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Caridina tashanica sp. nov., a new cave shrimp species (Decapoda, Atyidae) from sulphidic water in southwestern Iran

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Abstract

A new cave species of atyid shrimp of the genus *Caridina* H. Milne Edwards, 1837 was discovered during a survey of a subterranean habitat in southwestern Iran (Khuzestan Province, Tashan Cave). This is the first record of a cave atyid shrimp in Iran and the first documented occurrence of a *Caridina* species inhabiting sulphidic groundwater. Phylogenetic analyses and genetic distances support the status of *Caridina tashanica* **sp. nov.** as a distinct species, closely related to *C. shahrazadae*. Morphologically, the new species is characterised by reduced eyes and pigmentation, and by an extremely elongated rostrum with numerous teeth. Males have specific, triangular endopodite of pleopod I, and a rod-like appendix masculina of pleopod II with numerous long setae. Ovigerous females lay relatively large, oval, white eggs, which clearly indicate a landlocked life cycle. This study contributes to the knowledge of atyid shrimps in the Middle East and to the subterranean biodiversity of the sulphidic Tashan Cave ecosystem in Iran.

* These authors contributed equally to this work.

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Keywords
Atyids, groundwater, Middle East, subterranean, sulphidic, Tashan Cave

Introduction

Freshwater shrimps of the family Atyidae occur worldwide across a wide range of habitats, spanning from freshwater to mixohaline and from surface to subterranean habitats (De Grave et al. 2008; De Grave and Fransen 2011). The genus *Caridina* H. Milne Edwards, 1837 is the most species-rich within the atyids, currently comprising 364 nominal species (DecaNet. 2026: Assessed through WoRMS at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=240672 on 19 February 2026), with a wide distribution that includes the Indo-Malayan, Australasian, Afrotropical and Oceanian, and extending into parts of the eastern Palearctic realms (De Grave et al. 2015). In the Palearctic, the genus reaches its northwestern limit of distribution in the Middle East (Klotz et al. 2019), where the endemic monotypic Iraqi genus *Puteonator* (*P. iraqiensis* Gurney 1987), which closely resembles *Caridina*, also occurs. Although several subterranean species of *Caridina* have been described — predominantly from Southeast Asia — no cave shrimp of the genus has yet been recorded from the Middle East.

To date, four epigean species of atyid shrimps have been recorded in Iran: *Atyaephyra orientalis* Bouvier, 1913 (previously reported as *Atyaephyra desmarestii* (Millet, 1931)) and three species of the genus *Caridina*: *C. fossarum* Heller, 1862, *C. fernandoi* Arudpragasam & Costa, 1962, and *C. shahrazadae* Klotz, von Rintelen & Christodoulou, 2019. Despite these records, the atyid shrimp fauna of Iran remains poorly studied; particularly in subterranean habitats, where a high diversity of newly described subterranean taxa has recently been discovered (Reboleira et al. 2015; Mousavi-Sabet and Eagderi 2016; Malek-Hosseini and Zamani 2017; Malek-Hosseini et al. 2021), including several new subterranean crustaceans (e.g. Amphipoda, Isopoda) (Malek-Hosseini et al. 2023; Jugovic et al. 2024; Mamaghani-Shishvan et al. 2024), highlighting the region's high, but still largely unexplored subterranean biodiversity. To date, however, no subterranean decapods have been reported from Iran.

Recently, Klotz et al. (2019) conducted a comprehensive study of atyids from the Middle East, describing three new epigean *Caridina* species from freshwater habitats in Syria, Iraq and Iran. From western Iran, *C. shahrazadae* was described (Klotz et al. 2019), a species that was likely previously neglected due to its high morphological similarity to *C. fossarum*. Species of *Caridina* inhabit freshwater habitats along the Zagros Mountains (Fig. 1), one of Iran's principal mountain chains, extending from the northwest to the south of the country. This region comprises approximately one-fifth of Iran's land area and contains around 55% of the country's karstic carbonate rock formations (Reboleira et al. 2015). Such karstic landscapes are well known to harbour high subterranean diversity, including *Caridina* (e.g. Feng et al. 2021).

Here, we describe *Caridina tashanica* sp. nov., the first exclusively subterranean atyid shrimp recorded from Iran. This depigmented species with strongly reduced eyes

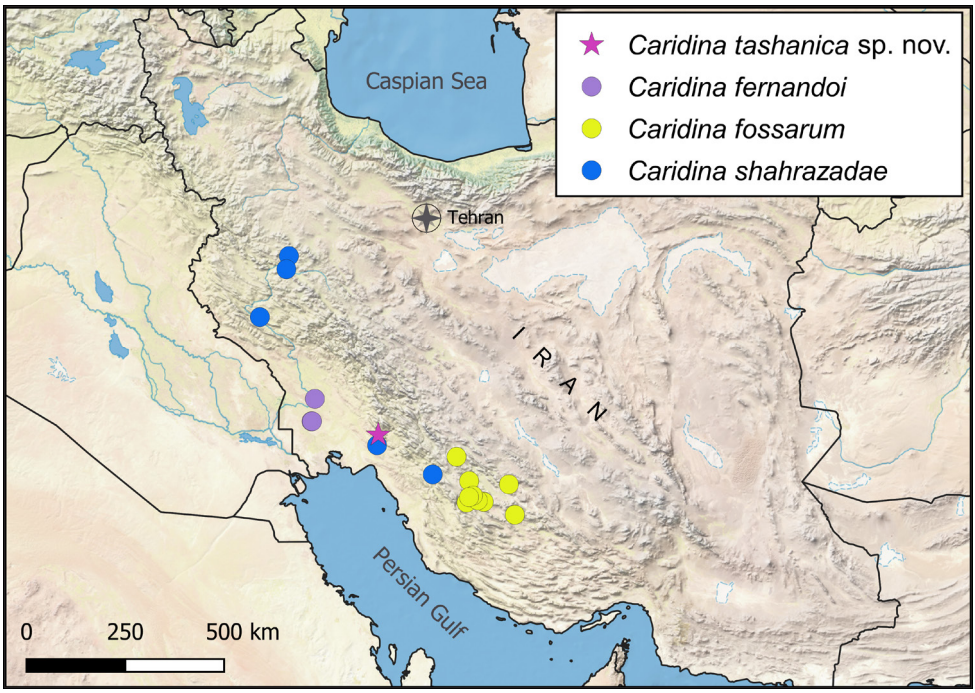

Figure 1. Distribution of *Caridina* species in Iran, including the type locality of the new cave shrimp species *Caridina tashanica* sp. nov. Distribution data are available in Suppl. material 1: table S2.

and eye pigmentation was discovered in a karstic cave system in the Zagros Mountains. It is not only the first cave shrimp known from Iran, but also the northwesternmost cave species of the genus and the first *Caridina* reported from sulphidic groundwater. We used molecular data to corroborate the distinctiveness of *Caridina tashanica* sp. nov. from previously described species and to assess its phylogenetic relationships with other *Caridina* from Iran. This finding represents a new insight into the diversity and biogeography of subterranean atyids in the Middle East and highlights the need for further speleobiological investigations in Iran's karstic areas.

Materials and methods

Cave and habitat description

Tashan Cave is part of the Tashan-Chah Kabootari cave system in Khuzestan Province, within the Zagros Mountains of southwestern Iran (30°52'10"N, 50°10'01"E, altitude 539 m above sea level; Fig. 1). It is a limestone cave representing a specific subterranean habitat characterised by several cave pools containing groundwater enriched with hydrogen sulphide (Fatemi et al. 2019). Several neighbouring wells and springs are fed

with sulphidic water from this aquifer. In recent years, groundwater sulphide ecosystems and their fauna have attracted scientific interest (e.g. Brad et al. 2021), as they host unique and highly adapted communities, often with remarkable taxonomic and functional diversity, particularly among crustaceans (Peterson et al. 2013; Por et al. 2013).

Sampling

Cave specimens were caught by hand net during field trips in Tashan Cave, Tashan County, Khuzestan Province, southwestern Iran by Mohammad Javad Malek Hosseini and Yaser Fatemi and preserved in 96% ethanol. Samples were collected during three field trips: 27 August 2016, 16 October 2017 and 17 March 2018. Epigean *Caridina fossarum* and *C. fernandoi* specimens were collected using the same method from a spring and river in Iran (Suppl. material 1: table S2). Most samples are stored in the Zoological collection at the University of Ljubljana, Biotechnical Faculty, Department of Biology, Slovenia, whereas two specimens (vouchers TB489 and TB486) were deposited in the National Museum of Natural History and Genetic Resources, Department of Environment, Tehran, Iran.

Morphological analysis

Animals were dissected and photographs of the body parts were taken under a stereomicroscope (Leica EZ4, digital camera Sony DXC390P) using the program LAZ EZ Ink, and measurements of morphological characters followed 73 metric and 17 meristic characters (see Jugovic et al. 2010a, 2010b, 2011 for a list of characters). Vector drawings were created from microphotographs using a graphic tablet (Wacom, Cintiq 13HD Creative Pen Display) in the freeware Krita 4.1.1. Each animal received a unique voucher number and the type specimen was deposited in the Zoological Collection at the University of Ljubljana, Biotechnical Faculty, Department of Biology, Slovenia (see Material examined). The abbreviation CL is used for carapace length, measured from the postorbital margin to the posterior margin of the carapace and RL for rostrum length, measured from the tip of the rostrum to the postorbital margin. The rostral dentition formula '(X+Y)/Z' denotes the number of teeth dorsally on the rostrum and carapace over the number of teeth ventrally on the rostrum. In the description we report values measured in the holotype, and ranges (min–max) for male (♂♂) and female (♀♀) material.

In ovigerous females, eggs were counted and measured as proposed by Oh and Hartnoll (2004); eggs were treated as ellipsoids and their volume was calculated using the formula: $4/3\pi r_1(r_2)^2$, where r_1 is half the major axis and r_2 is half the minor axis.

Molecular and phylogenetic analysis

Genomic DNA was isolated using the GeneElute Mammalian Genomic DNA Miniprep Kit (Sigma-Aldrich, USA) from one of the pereiopods and the rest of the specimens was kept for further morphological studies. Two mitochondrial regions (cytochrome *c* oxidase subunit I – COI and 16S rDNA) and one nuclear gene (histone H3) were

amplified. A list of PCR primers and PCR amplification protocols is available in Suppl. material 2. PCR products were purified using Exonuclease I and FastAP (Thermo Scientific, USA) according to the manufacturer's instructions. Each fragment was sequenced in both directions with the same primers as for amplification by Macrogen Europe (Amsterdam, the Netherlands) and sequence chromatograms were visually checked, assembled and edited in Geneious v11.1.5 (Biomatters, New Zealand). Sequences were aligned using MAFFT v7 (Katoh and Standley 2013), using the G-INS-I algorithm, and concatenated in Geneious. The total length of the concatenated dataset was 1533 bp. The most probable substitution model and the best partitioning scheme were selected in PartitionFinder v2.1.1 (Lanfear et al. 2012) and are included in Suppl. material 2.

To assess the phylogenetic position of the new *Caridina* species, we compiled a dataset of 18 specimens from the genus. As the genus *Caridina* is highly diverse, likely not monophyletic (Page et al. 2007a; von Rintelen et al. 2012), and in need of revision, the dataset comprised only putatively closely related species from the region from Africa, the Middle East to India and Sri Lanka. *Xiphocaris elongata* was used as the outgroup. The list of taxa and specimens, sample origin and GenBank Accession Numbers are provided in the Suppl. material 1: table S1.

Phylogenetic relationships were reconstructed using Bayesian inference (BI) with partition-specific settings in MrBayes 3.2.7 (Ronquist and Huelsenbeck 2003) and maximum likelihood (ML) in IQ-tree (Nguyen et al. 2015). Maximum likelihood analyses used partition specific settings on the IQ-web server (Trifinopoulos et al. 2016). The Bayesian MCMC tree search used partition-specific settings with two independent runs with four chains each run for 5 million generations, with trees sampled every 1000th generation. After reaching the stationary phase, the first 25% of trees were discarded and a 50% majority rule consensus tree was calculated from the remaining trees. Genetic distances for the 16S rDNA gene fragment and for the COI marker, where available, were estimated between *Caridina tashanica* sp. nov. and closely related species using the Kimura-2-parameter (K2P) model implemented in MEGA11 (Tamura et al. 2021).

Results

Phylogenetic analyses

Phylogenetic relationships among selected *Caridina* species, inferred from concatenated mitochondrial and nuclear data, showed *Caridina tashanica* sp. nov. within a well-supported clade that includes its sister species *C. shahrazadae*, as well as *C. fossarum*, *C. enkii* and *C. chauhani* (Fig. 2). The position of the latter species, however, was not well supported. Phylogenetic relationships inferred using both maximum likelihood and Bayesian inference did not recover *Caridina* species from Iran as monophyletic. However, it should be noted that the aim of the present phylogenetic analysis was to assess phylogenetic relationships among *Caridina* species from the Middle East, particularly from Iran. Assessing a phylogenetic relationships of *Caridina* from the Middle East

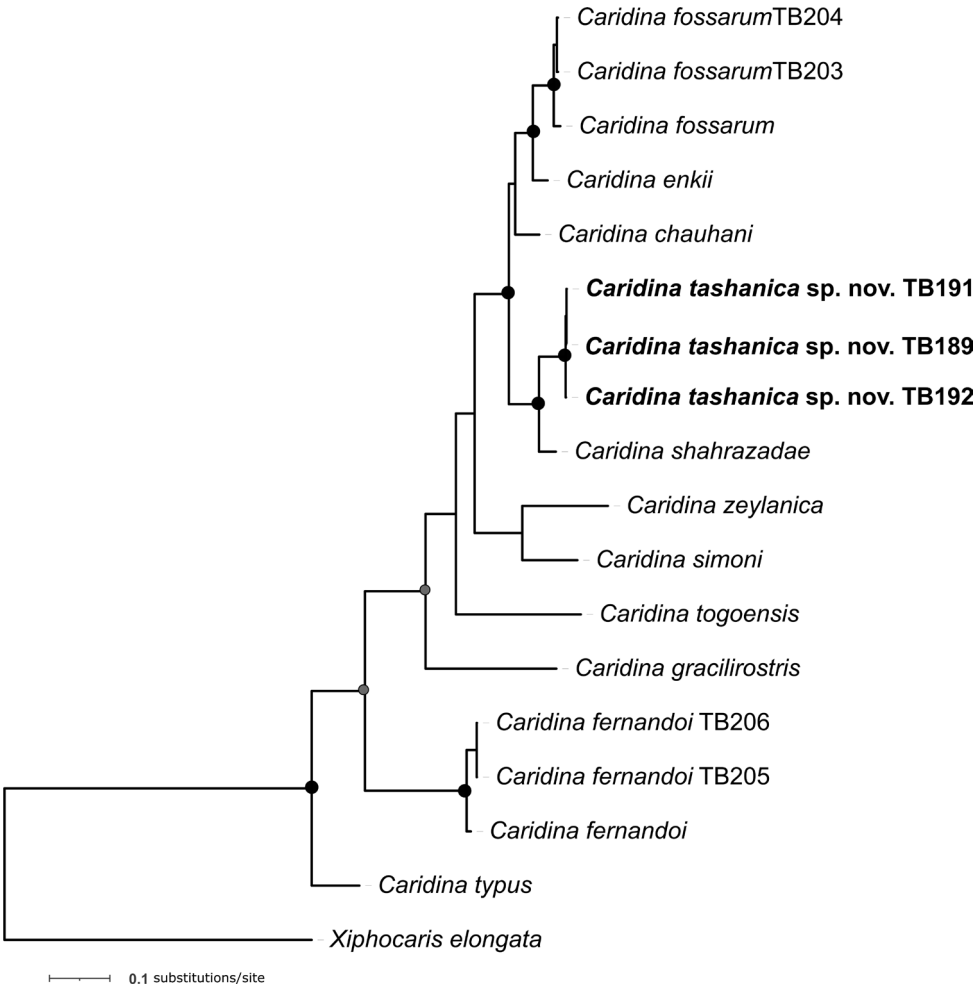

Figure 2. Phylogenetic relationships among *Caridina* species. The tree was constructed using Bayesian inference on concatenated mitochondrial (COI and 16S rDNA) and nuclear (H3) data. The posterior probabilities for the nodes are shown as circles: black = 1 and grey > 0.95. Maximum-likelihood analyses recovered the same topology with high node support.

within this highly diverse genus is beyond the scope of this study and would require a broader taxonomic and molecular framework (e. g. von Rintelen et al. 2012).

The Kimura 2-parameter (K2P) genetic distance in COI between *C. tashanica* sp. nov. and *C. fossarum* was 15.1%. The K2P interspecific distance in 16S rDNA between *C. tashanica* sp. nov. and its sister species *C. shahrazadae* was 3.7% (Suppl. material 2: table S3). The minimum genetic distance within a group of five species of *Caridina* (*C. fossarum*, *C. enkii*, *C. chauhani*, *C. tashanica* sp. nov. and *C. shahrazadae*) from Iran, Iraq and India was 3.1% between *C. fossarum* and *C. enkii* and the highest was 7.0% between *C. tashanica* sp. nov. and *C. enkii*.

Species description

***Caridina tashanica* Jugovic, Malek Hosseini & Zakšek, sp. nov.**
https://zoobank.org/3BE66B62-0808-4F1B-A766-79B1923741F4
Figs 3–5

Material examined. *Holotype*: • male, CL 3.19 mm (voucher number TB483), Tashan cave, Tashan-Chah Kabootari cave system in Khuzestan Province, southwestern Iran, (30°51'54"N, 50°10'29"E), 27 August 2016, coll. by Mohammad Javad Malek-Hosseini, Yaser Fatemi and Vahid Malek Hosseini.

***Paratypes*:** • 2 males and 1 female – male CL 4.17 (TB484) and 2.88 (TB485), female CL 3.86 mm (TB486), data same as holotype.

Other material. • 2 ovigerous females, CL 5.11 (TB487) and 4.69 mm (TB488); • 4 females, CL 5.43 mm (TB489), CL 4.72 mm (TB490), CL 3.42 mm (TB491), 2.95 mm (TB492), • 2 males CL 3.27 mm (TB493) and 3.09 mm (TB494), coll. Mohammad Javad Malek-Hosseini and Yaser Fatemi (16 October 2017). • 3 females and 3 males, coll. Mohammad Javad Malek-Hosseini and Yaser Fatemi (17 March 2018).

Diagnosis. *Caridina tashanica* sp. nov. is the only species of cave shrimp (depigmented and with strongly reduced eyes without pigmentation; Fig. 6) from Iran of the family Atyidae. It is characterised by an extremely long rostrum (Fig. 3) with numerous teeth (13–19+3–5/9–22), uropodal diaeresis with 7–10 spiniform setae and 4–6 pairs of dorsomarginal spiniform setae on the telson of which the distal pair is dorsomarginal-terminal. Propodus of pereiopod III and V bears only 7–14 and 9–18 spiniform setae, respectively, while dactylus of pereiopod V bears only 17–27 spiniform setae in a comb-like formation. Endopodite of male first pleopod is triangular and in females it is triangular with distal elongation, in both sexes without retinacular hooks. Appendix masculina slender (rod-like), ~ 2× wider than appendix interna and bearing small number of spiniform setae (9–15) that surpass the width of the appendix masculina. As all members of the genus *Caridina*, the newly proposed species has only a slightly excavated propodus on the second pereiopod.

Description of male holotype (first reported value) and other material (values in parentheses, where available).

***Cephalothorax and cephalic appendages*.** Carapace surface smooth and depigmented. Its length 3.2 mm (♂♂ 2.9–4.2 mm, median 3.2 mm; ♀♀ 2.9–5.4, median 4.9). Rostrum curved upwards and long (Fig. 3 C), for 1.4× (♂♂ 1.3–1.5; ♀♀ 1.38–1.39) overreaching the antennular peduncle, and overreaching also scaphocerite, 0.79× (♂♂ 0.79–1.00; ♀♀ 0.72–0.80) as long as carapace, with 14+4/11 (♂♂ 13–18+4–5/9–22; ♀♀ 16–19+3–5/13–21) teeth. Teeth on carapace along 21% (♂♂ 14–21%; ♀♀ 17–20%) of CL. Inferior orbital angle with well-developed antennal spine. Pterygostomian angle broadly rounded. Eyestalks still present but short, without pigmentation.

Antennular peduncle (Fig. 4 AI) 0.56× (♂♂ 0.56–0.70; ♀♀ 0.52–0.58) as long as carapace, first segment 1.71× (♂♂ 1.36–2.05; ♀♀ 1.78–2.19) as long as second segment, second segment 1.33× (♂♂ 1.19–1.59; ♀♀ 1.10–1.51) longer than third

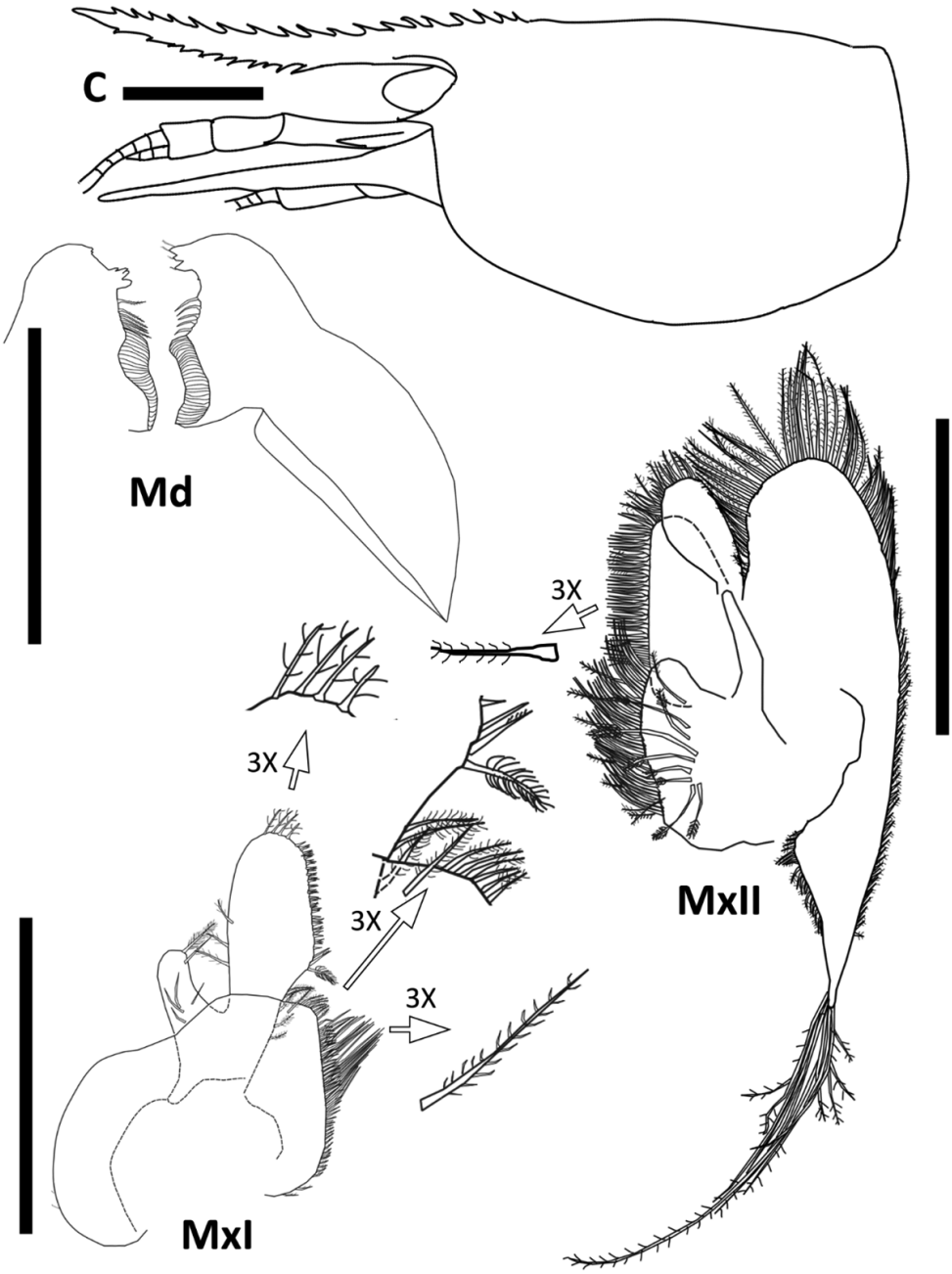

Figure 3. *Caridina tashanica* sp. nov. from Tashan Cave, southwestern Iran. Holotype male, cl 3.2 mm. C – carapace, Md – mandibles, MxI – maxilla I, MxII – maxilla II. Scale bars: 1 mm.

segment. First segment with nearly straight mesial margin with setose distal part. Mesial and lateral margins of second and third segment setose. Upper flagellum uniramous, lower flagellum slender, lengths of both flagella rather exceeding 200% of CL.

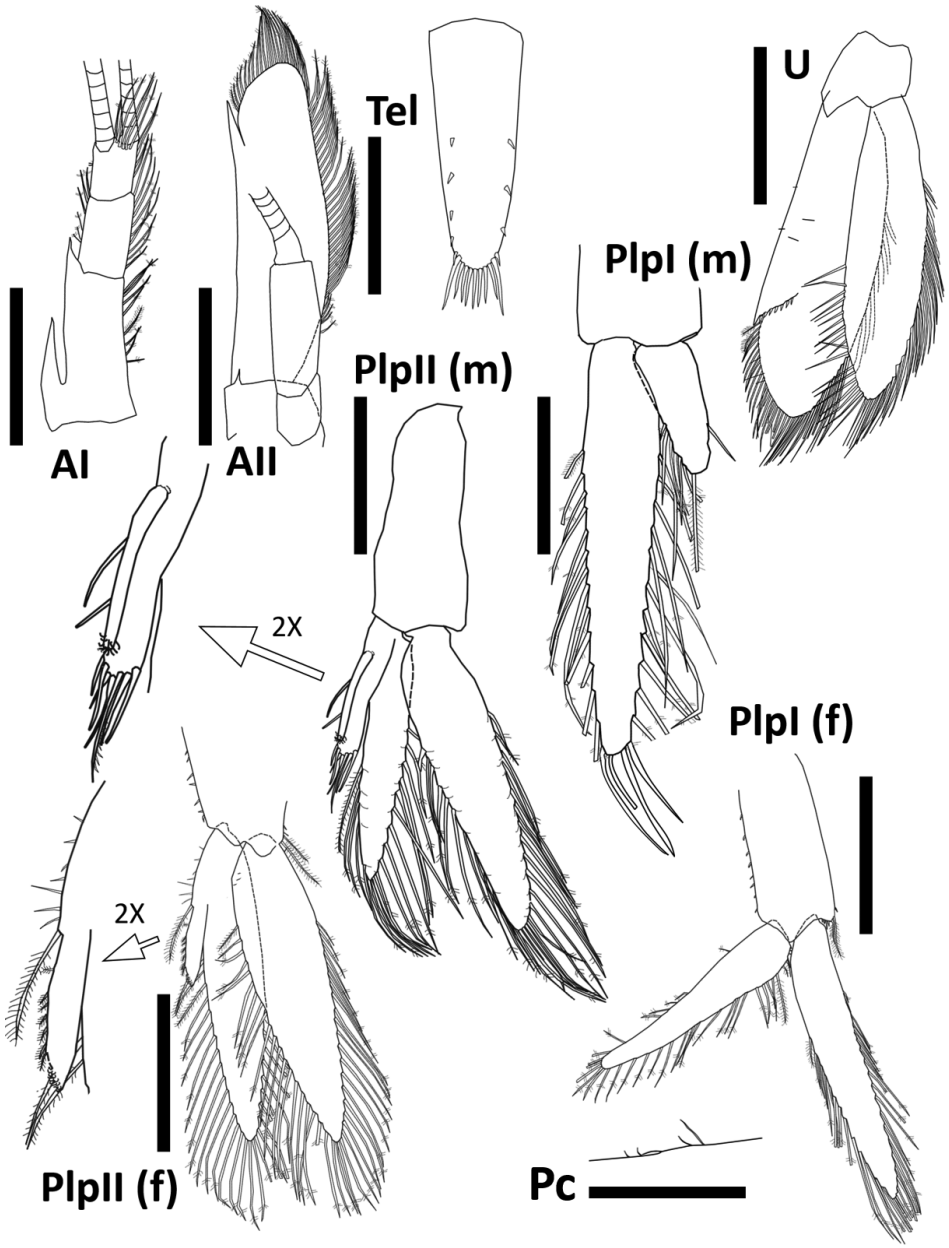

Figure 4. *Caridina tashanica* sp. nov. from Tashan Cave, southwestern Iran. Holotype male, cl 3.2 mm: AI – antenna I (antenna), AII – antenna II (antennula), Tel – telson, PlpI – pleopod I, PlpII – pleopod II, U – uropod (pleopod VI). Paratype female, cl 5.4 mm: PlpI – pleopod I, PlpII – pleopod II; m – male, f – female, Pc – pre-anal carina.

Stylocerite with broad base and slender, acute tip reaching to 0.77× (♂♂ 0.76–0.82; ♀♀ 0.64–0.82) of basal segment of antennular peduncle. Distolateral lobe of the second segment sharply pointed, its length 16% (♂♂ 14–18%; ♀♀ 15–19%) of peduncle length.

Antennal peduncle 0.41× (♂♂ 0.41–0.50; ♀♀ 0.36–0.44) as long as carapace, its scaphocerite (Fig. 4 AII) 3.51× (♂♂ 3.50–4.22; ♀♀ 3.68–4.38) as long as wide. Flagella length rather exceeding 200% of CL.

Abdominal somites, telson and uropods. Abdominal somites smooth, 1.58× (♂♂ 1.58–1.74; ♀♀ 1.32–1.60) carapace length. Sixth abdominal somite 0.42× (♂♂ 0.42–0.49; ♀♀ 0.34–0.44) carapace length, 1.72× (♂♂ 1.59–1.93; ♀♀ 1.64–1.84) as long as fifth somite, 0.84× (♂♂ 0.84–1.00; ♀♀ 0.70–1.03) as long as telson.

Telson (Fig. 4 Tel) length 3.09× (♂♂ 2.45–3.30; ♀♀ 2.86–3.49) as long as its proximal width, its proximal width 1.90× (♂♂ 1.45–1.97; ♀♀ 1.70–1.83) as wide as its distal width. Telson distal margin convex, with 4 (♂♂ 3–4; ♀♀ 3–5) pairs of dorsal spinules and one pair of dorsolateral spinules; distal end with 9 (♂♂ 8–10; ♀♀ 8–12) spines, sublateral pair distinctly shorter than lateral and inner spines.

Uropodal exopodite (Fig. 4 U) 3.15× (♂♂ 3.08–3.29; ♀♀ 2.93–3.14) as long as wide, its diaeresis (Fig. 4 U) with 7 (♂♂ 7–10; ♀♀ 9–10) movable spinules.

Pre-anal carina (Fig. 4 Pc) low, weakly developed, without a tooth or spine.

Mouthparts. Mandible with rather robust corpus, without palp. Mandibular pars incisiva (incisor process; Fig. 3 Md) stout, tapering distally, distal margin of 3 (3–4) teeth of different size. Teeth number on left and right mandible often different. Pars molaris stout and U-shaped with triturative surface.

Maxilla I (Fig. 3 MxI) palp slender truncated, with one long plumose seta at interodistal angle, one long spiniform subdistal seta and four simple setae on palp surface. Rectilinear outer margin of upper lacinia (basipodial endite) with numerous short strong cuspidate setae, curvilinear inner margin with few (3 in holotype) plumose setae and few on upper margin (4 in holotype). Lower lacinia (coxal endite) well developed, semicircular; outer margin with dense plumose and serrate setation.

Maxilla II (Fig. 3 MxII) with slender, simple, tapering palp with one simple seta distally. Basipodial endite bilobed; upper lobe narrower (~ 1/5 of lower lobe), margins with dense plumose setation, its surface without setation. Coxal endite fan-like, with dense plumose setae along its margin and scarcely set plumose setae on its surface. Scaphognatite well developed, broad, margin fringed with plumose setae, anterior lobe large, posterior lobe narrower, subtriangular, with a group of over 10 long plumose setae on lower distal part, the longest setae longer than the posterior lobe itself.

Maxilliped I (Fig. 5 MxpI) bears a finger-like palp; palp's distal margin with several plumose setae. Basipodial endite ~ 3× longer than coxal endite, its distal margin with dense rows of long plumose setae, almost rectilinear outer margin with row of subequally long papulose setae with scale-like setules. Mesial surface of basipodial endite with a sparsely set row of plumose setae. Coxal endite poorly developed, with short serrate and longer plumose setae along outer margin. Exopodite with large caridean lobe ~ 2× longer than flagellum. Lobe and flagellar margins and lobe ventral surface with plumose setation.

Maxilliped II (Fig. 5 MxpII) with well-developed endopodite. Dactylopropodus broad, with long plumose setae on upper superior margin, densely packed longer pappose and shorter serrate setae along almost rectilinear lower superior margin

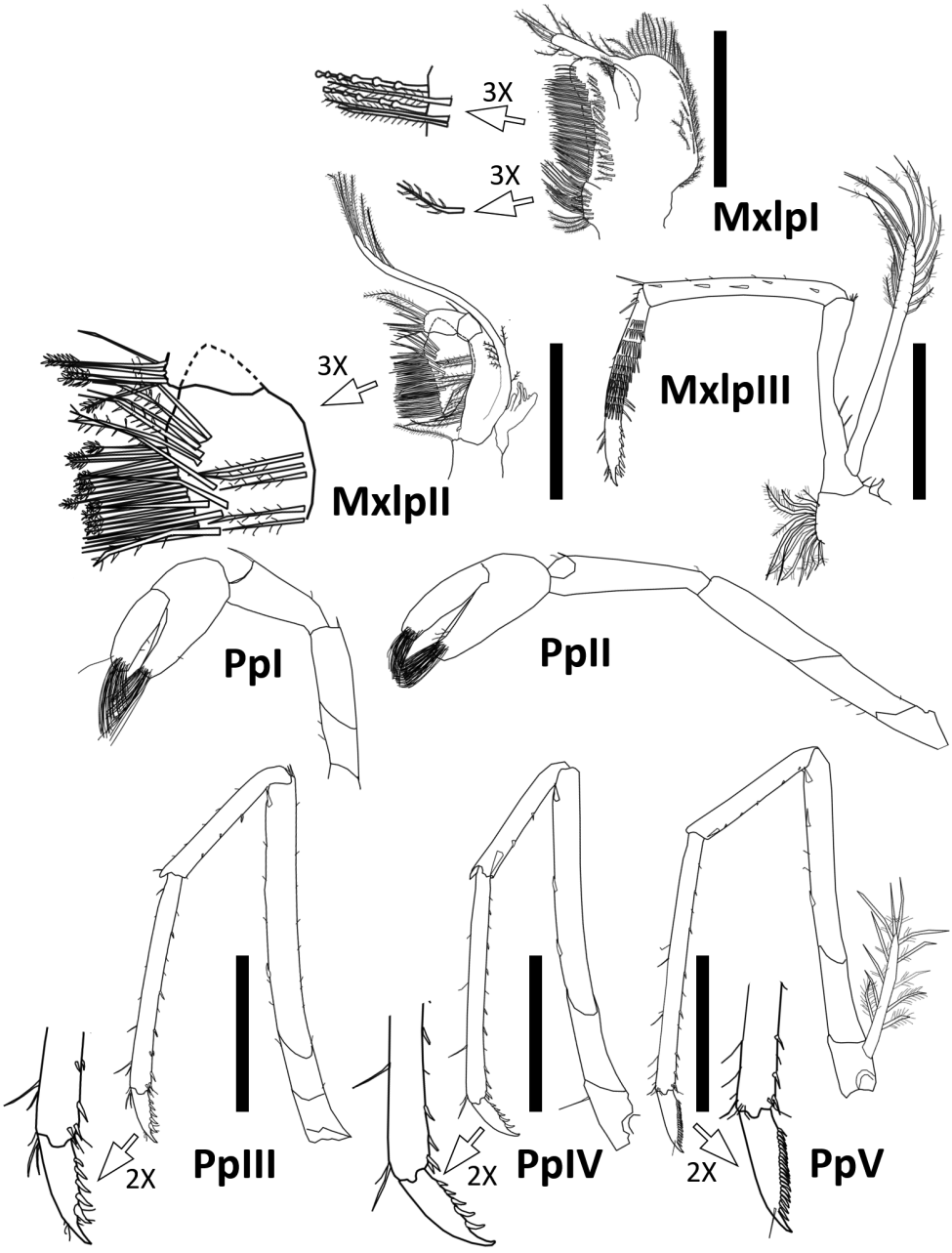

Figure 5. *Caridina tashanica* sp. nov. from Tashan Cave, southwestern Iran. Holotype male, cl 3.2 mm. MxlpI-III – maxilliped I–III, PpI-PpV – pereiopods I–V. Scale bars: 1 mm.

and some long submarginal plumose setae. Exopodite with well-developed flagellum, with plumose distal setae and serrate proximal setae. Well-developed comb-like podobranchium with ~ 6 branches.

Figure 6. Photo of two cave shrimps *Caridina tashanica* sp. nov. (both ovigerous females) from Tashan Cave, Khuzestan Province in southwestern Iran. Photo credit: YF and MJMH, photographed on 8 December 2018.

Maxilliped III (Fig. 5 MxpIII) with slender endopod, 1.19× (♂♂ 1.14–1.25; ♀♀ 1.01–1.10) as long as CL. Ischiomerus merged with basis, about 6.5× as long as wide, with few simple setae proximally on superior margin. Penultimate article slender, about 10× as long as wide and subequal in length to a preceding article, with few sparsely set spiniform setae on mesial surface and few simple setae on upper margin and distosuperior angle. Terminal article (dactylopropodus) about 10× as long as wide and equally long as ischiomerus, tapering distally, with strong apical dactylopropodal spine (claw). Distal ⅓ of inferior margin with ~ 6 subequal spiniform setae, proximal ⅔ of mesial surface and superior submarginal surface with transverse series of serrate setae. Exopodite tip reaching beyond basioischiomeral distal tip, robust flagellum with long plumose distal setae set distally on exopodite. Coxa with larger, well developed arthrobranchium (frequently damaged by dissection).

Pereiopods. First pereiopod (Fig. 5 PpI) sexually dimorphic in length (males > females), from base of article 2 (basis) to apex of article 6 (propodus, unmovable finger of chela) 0.87× (♂♂ 0.85–0.92; ♀♀ 0.73–0.80) length of carapace. Chela and carpus of first pereiopod stouter and broader than chela and carpus of second pereiopod (Fig. 5 PpII); maximal length of chela of first pereiopod 2.13× (♂♂ 1.91–2.15; ♀♀ 2.03–2.44) as long as wide, 1.38× (♂♂ 1.25–1.43; ♀♀ 1.12–1.52) length of carpus; chela with palm subcylindrical, slightly compressed, fingers with dense tuft of longer pappose and shorter serrate setae apically, tips of fingers rounded; dactylus 61% (♂♂ 52–

61; ♀♀ 46–59) of propodus maximal length; carpus slightly excavated distally, 1.11× (♂♂ 1.03–1.21; ♀♀ 0.95–1.15) length of merus. Merus longer than ischium, basis being the shortest segment of the pereiopods. First pereiopod without exopodite.

Second pereiopod (Fig. 5 PpII) sexually dimorphic in length (males > females), from base of article 2 (basis) to apex of article 6 (propodus, unmovable finger of chela) 1.13× (♂♂ 1.13–1.27; ♀♀ 1.02–1.07) length of carapace. Maximal length of chela of second pereiopod 2.12× (♂♂ 2.12–2.57; ♀♀ 2.22–2.48) as long as wide, 0.87× (♂♂ 0.87–0.96; ♀♀ 0.84–0.97) length of carpus; chela with palm subcylindrical, slightly compressed, fingers with dense tuft of longer pappose and shorter serrate setae apically, tips of fingers rounded; dactylus 59% (55–61; ♀♀ 54–64) of propodus maximal length; carpus slightly excavated distally, 1.11× (♂♂ 1.02–1.21; ♀♀ 1.02–1.08) length of merus. Merus longer than ischium, basis being the shortest segment of the pereiopods. Second pereiopod without exopodite.

Third pereiopod slender (Fig. 5 PpIII), sexually dimorphic in length (males > females), its length from base of article 2 (basis) to apex of article 7 (dactylus) 1.58× (♂♂ 1.58–1.83; ♀♀ 1.29–1.61) length of carapace. Dactylus terminating in one large claw with five (♂♂ 5–6; ♀♀ 6) accessory spines on flexor margin; propodus 4.10× (♂♂ 4.04–4.26; ♀♀ 4.46–4.89) as long as dactylus; carpus 0.67× (♂♂ 0.65–0.69; ♀♀ 0.65–0.70) as long as propodus, 0.55× (♂♂ 0.51–0.55; ♀♀ 0.54–0.60) as long as merus; merus 1.82× (♂♂ 1.82–1.95; ♀♀ 1.67–1.95) as long as carpus. Ischium is always longer than basis which is the shortest segment of the third pereiopod. Third pereiopod without exopodite. Propodus, carpus and merus bear 8 (♂♂ 7–12; ♀♀ 11–14), 3 (♂♂ 2–9; ♀♀ 3–6) and 2 (♂♂ 1–3; ♀♀ 0–3) spiniform setae, respectively. Ischium and basis bear no spiniform setae.

Fourth pereiopod (Fig. 5 PpIV) similar to third pereiopod, sexually dimorphic in length (males > females), its length from base of article 2 (basis) to apex of article 7 (dactylus) 1.54× (♂♂ 1.54–1.71; ♀♀ 1.36–1.52) length of carapace. Dactylus terminating in one large claw with five (♂♂ 5–7; ♀♀ 6) accessory spines on flexor margin; propodus 4.14× (♂♂ 4.02–4.85; ♀♀ 4.67–5.42) as long as dactylus; carpus 0.65× (♂♂ 0.60–0.68; ♀♀ 0.63–0.65) as long as propodus, 0.61× (♂♂ 0.51–0.61; ♀♀ 0.57–0.62) as long as merus; merus 1.65× (♂♂ 1.65–1.97; ♀♀ 1.61–1.74) as long as carpus. Ischium is always longer than basis which is the shortest segment of the fourth pereiopod. Fourth pereiopod without exopodite. Propodus, carpus and merus bear 11 (♂♂ 8–12; ♀♀ 9–15), 3 (♂♂ 2–6; ♀♀ 2–8) and 3 (♂♂ 0–4; ♀♀ 1–3) spiniform setae, respectively. Ischium and basis bear no spiniform setae.

Fifth pereiopod (Fig. 5 PpV) slender, sexually dimorphic in length (males > females), its length from base of article 2 (basis) to apex of article 7 (dactylus) 1.61× (♂♂ 1.55–1.68; ♀♀ 1.33–1.57) length of carapace. Dactylus terminating in one large claw with a series of 19 (♂♂ 17–27; ♀♀ 23–26) spiniform setae forming a comb on flexor margin; propodus 3.89× (♂♂ 3.68–4.37; ♀♀ 3.74–4.51) as long as dactylus; carpus 0.55× (♂♂ 0.52–0.55; ♀♀ 0.53–0.54) as long as propodus, 0.68× (♂♂ 0.61–0.68; ♀♀ 0.64–0.67) as long as merus; merus 1.46× (♂♂ 1.46–1.63; ♀♀ 1.48–1.55) as long as carpus. Ischium is always longer than basis which is the shortest segment of the

fifth pereiopod. Fifth pereiopod exceptionally with exopodite. Propodus, carpus and merus bear 12 (♂♂ 9–12; ♀♀ 10–18), 6 (♂♂ 2–6; ♀♀ 4–6) and 3 (♂♂ 1–3; ♀♀ 2) spiniform setae, respectively. Ischium and basis bear no spiniform setae.

Pleurobranchs present on all pereiopods.

Pleopods. Endopodite of male first pleopod (Fig. 4 PlpI(m)) triangularly elongated, 0.34× (0.34–0.36) as long as exopodite, without visible appendix interna and no retinacular hooks. Only few (1–7) simple setae along endopodite margins.

Appendix masculina on male second pleopod (Fig. 4 PlpII(m)) slender, 0.53× (0.42–0.59) as long as endopodite, with some long spines on inner and numerous long spines (surpassing the width of the appendix masculina) on distal margin (9–15 along the margins), appendix interna ~ half slender than appendix masculina but almost as long as apendix masculina, bearing ~ 10 (9–15) retinacular hooks. Exopodite 1.21× (1.06–1.21) longer than endopodite.

Endopodite of female first pleopod (Fig. 4 PlpI(f)) slender and distally elongated, 0.71–0.82× (smallest measured female: 0.27×, CL 3.9 mm) as long as exopodite, the distal elongation probably representing appendix interna but without retinacular hooks. Female second pleopod (Fig. 4 PlpII(f)) similar to the male second pleopod; its exopodite 1.02–1.11× as long as endopodite, appendix interna 0.26–0.30× as long as endopodite, without appendix masculina but with slender appendix interna bearing 8–16 retinacular hooks.

Sexual dimorphism. Besides sexually dimorphic pleopods I–II that shrimps use in reproduction (Fig. 4), we noticed sexual size dimorphism (females > males, compare CLs in Material examined) and significantly longer (relatively to CL, see Description) pereiopods in males than females. It is possible that the smallest shrimps in our sample were subadults, but a larger sample would be needed to ascertain this assumption.

Reproductive biology. Ovigerous females with 12–17 (n=2) oval white eggs; size of eggs 0.97–1.36 × 0.73–0.97 mm and volume 2.68–5.13 mm^3. No eyes could be noticed in the eggs of neither of the two ovigerous females. Species of *Caridina* with relatively large eggs, such as *C. tashanica* sp. nov., usually lack a planktonic larval stage and are indicative of a landlocked freshwater habitats and life cycle (Lai and Shy 2009, Chiao-Chuan et al. 2011).

Etymology. The species epithet *tashanica*, a feminine Latinized adjective, originates from the name of the type locality, Tashan Cave.

Distribution. *Caridina tashanica* sp. nov. is known only from the Tashan Cave in Zagros Mountains in southwestern Iran (Fig. 1).

Remarks. Up to now, four species of atyid shrimps have been recorded from Iran, neither of them being exclusively subterranean. These are *Atyaephyra orientalis* Bouvier, 1913 (reported as *A. desmarestii* by Gorgin 1996), and three *Caridina* species, namely *C. fernandoi* Arudpragasam & Costa, 1962 (reported as *C. babaulti basrensis* by Al-Adhub & Hamzah, 1987), *C. fossarum* Heller, 1862 and *C. shahrazadae* Klotz, von Rintelen and Christodoulou 2019. Recently, *Caridina enkii* was described from neighbouring Iraq although there is some uncertainty about the origin of the type material (Klotz et al. 2019). All the above-mentioned species are epigean and have well

developed, pigmented eyes and pigmented body. While colouration is present but unknown for *C. fossarum*, *C. shahrazadae*, *C. enkii* (Klotz et al. 2019) and *C. peninsularis* Kemp, 1918, their eyes are known to be well pigmented, whereas in *Caridina tashanica* sp. nov. both eye and body pigment are lacking. In *C. chauhani* and *C. fernandoi* the pattern of body colour is variable (Arudpragasam and Costa 1962) and often mimics the environment, which is characteristic for many *Caridina* species. In *C. fernandoi*, eyes are pigmented and have dilated cornea. Phylogenetically, *Caridina tashanica* sp. nov. is a sister species to the epigean *C. shahrazadae* (see Results), which was found from a locality not far from Tashan cave. One of *C. shahrazadae* locations (Klotz et al. 2019) from Khuzestan Province (road between Behbahan and Ramhormoz, 30°39'N, 50°09'E;) is about 25 km east of the Tashan cave (Fig. 1).

Exopods on pereiopods are absent in *C. tashanica* sp. nov., which is consistent with the typical morphology of *Caridina*. Well-developed pereiopodal exopods are characteristic of basal atyid genera (e.g., *Paratya*, *Atyaephyra*, *Syncaris*), but are generally lacking in *Caridina* (De Grave and Page 2014). The rare occurrence of an exopod in *C. wilkinsi* (and occasionally in *C. thermophila*; Calman (1926), Riek (1953)) has been interpreted as an evolutionary reversal rather than a character of generic significance. The absence of exopods in the present species therefore supports its placement within *Caridina* (De Grave and Page 2014).

A more detailed comparison of morphological characters with other closely related *Caridina* species from Middle East and South Asia is available in Suppl. material 2.

Discussion

Diversity and morphology of *Caridina* shrimps in the Middle East

The discovery of *Caridina tashanica* sp. nov., the first subterranean atyid species from Iran, raises the number of *Caridina* species known from the Middle East to seven. All previously known Middle East *Caridina* are epigean, although Zare et al. (2011) reported *C. fossarum* as inhabiting subterranean habitats, which is likely a misinterpretation of the original description (Karami and Gorgin 2000). The complete absence of body and eye pigmentation in *Caridina tashanica* sp. nov. represents a case of troglomorphy, adaptation typical for stygobiotic atyids found in karstic systems worldwide (Holthuis 1993; Page et al. 2007a; von Rintelen et al. 2012). Exclusively subterranean atyids are relatively common, i.e. found in approximately 20 genera, including *Caridina* (Holthuis 1993, Page et al. 2007b; see Jugovic et al. 2019) and have evolved several times independently (von Rintelen et al. 2012). Up to now, at least 25 subterranean species of *Caridina* have been described, mostly from the extensive karst regions of southern China (Cai and Ng 2018). More recently, cave shrimps were also described from nearby Vietnam (Tu et al. 2021) as well as from the Andaman and Nicobar Islands (Vijayamma et al. 2021).

The monotypic genus *Puteonator* (*P. iraqiensis*) from subterranean habitats in nearby Iraq should also be noted due to its close morphological resemblance to *Caridina*,

geographic proximity, and anchialine habitat (see Table 1). However, assessing its relationship to the newly described *C. tashanica* sp. nov. or a possible congeneric status is beyond the scope of this study and would require a comprehensive taxonomic revision of *Caridina* (von Rintelen et al. 2012; De Grave and Page 2014).

Table 1. Comparison between five *Caridina* species and *Puteonator iraqiensis* from Iran and Iraq (References: [1]Klotz et al. 2019; [2]Arudpragasam and Costa 1962; [3]Pandya and Richard 2019; [4]Gurney 1987); * for rostral formula, see Materials and methods.

Character	*C. fossarum*[1]	*C. enkii*[1]	*C. fernandoi*[1,2,3]	*C. shahrazadae*[1]	*C. tashanica* sp. nov.	*P. iraqiensis*[4]
Habitat	Epigean; freshwaters (rivers, springs, lakes)	Epigean; freshwater streams	Epigean; freshwater streams	Epigean; freshwaters	Subterranean, cave pools	Subterranean, groundwater (wells)
Body and eye pigmentation	Present, but coloration unknown	Present, but coloration unknown	Present, variable (mostly dark-brown to black with a light mid-dorsal stripe)	Present, but coloration unknown	Completely absent (troglomorphic)	Body pigmentation absent, eyes reduced, without corneal facets or pigment
Rostrum length	Moderate, reaching to or slightly overreaching (most specimens) scaphocerite/ antennular peduncle	Moderate, reaching to or slightly overreaching scaphocerite/ antennular peduncle	Moderate, not to the end of antenullar peduncle or scaphocerite	Moderate to short; reaching do distal margin of scaphocerite in most specimens, in some to distal end of antennular peduncle	Long, clearly exceeding scaphocerite	Short, not reaching as far as third segment of antennular peduncle
Rostral dentition	Dorsal and ventral teeth present Formula*: 15-21+2-6/5-13	Dorsal and ventral teeth present Formula: 17-18+2-5/5-8	Dorsal and ventral teeth present Formula: 11-15+5-6/appr.6	Dorsal and ventral teeth present Formula: 13-26 throughout dorsal margin/3-10	More numerous dorsal teeth, longer distal part Formula: 13–19+3–5/9–22	Without dentition Formula: 0+0/0
Sexual dimorphism (propodi of pereiopods III–IV)	Strong; propodi distally dilated with numerous spiniform setae in males	Strong; propodi distally dilated with numerous spiniform setae in males	Absent	Slight difference in setation and dilatation of propodi (males > females)	Absent	Strong; propodi distally dilated with numerous spiniform setae in males
Sexual dimorphism (pereiopods I–V length)	Not reported	Not reported	Not reported	Not reported	Males with generally longer pereiopods I–V than females (possibly adaptation to cave life / mating)	Not reported
Pleopod I endopodite (male)	Appendix interna well developed, retinacular hooks present	Appendix interna well developed, retinacular hooks present	Appendix interna well developed, retinacular hooks present	Appendix interna reduced	Appendix interna reduced, endopodite sparsely setose	Appendix interna well developed, retinacular hooks present
Setation of pleopod I endopodite	Dense, mainly at basal part of its inner margin	Dense, with long simple setae on outer margin, with somewhat shorter simple setae on inner margin	Dense (but see Fig. 3 in [3])	Moderate, >30 setea along margin	Sparse (≈ ½ of other Middle East *Caridina*), up to ca. 7 setae along margin	Lateral plumose setae on inner and outer margins
Ecology	Surface-dwelling	Surface-dwelling	Surface-dwelling	Surface-dwelling	Cave-dwelling, troglomorphic traits (depigmentation, eye reduction, elongate appendages); co-occurs with cave fish *Garra tashanensis*	Anchialine habitat at depth 160 m

A comparative overview of the main diagnostic characters among *C. fossarum*, *C. enkii*, *C. fernandoi*, *C. shahrazadae* and *C. tashanica* sp. nov. is presented in Table 1. The new species can be readily distinguished from all its Middle Eastern congeners by complete depigmentation, lack of eyes, elongate pereiopods, and the absence of sexual dimorphism in the walking legs. The latter trait contrasts strongly with the pronounced dimorphism in *C. fossarum* and *C. enkii*, in which males possess distinctly dilated and spinose propodi III–IV. In contrast, *C. shahrazadae* and *C. tashanica* sp. nov. both lack such dimorphism, suggesting either a secondary loss of this feature or independent evolutionary reduction in separate lineages.

Further evidence of affinity between *C. tashanica* sp. nov. and *C. shahrazadae* lies in the structure of male pleopods I–II. Both species possess an endopodite of pleopod I with an undeveloped appendix interna, in contrast to the well-developed appendix interna seen in *C. fossarum*, *C. enkii* and *C. fernandoi* (Table 1). Additionally, *C. tashanica* sp. nov. shows extremely sparse setation on the male pleopod I endopodite, approximately half that observed in other Middle Eastern *Caridina*, which may further indicate specialization linked to its subterranean habitat.

The rostrum of *C. tashanica* sp. nov. is long and armed with numerous dorsal teeth, exceeding that of its epigean sister species *C. shahrazadae*. Rostral elongation in atyid shrimps has been associated with ecological or behavioural pressures, such as predation risk (Covich et al. 2009; Jugovic et al. 2010b; Mazancourt et al. 2017). The presence of the cave fish *Garra tashanensis* (Mousavi-Sabet et al. 2016) within the same habitat may thus represent a potential selective pressure contributing to this feature.

Cave shrimps in sulphidic groundwaters

Cave systems fed by hydrogen sulphide-rich groundwater are unique chemoautotrophy-based ecosystems that rely primarily on microbial primary production (Sarbu 2000; Engel 2007). Such sulphidic subterranean habitats are rare, but have been documented in several karst regions with endemic and highly diverse faunas, representing hotspots of subterranean biodiversity (Engel 2007; Brad et al. 2021; Urák et al. 2025). Despite the broad ecological range of *Caridina* species inhabiting a very diverse range of habitats, to our knowledge none has been previously reported from sulphidic waters. Records of any other atyid shrimp inhabiting toxic hydrogen sulphide layers are also extremely rare. One exception is *Xiphocaridinella jusbaschjani*, the cave shrimp from the Caucasus, which was observed in shallow hydrogen sulphide pools where aggregations of cave shrimps were possibly feeding on sulphide-oxidising bacteria (Marin and Sokolova 2014). Studies of food webs based on stable isotopes in other subterranean shrimps of the family Atyidae, such as *Stygiocaris* from Australia (Humphreys 1999) and *Typhlatya pearsei* from anchialine caves of the Yucatan Peninsula in Mexico (Duran and Alvarez 2025), have suggested and demonstrated their feeding on sulphide-oxidising chemoautotrophic bacteria. These bacteria are common in anchialine systems, thus making these systems at least partially independent from the surface.

Tashan Cave is a natural limestone cave with active sulphur springs (Malek-Hosseini et al. 2023), likely supporting a similar chemoautotrophic-based ecosystem. *Caridina tashanica* sp. nov. was found exclusively in a single pool (Fig. 7) within this system, possibly in close association with bacterial mats. In addition to *C. tashanica* sp. nov., the Tashan Cave fauna includes other subterranean crustaceans and the cave fish *Garra tashanensis* (Mousavi-Sabet et al. 2016), highlighting its exceptional biodiversity and the importance of the system. Another sulphidic cave ecosystem hosting cave shrimps (Decapoda: Typhlocarididae) is Ayyalon Cave in Israel, where *Typhlocaris ayyaloni* occurs (Tsurnamal 2008; Por et al. 2013).

The discovery of *C. tashanica* sp. nov. thus extends the ecological limits of the genus *Caridina* and is another rare example of an atyid shrimp inhabiting sulphidic groundwater. It also highlights the importance of continued speleobiological exploration and conservation of the Tashan Cave system, which may still harbour additional undescribed taxa. Iranian subterranean fauna exhibits a high level of endemism and is therefore of great conservation importance. Although caves, wells and karstic springs in Iran have been poorly studied, most of so far known subterranean species are restricted to single sites. This pattern likely reflects both long-term isolation and fragmented nature of subterranean habitats. The description of a cave shrimp species from the Tashan Cave system adds another subterranean species to this unique habitat, which urgently needs conservation, as numerous threats such as pollutants and human visits are endangering it (Malek-Hosseini et al. 2023).

Figure 7. Habitat of *Caridina tashanica* sp. nov., hydrogen sulphide-rich pool inside the Tashan cave in southwestern Iran. Photo credit: YF.

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Supplementary material 1

Sample data and occurences

Authors: Jure Jugovic, Mohammad-Javad Malek Hosseini, Yaser Fatemi, Jean-François Flot, Matjaž Kuntner, Valerija Zakšek

Data type: (measurement/occurrence/multimedia/etc.)

Explanation note: **table S1.** List of samples used in phylogenetic analyses along with GenBank Accessions. **table S2.** Collected records of atyid shrimp species in Iran used for distribution map.

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Link: https://doi.org/10.3897/subtbiol.55.184889.suppl1

Supplementary material 2

Molecular laboratory protocols & genetic distances, morphological data

Authors: Jure Jugovic, Mohammad-Javad Malek Hosseini, Yaser Fatemi, Jean-François Flot, Matjaž Kuntner, Valerija Zakšek

Data type: (measurement/occurrence/multimedia/etc.)

Explanation note: Detailed molecular laboratory protocols, detailed morphological comparison of *Caridina tashanica* sp. nov. with other species in a region and estimated genetic distances of closely related Caridina species in Middle East and India.

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