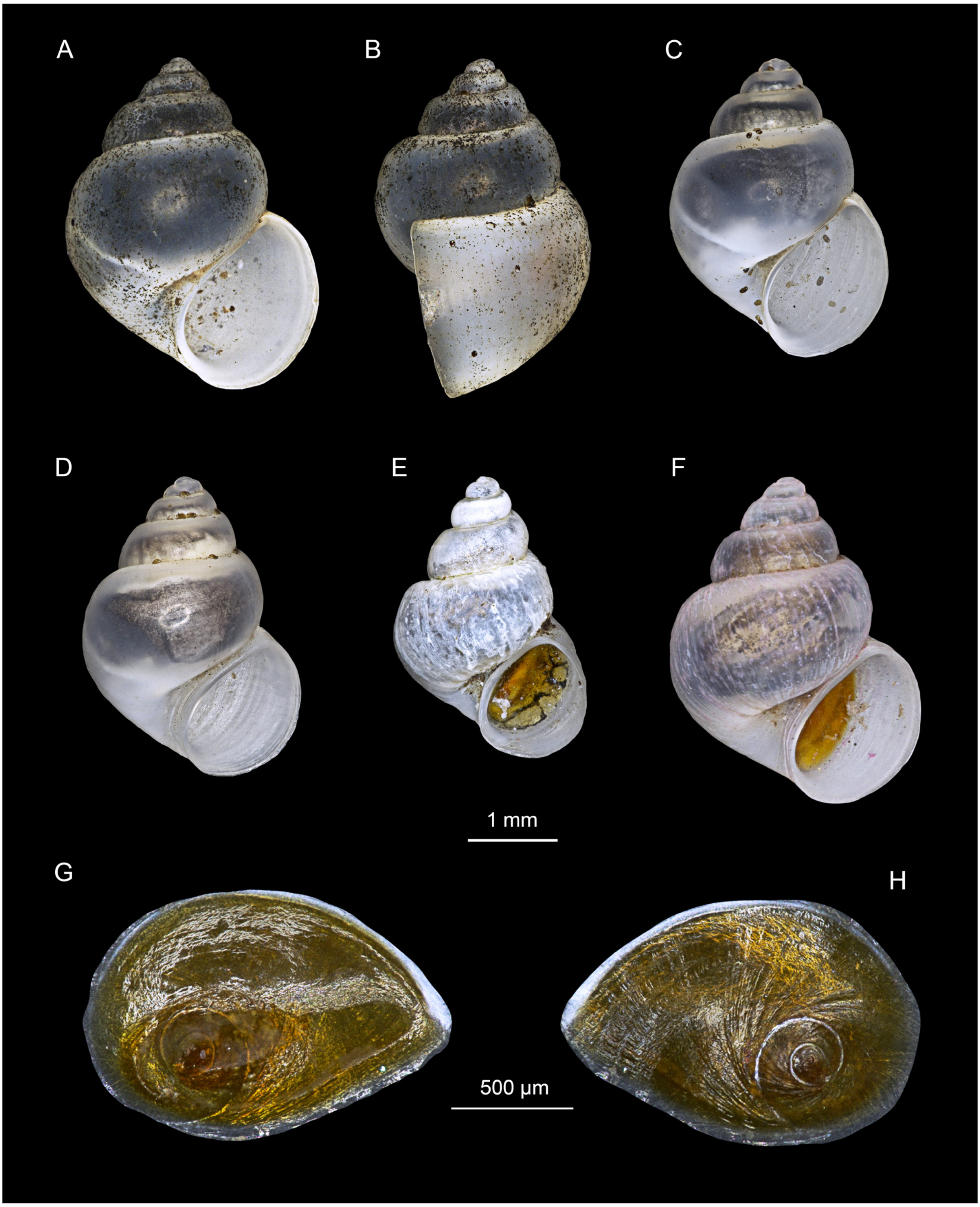


Fig. 26. Shells and operculum of *Mercuria lupiaensis* Miller & Delicado sp. nov. **A–B**. Holotype (MNCN 15.05/200123H), frontal and lateral views. **C–D**. Paratypes (MNCN 15.05/200123P). **C–D, G–H**. Specimens from Giammateo Creek, Frigole, Lecce. **E**. Specimen from the spring in Torre Castiglione, Ionian Coast, Porto Cesareo, Apulia (UGSB 16237). **F**. Specimen from Palude del Capitano Pond, San Isidoro, Ionian coast, Nardò, Apulia (UGSB 16236). **G**. Operculum, inner side. **H**. Operculum, outer side.

than wide, with the unpigmented intestine surrounding its distal part and continuing on as a straight rectum (Fig. 28H).

Male genitalia. Prostate gland bean-shaped, about 2 times as long as wide (Supp. file 2: Table S18), connected by the posterior vas deferens to a convoluted seminal vesicle and the testis (Fig. 28F). Penis darkly pigmented, gradually tapering, attached to the central area of the neck; penial appendix unpigmented or slightly pigmented at the junction with the distal end of the penis. Penial appendix ovate, smaller than the penis, base narrow, medially positioned on the inner edge of the penis (Fig. 28C–E).

Female genitalia. Glandular oviduct 2.5 times as long as wide; albumen gland and capsule gland about the same size (Fig. 28A–B); bursa copulatrix elongate, ca 2 times as long as wide (Supp. file 2: Table S17); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal receptacle pyriform, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct (Fig. 28B).

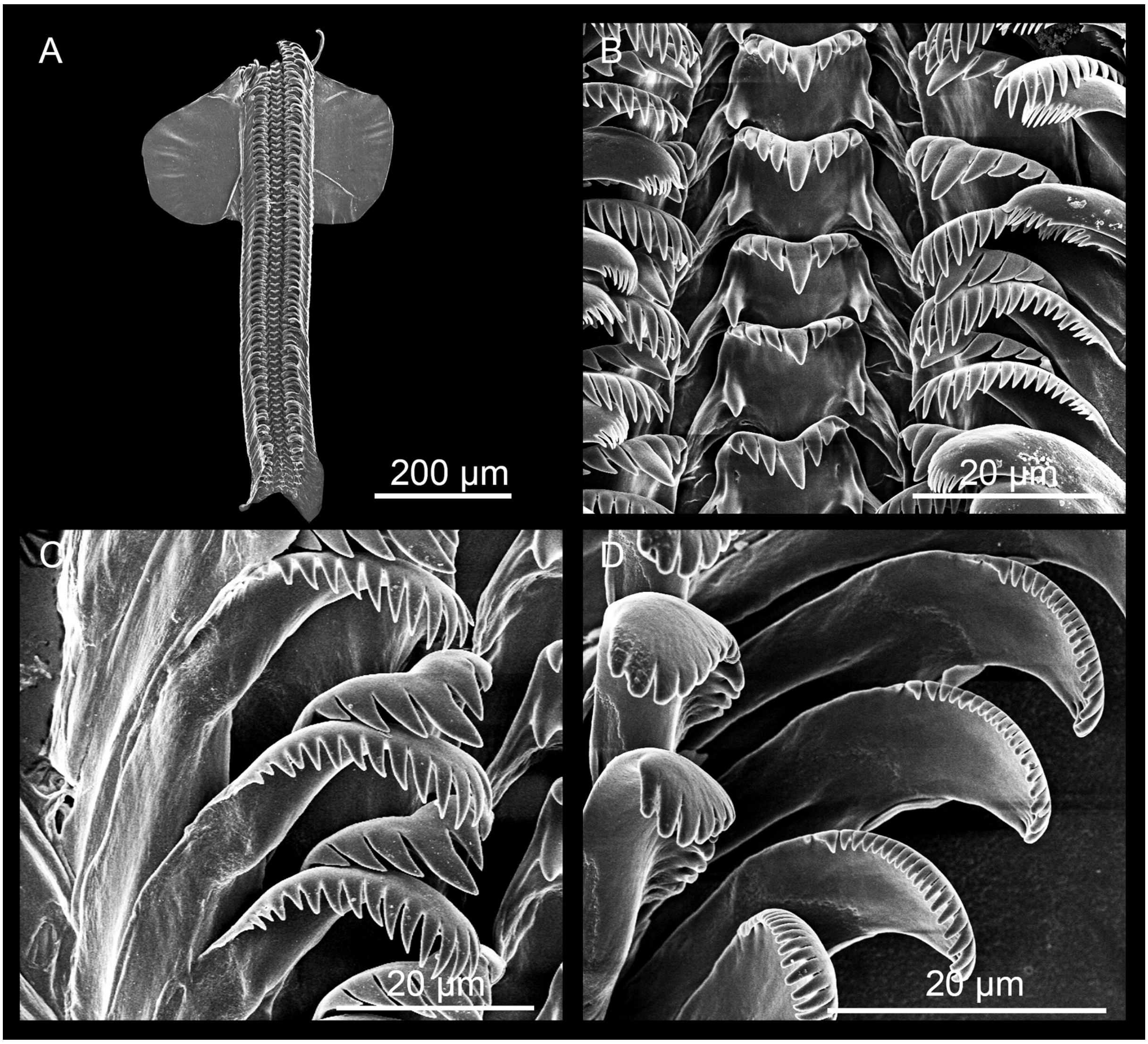


Fig. 27. Radula of the *Mercuria lupiaensis* Miller & Delicado sp. nov. from Giammateo Creek, Frigole, Lecce. **A**. General view of the radular ribbon. **B**. Overview of radular teeth rows. **C**. Detailed view of the lateral and inner marginal teeth. **D**. Detailed view of the outer marginal teeth.

Nervous system. Pigmented, elongate (mean RPG ratio = 0.53; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size (Fig. 28I).

Ecology and distribution

The species is only known from the three nearby localities in the Salento Peninsula in the region of Apulia, Italy. The ecology of the species is not well known. The species was found in very clear running waters, close to the coastal margins. Co-occurring species are *Pseudamnicola conovula* (Frauenfeld, 1863), *Eupaludestrina stagnorum* (Gmelin, 1791) and *Bithynia leachii* (Sheppard, 1823).

Remarks

Mercuria lupiaensis sp. nov. now represents the easternmost species of the genus and potentially the second species reported in the Apennine Peninsula. The species *M. similis* has been documented from the Sale Basin (Bodon *et al.* 2005; Cianfanelli & Bodon 2017), the first species of *Mercuria* described from the Apennine Peninsula. Despite that the new species and *M. similis* have a similar shell shape; they can be easily distinguished by differences in the penial appendix: in *M. similis*, it is large, triangular and highly pigmented, whereas in *M. lupiaensis*, it is small, sometimes very small, ovate and slightly pigmented or unpigmented. In the new species, the albumen and capsule glands are about the same size, whereas, in *M. similis*, the albumen gland is longer than the capsule gland. They also present differences in the bursa copulatrix: elongate and about 2 times as long as wide in *M. lupiaensis* and pyriform to elongate and 3 times as long as wide in *M. similis.*

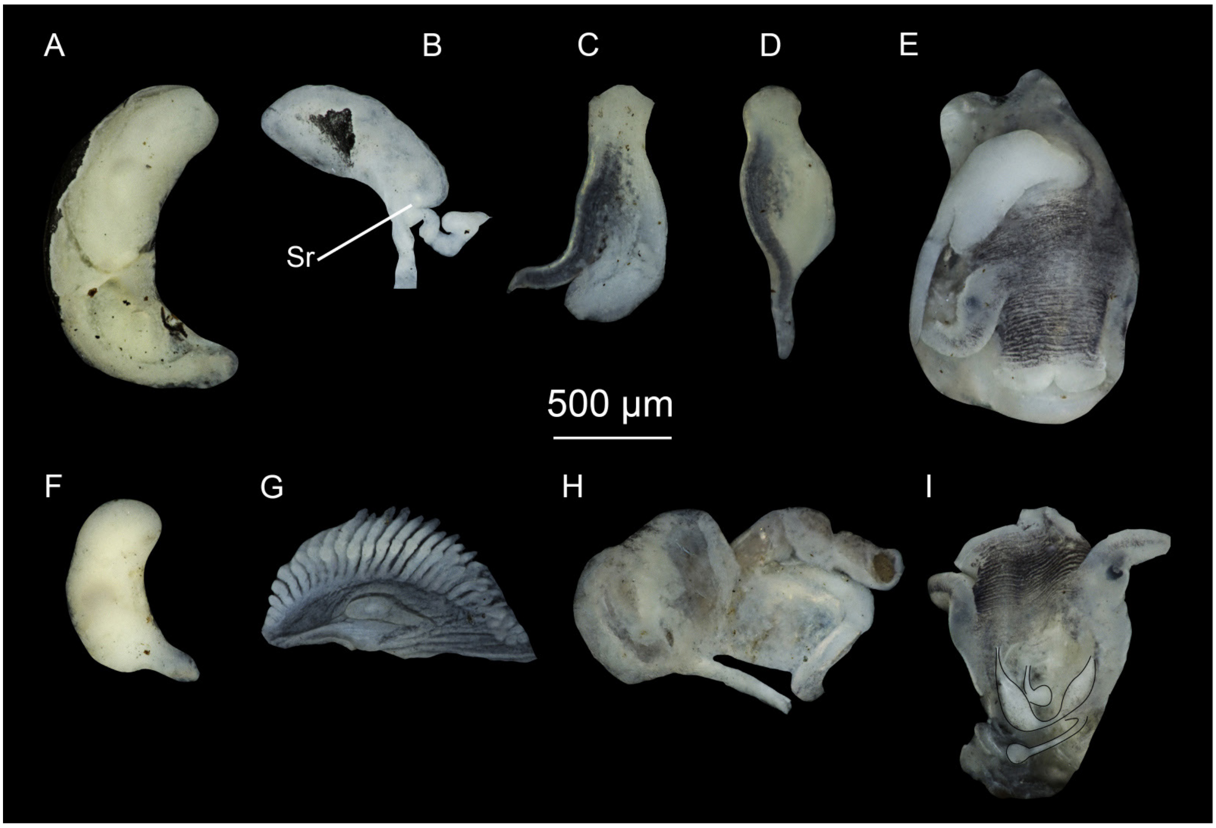


Fig. 28. Anatomy of *Mercuria lupiaensis* Miller & Delicado sp. nov. from Giammateo Creek, Frigole, Lecce. **A–B**. Female genitalia indicating the seminal receptacle (Sr). **C–D**. Penis. **E**. Head of a male. **F**. Prostate gland. **G**. Ctenidium and osphradium. **H**. Stomach. **I**. Head with perioesophageal ring attached.

Mercuria lupiaensis sp. nov. can be further distinguished from the phylogenetically closely related species *M. veronicae* sp. nov. by its smaller size, lighter dorsal pigmentation, similarly sized capsule and albumen glands (albumen gland longer than capsule gland in *M. veronicae*), a penial appendix that is shorter than the distal end of the penis and a smaller number of cusps on the central teeth.

The sequence divergence estimates of COI showed that the species is most closely related to *M. veronicae* sp. nov. (mean divergence of 3.9%) and most distantly to *M. midarensis* (with a mean divergence of 9.3%) (Miller *et al.* 2022).

Mercuria veronicae Miller, Khalloufi & Delicado sp. nov.

urn:lsid:zoobank.org:act:986C0653-973B-4C3D-9A4A-C6A216321EBE
Figs 29–31; Supp. file 2: Tables S14–S18

Diagnosis

Shell ovate-conic; aperture obliquely ovate; periostracum whitish to pale grey; central radular tooth formula (5)4-C-4(5)/1-1; female genitalia with a bursa copulatrix pyriform to elongate, ca 2 times as long as wide; seminal receptacle elongate; penis darkly pigmented; penial appendix slightly pigmented, ovate, shorter than or equal in length to the distal end of the penis, medially positioned on the inner edge of the penis; nervous system pigmented, elongate (mean RPG ratio = 0.55); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 11 times as long as pleuro-suboesophageal one.

Etymology

After Veronica Ruiz, the first author's grandmother.

Type material

Holotype

TUNISIA • sex unknown (preserved in ethanol 80%); Tozeur, Tamerza, Oasis Waterfall. El Waha Spring; MNCN 15.05/200124H.

Paratypes

TUNISIA • 3 specs (preserved in ethanol 80%); same collection data as for holotype; MNCN 15.05/200124P • 15 specs (preserved in ethanol 80%, 6 dissected and 1 processed for DNA sequencing); same collection data as for holotype; UGSB 17271.

Additional material examined

TUNISIA • 15 specs; Tozeur, Tamerza, Big Waterfall, Lekbir Spring; UGSB 17274 • 4 specs; Tozeur, Echbika, Echbika Waterfall, Echbicka Spring; UGSB 17276.

Additional locality information provided in Supp. file 1: Table S1.

Type locality

El Waha Spring, Oasis Waterfall, Tamerza, Tozeur, Tunisia, 34.381933° N, 7.933450° E, 278.67 m a.s.l.

Description

MEASUREMENTS. Holotype: SL = 4.87 mm, SW = 3.56 mm, SL/SW = 1.36, AH = 2.03 mm, SL-LBW = 1.40 mm, WBW = 2.96 mm, AL = XX mm, AW = 2.06 mm, WPW = 1.67 mm, WAW = 0.85 mm.

SHELL. Ovate-conic, whorls 4–5, height 3.25–5.3 mm, width 2.5–4 mm (Fig. 29A–F; Supp. file 2: Table S14); periostracum whitish to pale grey; protoconch of 1.5 whorls, ca 250 µm wide, nucleus

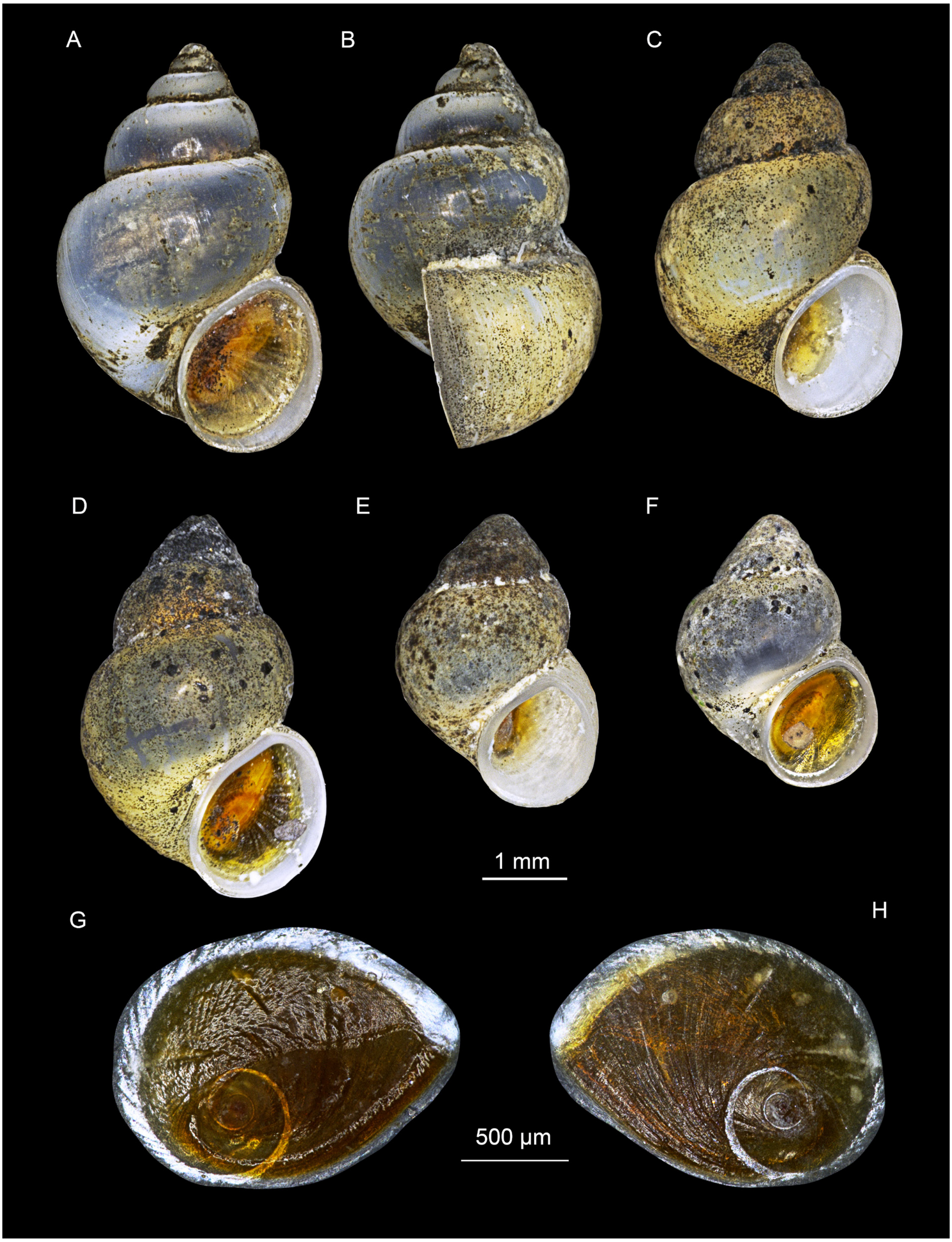


Fig. 29. Shells and operculum of *Mercuria veronicae* Miller, Khalloufi & Delicado sp. nov. **A–B**. Holotype (MNCN 15.05/200124H), frontal and lateral views. **C–D**. Paratypes. **C**. MNCN 15.05/200124P. **D**. UGSB 17271. **A–D, G–H**. El Waha Spring, Oasis Waterfall, Tamerza, Tozeur. **E–F**. Lekbir Spring, Big Waterfall, Tamerza, Tozeur. **G**. Operculum, inner side. **H**. Operculum, outer side.

ca 150 µm wide; teleoconch whorls slightly convex, separated by a deep suture; body whorl large, convex, occupying about two-thirds of the total shell length; aperture obliquely broad ovate, complete; inner lip thicker than outer lip; aperture margin straight; inner lip touching the body whorl; umbilicus narrow, not covered by the inner lip.

Operculum. As for the genus, orange to brown, sometimes yellowish, about two whorls; muscle attachment oval, located near the nucleus (Fig. 29G–H).

Radula. Length intermediate, ca 750 µm long (35% of total shell length), containing about 60 rows of teeth (Fig. 30A). Central tooth formula (5)4-C-4(5)/1-1, central cusp V shaped, cutting edge concave (Fig. 30B–C). Lateral tooth formula (3)4-C-4(3), central cusp V shaped and slightly longer than the central tooth one. Inner marginal teeth with 11–15 cusps; outer marginal teeth with 21–25 cusps (Fig. 30D). Radular data were collected from the following specimens: UGSB 17271 – El Waha Spring,

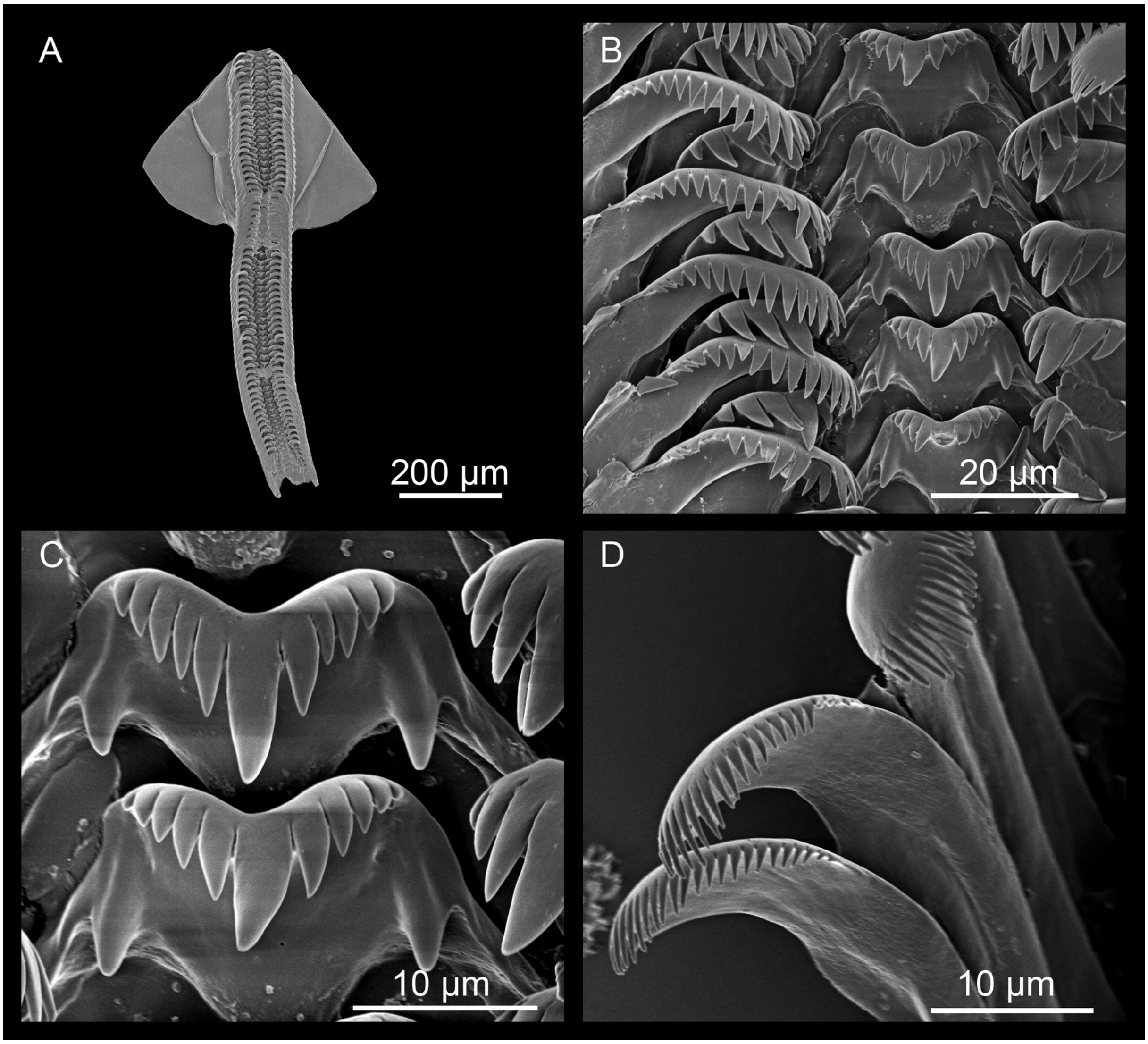


Fig. 30. Radula of the *Mercuria veronicae* Miller, Khalloufi & Delicado sp. nov. from El Waha Spring, Tozeur. **A**. General view of the radular ribbon. **B**. Overview of radular teeth rows. **C**. Detailed view of the central teeth. **D**. Detailed view of the outer marginal teeth.

Oasis Waterfall, Tamerza, Tozeur, Tunisia; UGSB 17274 – Lekbir Spring, Big Waterfall, Tamerza, Tozeur, Tunisia; UGSB 17276 – Echbicka Spring, Echbika Waterfall, Echbika, Tozeur, Tunisia.

Pigmentation and anatomy. Animal darkly pigmented (Fig. 31A, D); head and tentacles dark brown, pigmentation lighter on eye lobes, snout and neck; snout about as long as wide, approximately parallel-sided, with medium distal lobation. Ctenidium occupying almost the total length of the pallial cavity; 28–33 gill filaments; filaments broad, triangular, fused at the base by an epithelium (Fig. 31B). Osphradium elongate, more than 3 times as long as wide, positioned opposite middle of ctenidium. Stomach almost as long as wide with two chambers almost equal in size (Supp. file 2: Table S16); style sac longer than wide, with the unpigmented intestine surrounding its distal part and continuing on as a straight rectum (Fig. 31C).

Male genitalia. Prostate gland bean-shaped, about 2 times as long as wide (Supp. file 2: Table S18). Pallial vas deferens emerge close to both the anterior edge of the prostate and the external margin of the penis (Fig. 31F). Penis darkly pigmented, gradually tapering, attached to the neck behind the right eye, distal end of the penis broad, triangular; penial appendix pyriform, shorter than or about to the

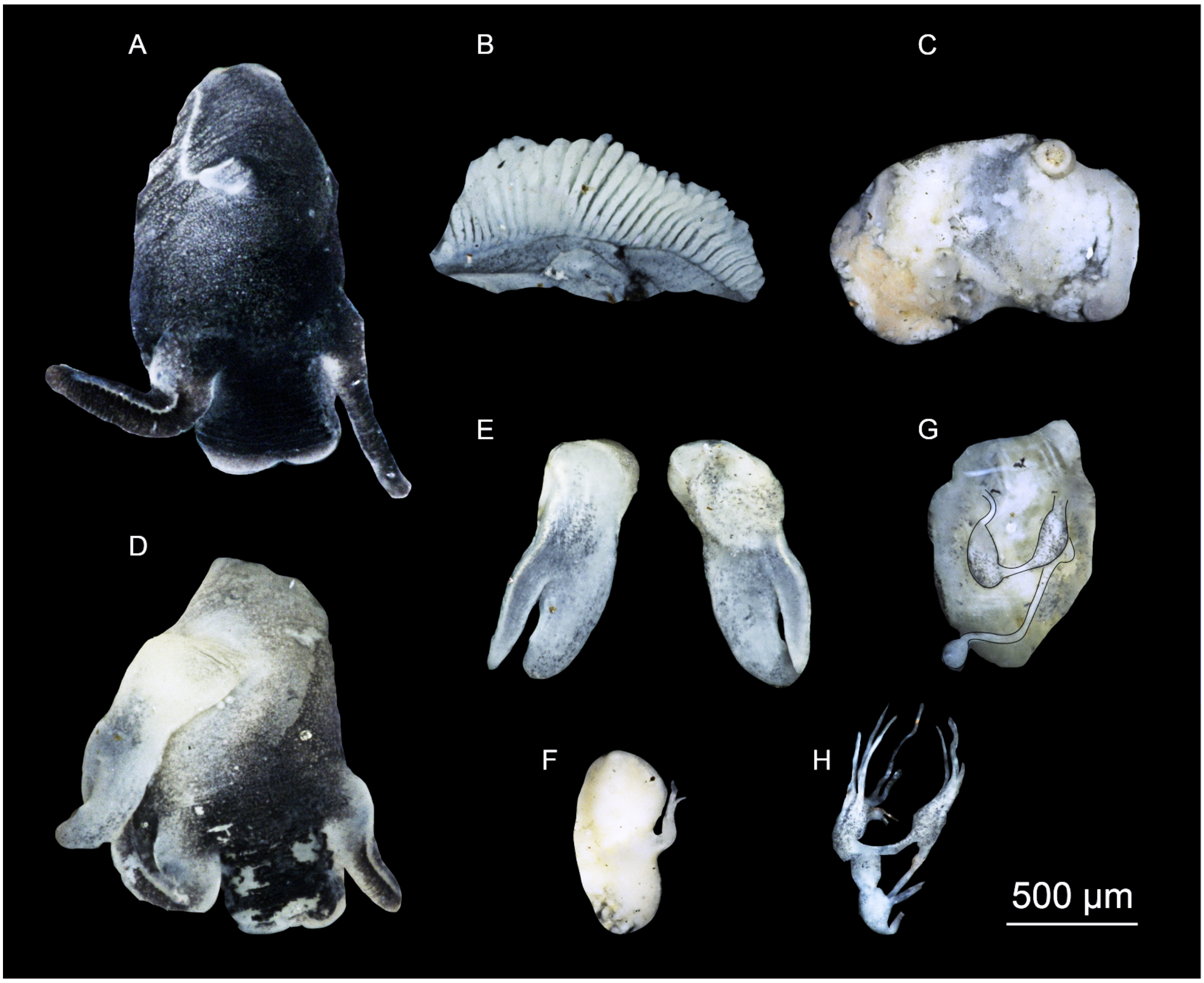


Fig. 31. Anatomy of the *Mercuria veronicae* Miller, Khalloufi & Delicado sp. nov. from Spring El Waha, Tozeur, Tunisia. **A**. Head. **B**. Ctenidium and osphradium. **C**. Stomach. **D**. Head of a male. **E**. Penis. **F**. Prostate gland. **G**. Head with perioesophageal ring attached. **H**. Perioesophageal ring.

same length as the distal end of the penis, slightly pigmented at the junction with the penis, medially positioned on the inner edge of the penis (Fig. 31D–E).

Female genitalia. Glandular oviduct 2.5 times as long as wide, albumen gland longer than capsule gland; bursa copulatrix elongate, ca 2 times as long as wide (Supp. file 2: Table S17); bursal duct shorter than bursa copulatrix; renal oviduct unpigmented, highly coiled with three loops; seminal receptacle elongate, with a short duct, positioned on the distal part of the renal oviduct just above the junction with the bursal duct.

Nervous system. Pigmented, elongate (mean RPG ratio = 0.55; see Supp. file 2: Table S15); cerebral ganglia approximately equal in size; pleuro-supraoesophageal connective ca 11 times as long as pleuro-suboesophageal one (Fig. 31G–H).

Ecology and distribution

The studied samples of this species come from three localities in the Tozeur region, north of the Chotts, but its distribution extends to other regions around the Chotts el Gharsa and Djeride (Gafsa, Kebili, Nefzaoua and Gabes). It occurs in streams, springs and irrigation ditches of the oasis areas. This species is present at a high density (more than 3000 ind./m^2) on the edge of the streams, where the flow is low and the substrate muddy, and attached to aquatic plants. The main streams of Tamarza (Oued Frid) and Echbika (Oued Echbika) are highly saline (conductivity 8667 and 3945 µS/cm, respectively) and flow over an alluvial and clayey-sandy substrate of the Plio-Quaternary, with a predominance of sulphate-sodium, gypsum and phosphorites (Abidi 2007). Co-occurring species are *Galba truncatula*, *Physella acuta* (Draparnaud, 1805) (in low abundance), *Eupaludestrina* spp., *Melanoides tuberculata* (O.F. Müller, 1774), *Melanopsis douvillei* Pallary, 1916 and *Melanopsis praemorsa* (Linnaeus, 1758) (in high abundance).

Remarks

Intraspecies morphological differences were observed mainly in the penial features of males from the same population (Fig. 31D–E). Some individuals have a much-atrophied penis. Such variation may be parasite-induced, similar to the case reported in another species of *Mercuria* (Boulaassafer *et al.* 2018). Parasitized females also presented an atrophied pallial oviduct, making it difficult to conduct a complete anatomical study. The pigmentation of the penis is also very variable, ranging from very slight to pronounced dark pigmentation at the junction between the appendix and distal end of the penis.

Mercuria veronicae sp. nov. differs from the phylogenetically closely related species *M. lupiaensis* sp. nov. and *M. melitensis* by having a high-spired shell and a more elongated bursa copulatrix compared with *M. lupiaensis* and thinner inner and outer shell lips compared with the characteristically thick ones of *M. melitensis* (Glöer *et al.* 2015). *Mercuria veronicae* also has a long, triangular and more pigmented penial appendix compared with the short (to very short), ovate and slightly pigmented or unpigmented one in *M. lupiaensis.* In *M. melitensis*, the penial appendix is only as long as the distal end of the penis. Compared with other geographically proximate species, *M. veronicae* resembles *M. pycnocheilia* (Bourguignat, 1862) in shell shape, although the latter presents a thicker inner shell lip (see Glöer *et al.* 2010) and the former, has smaller-sized shells. In addition, Glöer *et al.* (2010) and Glöer (2019) noted the acute apex of *M. pycnocheilia* (Bourguignat, 1862), which is not present in *M. veronicae.* Shell shape features also distinguish the new species from *M. globulina* (Letourneux & Bourguignat, 1887), which has a larger, more slender shell, and *M. bourguignati* Glöer, Bouzid & Boeters, 2010, which has a larger shell and smaller aperture (about half the shell length in *M. bourguignati* vs about three quarters the shell length in *M. veronicae*). The anatomy of these geographically proximate species is unknown.

According to our sequence divergence estimates of COI, *M. veronicae* sp. nov. is most similar to *M. lupiaensis* sp. nov. (average divergence of 3.9%) and diverges most with *M. tensiftensis* (by 8.4%) (Miller *et al.* 2022).

Discussion

Diagnostic characters for species of *Mercuria*

As seen in other hydrobiid genera (Arconada 2000; Arconada & Ramos 2006; Bodon & Cianfanelli 2012; Delicado *et al.* 2012; Delicado & Hauffe 2022), our morphological observations highlight the problematic nature of identifying species of *Mercuria* using only shell features. In this study, we used geometric morphometrics to describe the shell shape of over 1100 individuals from 35 populations and predicted that differences in shell shape may be congruent with the delimited morphospecies. From a total of eight species, two pairs of species could not be resolved using this methodology (*M. carrillorum* sp. nov. from *M. tachoensis*, and *M. egarensis* sp. nov. from *M. balearica*); however, the remaining four studied species were recovered as independent clusters (see Fig. 3). According to these findings, only 50% of the analysed species were successfully delimited based on the shell morphometry. Therefore, we conclude that this structure, whether studied through geometric or classic morphometry, cannot be used to achieve a complete understanding of species diversity in *Mercuria*. Giusti *et al.* (1995) emphasised that the taxonomy of this genus should be taken with caution, given the high morphological variability of the shell, and our data corroborate this assertion. In our study, some species (i.e., *M. tachoensis*, *M. similis* and *M. balearica*) presented a high level of interpopulation variability in the shell shape (Fig. 3), which was not observed in the remaining species, in part, due to their poorly known distribution. However, all of the species studied here do have, to some degree, high variability in shell dimensions (Supp. file 1: Table S1, Supp. file 2: Tables S5, S9, S13). We cannot rule out the possibility that this phenomenon is due to sexual dimorphism, which is generally common in Caenogastropoda (Davis & McKee 1989; Bichain *et al.* 2007; Falniowski *et al.* 2007; Reichenbach *et al.* 2012; Páll-Gergely *et al.* 2020), or to parasitism (Boulaassafer *et al.* 2018). Further studies would be necessary to test which underlying mechanism is responsible for the variability in shell dimensions.

In *Mercuria*, the colour of the operculum, thought to be dark brown, has been used as a taxonomic criterion to assign species to this group (Boeters & Falkner 2017); however, this character status can vary among species. For instance, we found that, for some species presenting an orange to brown operculum, some specimens had a yellowish operculum (i.e., in *M. tachoensis*, *M. balearica*, *M. egarensis* sp. nov., *M. felixi* sp. nov. and *M. veronicae* sp. nov.). In other species, the orange to brown coloured operculum was observed for all specimens (i.e., *M. similis*, *M. carrillorum* sp. nov. and *M. lupiaensis* sp. nov.).

Substantial variability was also observed in characters related to the reproductive system (e.g., penis, penial appendix and bursa copulatrix). In particular, we observed intraspecific differences in the shape and size of these characters. The use of these characters has been indiscriminate, leading to misclassifications and an overestimation of the species richness of *Mercuria* (Giusti *et al.* 1995). Interestingly, Boulaassafer *et al.* (2018) observed specimens of *M. tensiftensis* with marked atrophy of the penis or with prostatic hyperplasia and concluded that the size variability of the penis and prostate gland in this species may be caused by parasitism. In our study, however, we did not find any evidence of parasitism in any of the populations studied from the Iberian Peninsula, France, the Balearic Islands, although some parasite specimens were found in the Italian populations. Holyoak *et al.* (2017) found that allometric growth of the penis and the penial appendix is a source of variability in the reproductive system of *M. tachoensis*, and highlighted how this system varies according to the maturation time of the specimens. We observed a similar phenomenon in *M. similis* (see Fig. 7A–F), however, their growth could not be correlated with different maturation periods since we did not sequentially sample the population over time.

Taxonomic reappraisal of the studied species of *Mercuria*

Hydrobiids, in general, present high levels of homoplasy due to convergence in shell characters and the simplicity of their structures, which makes the recognition of species boundaries difficult (Hershler 1994; Bodon *et al*. 2001; Falniowski 2018). The assignment of hydrobiid species to a genus should follow an integrative taxonomic approach (Dayrat 2005) as morphological studies alone cannot resolve the systematics of the group, particularly given that many of these studies have been based on shell characters (colour and measurements) proven to be highly variable within populations (Wilke *et al.* 2000; Wilke & Falniowski 2001; Barszcz 2004) and therefore insufficient for proper species delimitation.

Based on our observations, we have identified characters previously considered diagnostic as insufficient to distinguish between species of *Mercuria*; therefore, we used integrative taxonomy to address some unresolved taxonomic questions about species of this genus:

Mercuria confusa as a synonym of *M. similis*

Assessing the taxonomic status of populations of *Mercuria* is further hampered by the inability to accurately identify the type material of the widespread species. Several species of *Mercuria* were described in the Mediterranean region in the nineteenth century (Poiret 1801; Draparnaud 1805; Risso 1826; Frauenfeld 1863; Paladilhe 1869; Bourguignat 1876), however, the taxonomic status and location of some of their type materials remain elusive. One such case involves the taxonomic uncertainty surrounding the type species of the genus, *M. confusa* (Frauenfeld, 1863), and *M. similis*. These two names were synonymised by Boeters & Falkner (2000) when these authors assigned the lectotype of *M. confusa* (currently deposited under lot number NHMW-MO 92596 at the Natural History Museum in Vienna; Eschner *et al.* 2020) as the neotype of *M. similis*. The justification for this synonymisation, which reduced the number of recognised species of *Mercuria*, was based on the similarity in height of two shells (i.e., the lectotype of *M. confusa* and the shell illustrated by Draparnaud (1805) in the original description). As supported by our geometric morphometric analysis and shell measurements, shell features cannot be used to reliably distinguish species of *Mercuria*, diminishing confidence in this synonymy. Despite this, our morphological and molecular data have delimited only one species, a finding that, without more data, would support the hypothesis that only a single species of *Mercuria* is present across southern France (i.e., "Gallia meridionalis"). These findings refute past interpretations about the presence of *M. meridionalis* (Risso, 1826) and *M. similis* in southern France, and their geographic distributions being separated by the Rhône River (Boeters & Falkner 2017).

Genus assignment for *Amnicola emiliana*

Our study confirms that the populations of *Mercuria* sampled by Boeters (1988) from southern France, southern Spain and the Balearic Island of Majorca are conspecific and likely all correspond to *M. similis*. Boeters (1988) initially assigned the specimens from these populations to *M. emiliana* (Paladilhe, 1869) but later identified them as belonging to *M. similis* (Boeters & Falkner 2017). The species *M. emiliana* was recently combined with the genus *Pseudamnicola* and the species was re-named as *P. emilianus* by Boeters & Falkner (2017). This taxonomic change was based on differences found in the colouration and size of the shell between the neotype assigned by these authors (i.e., MNHN-IM-2000-32541; Boeters & Falkner 2017) and other specimens of *M. similis* sampled from four proximal localities (see Boeters & Falkner 2017: table s6).

The assignment of *M. emiliana* to *Pseudamnicola* may be erroneous for several reasons. First, Boeters & Falkner (2017) designated a neotype for *Amnicola emiliana*, stating that syntypes of this species might be lost. However, Breure & Audibert (2017) declared this designation invalid as the original syntypes of *A. emiliana* can be found at the University of Montpellier under the lot number UM.PDL.003. Second, the decision for the species combination was based on only two shell measurements of three shells (which are probably not adults) and shell colouration, an insufficient character for genus assignment. According to Boeters & Falkner (2017), the neotype is too small (2.75 mm) to be a member of *Mercuria*, although, in table s6 of their study, they reported shells of *M. similis* from Port-La-Nouvelle ranging in size from 2.75 to 3.85 mm. We also found numerous individuals of *Mercuria* that are 2.75 mm high. Boeters & Falkner (2017) also claimed that Paladilhe (1869), in his original description of the species, stated the colour of the shell as "cornée" [corneous] and not milky as in *Mercuria*, and the operculum as corneous instead of chestnut brown. However, it is worth mentioning that all *Amnicola* species described by Paladilhe (1869) presented corneous shells and similar shell dimensions (Fig. 32). Moreover, we observed both types of shell and operculum colourations among the studied populations of *M. similis* (see Fig. 4 for shell morphotypes and differences in operculum colouration). Therefore, based on our observations, we consider these particular shell features insufficient to assign the species *A. emiliana* to *Pseudamnicola*. Boeters & Falkner (2017: 252) acknowledged the vagueness of their proposed taxonomic act: "The fact that *Amnicola emiliana* belongs to *Pseudamnicola* confronts us with a lot of questions which can only be mentioned in this context but will not be solved here". Given the difficulty of determining the precise taxonomic status of *A. emiliana* based on the shell characteristics of a designated neotype from a lot other than the type material, we consider it more appropriate to base the assignment of the taxonomic status of this species on populations found later in the region of the type locality. We found specimens of *M. similis* in areas close to the type locality and in Font de Estramar, another locality mentioned in the original description of the species. Therefore, we consider that *A. emiliana* is more likely a representative of *Mercuria*.

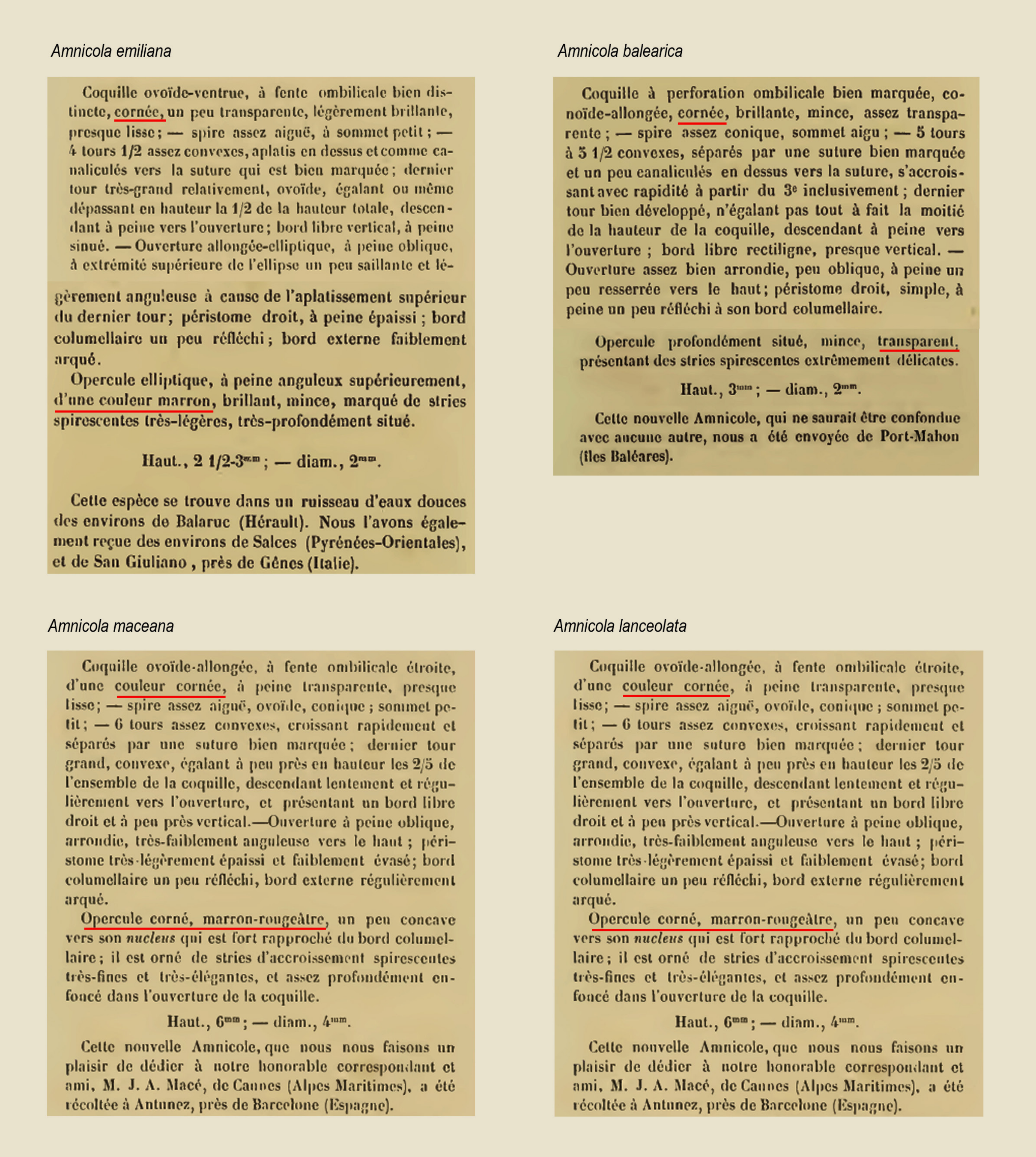
Taxonomy and geographic distribution of *M. tachoensis*

The populations of *Mercuria* sampled along the Atlantic coast of Europe and the British Isles were found to belong to the same species. The high morphological similarities found among these populations suggest the need for a taxonomic re-evaluation of some previously published records of *Mercuria*. Moreover, topotypes or near topotypes of the oldest known species, *M. tachoensis*, collected from localities surrounding the city of Lisbon in Portugal also grouped within the same species clade (Miller *et al.* 2022), suggesting that all of these populations may be of *M. tachoensis*. Despite exhaustive sampling, the species *M. edmundi* was not found in either of the two locations mentioned by Boeters (1986, 1988) and the localities mentioned for both *M. edmundi* and *M. tachoensis* in Lisbon have disappeared.

Subsequent sampling campaigns carried out in other parts of the city, including the civil parish of Ajuda and the Jardim Botânico da Ajuda, did not yield any evidence confirming the presence of these species in these localities [Rui M. da Costa Mendes pers. com.]. Neither did our survey of the vicinities of Burgau, Lagos and Praia da Figuera, Portugal. Holyoak *et al.* (2017) previously proposed the synonymy of *M. edmundi* with *M. tachoensis* based on conchological and anatomical characters, however, Miller *et al.* (2022) were unable to directly support their synonymy with molecular data.

According to the DNA-sequence data published by Miller *et al.* (2022), the population previously reported as *M. bayonnensis* from a stream in Bidart by Boeters & Falkner (2017) are actually conspecific with other populations of *M. tachoensis*. *Mercuria bayonnensis* was originally described from Lake Moriscot, in La Negresse, France (Locard 1894), and later, Boeters & Falkner (2017) expanded the known range of the species to the localities of Bidart, Biarritz, La Nive, Le Teich and La Tresne, in France, and the city of Bilbao, in Spain. In both the original description and the aforementioned article, the authors described the species as having a conical shell and a short, pigmented penis. However, *M. tachoensis* is also described as having a short, pigmented penis and conical shell (Boeters 1988), and all of the male individuals that we dissected from Bidart and Mouguerre presented short pigmented penises. Given that the species was not found in the type locality, it was not included in previous molecular analyses. Therefore, until material from the type locality can be integrated into our study, it is not possible to know with certainty whether *M. bayonnensis* is *M. tachoensis* or another species.

Miller *et al.* (2022) also found *M. tachoensis* in some localities previously reported for *M. anatina*. The type locality of the latter species is the “l’embouchure de la Somme” (‘the mouth of Somme River’) and “Les environs de Paris” (“the surroundings of Paris”), France (Poiret 1801). Despite many surveys of areas surrounding Paris, the species has not been found again in the area of the type locality (Boeters & Falkner 2017). However, morphological and molecular data of the populations living in this area will



Amnicola emiliana

Coquille ovoïde-ventrue, à fente ombilicale bien distincte, cornée, un peu transparente, légèrement brillante, presque lisse ; — spire assez aiguë, à sommet petit ; — 4 tours 1/2 assez convexes, aplatis en dessus et comme canaliculés vers la suture qui est bien marquée ; dernier tour très-grand relativement, ovoïde, égalant ou même dépassant en hauteur la 1/2 de la hauteur totale, descendant à peine vers l’ouverture ; bord libre vertical, à peine sinué. — Ouverture allongée-elliptique, à peine oblique, à extrémité supérieure de l’ellipse un peu saillante et légèrement anguleuse à cause de l’aplatissement supérieur du dernier tour ; péristome droit, à peine épaissi ; bord columellaire un peu réfléchi ; bord externe faiblement arqué.

Opercule elliptique, à peine anguleux supérieurement, d’une couleur marron, brillant, mince, marqué de stries spirescentes très-légères, très-profondément situé.

Haut., 2 1/2-3^{mm} ; — diam., 2^{mm}.

Cette espèce se trouve dans un ruisseau d’eaux douces des environs de Balaruc (Hérault). Nous l’avons également reçue des environs de Salces (Pyrénées-Orientales), et de San Giuliano, près de Gênes (Italie).

Amnicola balearica

Coquille à perforation ombilicale bien marquée, conoïde-allongée, cornée, brillante, mince, assez transparente ; — spire assez conique, sommet aigu ; — 5 tours à 5 1/2 convexes, séparés par une suture bien marquée et un peu canaliculés en dessus vers la suture, s’accroissant avec rapidité à partir du 3^{e} inclusivement ; dernier tour bien développé, n’égalant pas tout à fait la moitié de la hauteur de la coquille, descendant à peine vers l’ouverture ; bord libre rectiligne, presque vertical. — Ouverture assez bien arrondie, peu oblique, à peine un peu resserrée vers le haut ; péristome droit, simple, à peine un peu réfléchi à son bord columellaire.

Opercule profondément situé, mince, transparent, présentant des stries spirescentes extrêmement délicates.

Haut., 3^{mm} ; — diam., 2^{mm}.

Cette nouvelle Amnicole, qui ne saurait être confondue avec aucune autre, nous a été envoyée de Port-Mahon (Iles Baléares).

Amnicola maceana

Coquille ovoïde-allongée, à fente ombilicale étroite, d’une couleur cornée, à peine transparente, presque lisse ; — spire assez aiguë, ovoïde, conique ; sommet petit ; — 6 tours assez convexes, croissant rapidement et séparés par une suture bien marquée ; dernier tour grand, convexe, égalant à peu près en hauteur les 2/5 de l’ensemble de la coquille, descendant lentement et régulièrement vers l’ouverture, et présentant un bord libre droit et à peu près vertical. — Ouverture à peine oblique, arrondie, très-faiblement anguleuse vers le haut ; péristome très-légèrement épaissi et faiblement évasé ; bord columellaire un peu réfléchi, bord externe régulièrement arqué.

Opercule corné, marron-rougeâtre, un peu concave vers son *nucleus* qui est fort rapproché du bord columellaire ; il est orné de stries d’accroissement spirescentes très-fines et très-élégantes, et assez profondément enfoncé dans l’ouverture de la coquille.

Haut., 6^{mm} ; — diam., 4^{mm}.

Cette nouvelle Amnicole, que nous nous faisons un plaisir de dédier à notre honorable correspondant et ami, M. J. A. Macé, de Cannes (Alpes Maritimes), a été récoltée à Antunez, près de Barcelone (Espagne).

Amnicola lanceolata

Coquille ovoïde-allongée, à fente ombilicale étroite, d’une couleur cornée, à peine transparente, presque lisse ; — spire assez aiguë, ovoïde, conique ; sommet petit ; — 6 tours assez convexes, croissant rapidement et séparés par une suture bien marquée ; dernier tour grand, convexe, égalant à peu près en hauteur les 2/5 de l’ensemble de la coquille, descendant lentement et régulièrement vers l’ouverture, et présentant un bord libre droit et à peu près vertical. — Ouverture à peine oblique, arrondie, très-faiblement anguleuse vers le haut ; péristome très-légèrement épaissi et faiblement évasé ; bord columellaire un peu réfléchi, bord externe régulièrement arqué.

Opercule corné, marron-rougeâtre, un peu concave vers son *nucleus* qui est fort rapproché du bord columellaire ; il est orné de stries d’accroissement spirescentes très-fines et très-élégantes, et assez profondément enfoncé dans l’ouverture de la coquille.

Haut., 6^{mm} ; — diam., 4^{mm}.

Cette nouvelle Amnicole, que nous nous faisons un plaisir de dédier à notre honorable correspondant et ami, M. J. A. Macé, de Cannes (Alpes Maritimes), a été récoltée à Antunez, près de Barcelone (Espagne).

Fig. 32. Comparison among original descriptions of *Mercuria emiliana* (Paladilhe, 1869), *M. balearica* (Frauenfeld, 1865), *M. maceana* (Paladilhe, 1869) and *Amnicola lanceolata* Paladilhe, 1869 taken from Paladilhe (1869). Red lines remark the colour of the shells and operculum according to the author’s criterion.

be needed to clarify the taxonomic status of *M. anatina* and its validity as a species. This is particularly important because if the type populations of *M. tachoensis* and *M. anatina* are found to be conspecific (i.e., belonging to the same nominal taxon), this would invalidate the name *M. tachoensis*, as *M. anatina* is an older name. Until such empirical evidence is collected, we consider *M. tachoensis* to be the proper name of the species delimited and assigned to this taxon by Miller *et al.* (2022) based on molecular analyses including topotype specimens of *M. tachoensis*.

Boeters & Falkner (2017) assigned three populations of *Mercuria* located in the Netherlands to *M. anatina*. We sampled a population from one of these localities, the distributary of Oude Maas in Hoogvliet, Netherlands. Previous molecular findings (Miller *et al.* 2022) and our morphological studies of these specimens indicate that they belong, for now, to a population of *M. tachoensis*.

The systematics of populations of *Mercuria* that occur in the British Islands has always been confusing as many authors have attributed these populations, seemingly indiscriminately, to species distributed over the Mediterranean (i.e., *M. similis*) or in Atlantic coastal streams (i.e., *M. anatina*). Kerney (1999) and Anderson & Rowson (2020) cited all of the collected populations as *M. confusa*. Further assignations corrected the name, at least for the cases involving *M. similis*, though the authors cautiously named the species as *M.* cf. *similis* (Anderson 2005; Byrne *et al.* 2009). Kadolsky (2011) attributed populations occurring in the Arun River to *M. anatina*. The molecular survey by Miller *et al.* (2022), which included a population from this river and another from Barking, London, indicates that these snails are conspecific and probably *M. tachoensis*.

Morphological and DNA-sequence data have revealed that *M. tachoensis* is distributed along a large section of the Atlantic coastal area of Europe and in the British Islands. A similar geographic distribution pattern has also been documented in other freshwater taxa, including fishes (Reyjol *et al.* 2007), the genus *Unio* Philipsson, 1788 (Unionidae: Bivalvia) (Araujo *et al.* 2017) and the genus *Theodoxus* Montfort, 1810 (Neritidae: Gastropoda) (Sands *et al*. 2019). In this pattern, the Atlantic slope presents lower species richness compared with the Mediterranean region, consistent with our observations of *Mercuria*, and its higher diversity in the latter region.

Identified species of *Mercuria* after using an integrative approach

Our assignment of the collected populations to species using an integrative approach changes the number of species that should be currently recognised, and the extent of their distributions. Although Boeters & Falkner (2017) found a total of six species of *Mercuria* (i.e., *M. bayonnensis*, *M. baudoniana* (Gassies, 1859), *M. sarahae* (Paladilhe, 1869), *M. anatina*, *M. similis* and *M. meridionalis*) in the continental area of France, in our study, which included populations of four of these species (i.e., *M. bayonnensis*, *M. anatina*, *M. similis* and *M. meridionalis*), we could only identify two species (here assigned to *M. tachoensis* and *M. similis*). For the Iberian Peninsula and the Balearic Islands, Boeters (1988), Glöer *et al.* (2015) and Boeters & Falkner (2017) mentioned a total of six species (*M. tachoensis*, *M. edmundi*, *M. similis*, *M. balearica*, *M. bayonnensis* and *M. emiliana*). In our study, we found evidence for only three of these species (i.e., *M. tachoensis*, *M. similis* and *M. balearica*), which appear to have a wider distribution than previously thought. The inclusion of new populations from the Iberian Peninsula has revealed the existence of three newly discovered species (*M. egarensis* sp. nov., *M. carrillorum* sp. nov. and *M. felixi* sp. nov.). Likewise, new populations from the Italian Peninsula have uncovered a newly discovered species (*M. lupiaensis* sp. nov.).

According to our classic and geometric morphometric results, we found that the shell of *Mercuria* presents wide intra- and interspecific variability, thus evidencing that this character should not be used alone to propose species hypotheses. Similar results were found for the colour of the operculum. A high level of variability was also found in the reproductive system in characters associated with the penis, penial appendix and bursa copulatrix, indicating that these characters should be used with caution to delimit species of the genus. To this end, we propose wherever is possible, as an alternative, the use of an integrative taxonomic approach incorporating data from other sources of information to the proper species hypotheses such as DNA, ecology, ethology, and geometric morphometrics.

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Supplementary material

Supp. file 1. Table S1. Information on the sampling locations of the studied populations as well as collection numbers at the MNCN and UGSB. https://doi.org/10.5852/ejt.2023.866.2107.8853

Supp. file 2. Dimensions of the species of *Mercuria* Boeters, 1971 included in this paper.
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Table S2. Shell dimensions (mm) of *Mercuria similis* (Draparnaud, 1805).

Table S3. Dimensions of the osphradium, ctenidium and anterior digestive system (mm) in *Mercuria similis* (Draparnaud, 1805).

Table S4. Female genitalia measurements (mm) recorded in *Mercuria similis* (Draparnaud, 1805).

Table S5. Male genitalia measurements (mm) recorded in *Mercuria similis* (Draparnaud, 1805).

Table S6. Shell dimensions (mm) of *Mercuria tachoensis* (Frauenfeld, 1865).

Table S7. Dimensions of the osphradium, ctenidium and anterior digestive system (mm) in *Mercuria tachoensis* (Frauenfeld, 1865).

Table S8. Female genitalia measurements (mm) recorded in *Mercuria tachoensis* (Frauenfeld, 1865).

Table S9. Male genitalia measurements (mm) recorded in *Mercuria tachoensis* (Frauenfeld, 1865).

Table S10. Shell dimensions (mm) of *Mercuria balearica* (Paladilhe, 1869).

Table S11. Dimensions of the osphradium, ctenidium and anterior digestive system (mm) in *Mercuria balearica* (Paladilhe, 1869).

Table S12. Female genitalia measurements (mm) recorded in *Mercuria balearica* (Paladilhe, 1869).

Table S13. Male genitalia measurements (mm) recorded in *Mercuria balearica* (Paladilhe, 1869).

Table S14. Shell dimensions (mm) of *Mercuria* spp.

Table S15. Nervous system measurements (mm) and RPG ratios (average per species) of *Mercuria* spp.

Table S16. Dimensions of the osphradium, ctenidium and anterior digestive system (mm) in *Mercuria* spp.

Table S17. Female genitalia measurements (mm) recorded in *Mercuria* spp.

Table S18. Male genitalia measurements (mm) recorded in *Mercuria* spp.