










Research article

urn:lsid:zoobank.org:pub:978DD0AA-D9D2-4708-9D57-45CC082617B4

A second species of *Stenasellus* Dollfus, 1897 (Isopoda, Stenasellidae) from sulfidic groundwater of Iran described using morphological and molecular methods

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Abstract. We report on a new species of *Stenasellus* Dollfus, 1897 (Isopoda, Stenasellidae) from groundwater of Iran. *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. inhabits the Chah Kabootari Cave that is adjacent to the Tashan Cave, the type locality of the first recorded species of Stenasellidae from Iran, *Stenasellus tashanicus* Khalaji-Pirbalouty, Fatemi, Malek-Hosseini & Kuntner, 2018. Both caves are fed by sulfidic groundwater and belong to the Tashan-Chah Kabootari species-rich aquifer on the Zagros Mountains. Both species are characterized by a large body size (≥ 20 mm), a female-biased sexual size dimorphism, and a distinct black-pigmented Bellonci's organ. *Stenasellus stygopersicus* differs from *S. tashanicus* by a short and wide protopodite of pleopod I, setae set essentially along the apical margin of pleopod I exopodite, the subequal length and width of the male pleopod II protopodite, and deeply bilobed endopodites of pleopods III–V. Molecular evidence suggests that while *Stenasellus stygopersicus* is sister to *S. tashanicus*, the species are genetically distinguishable, with divergence time estimates ranging from 23 to 39.8 Ma.

Keywords. Biodiversity, phylogeny, Stenasellidae, groundwater, sulfidic cave.

Jugovic J., Malek-Hosseini M.J., Issartel C., Konecny-Dupré L., Kuntner M., Fatemi Y., Flot J.-F., Douady C.J. & Malard F. 2024. A second species of *Stenasellus* Dollfus, 1897 (Isopoda, Stenasellidae) from sulfidic groundwater of Iran described using morphological and molecular methods. *European Journal of Taxonomy* 968: 256–274. <https://doi.org/10.5852/ejt.2024.968.2733>

Introduction

Groundwater, the largest freshwater habitat on Earth, harbors a high diversity of living forms including viruses, prokaryotes, microeukaryotes, and metazoans (Marmonier *et al.* 2023). The discovery and description of groundwater metazoan specialists, i.e., animals that are strictly confined to groundwater during at least a part of their life cycle (Culver *et al.* 2023), has intensified worldwide over the last four decades (Malard 2022). However, there is still considerable variation in the description and understanding of groundwater biodiversity patterns among continents, as fewer studies have been conducted in Asia and Africa compared with Europe, America, and Australia (Zagmajster *et al.* 2018). Approximately 70% of the 51 subterranean (46 aquatic and five terrestrial) metazoan species known from Iran have been described over the last decade (Malek-Hosseini & Zamani 2017; Malek-Hosseini *et al.* 2022, 2023a, 2023b). Of the 46 groundwater species, 39 are crustaceans, including 24 amphipods and 12 copepods but only 3 isopods. The three groundwater isopods known from Iran are *Microcharon raffaellae* Pesce, 1979 (Lepidocharontidae), collected in a well at Shahr-e-Kord city, Chaharmahal and Bakhtiari Province, *Asellus (Asellus) ismailsezarrii* Malek-Hosseini, Jugovic, Fatemi & Douady, 2022 from Ganow spring, Khuzestan Province, and *Stenasellus tashanicus* Khalaji-Pirbalouty, Fatemi, Malek-Hosseini & Kuntner, 2018 (Stenasellidae) collected in Tashan Cave, Khuzestan Province.

Stenasellidae Dudich, 1924 contains 10 genera and 72 species worldwide, all of them eyeless, depigmented and strictly confined to groundwater (Magniez 1999, 2005; Malard *et al.* 2014). The areal distribution of this family extends longitudinally from Mexico to Borneo (Indonesia) and latitudinally from Java (Indonesia) to Slovenia. The genus *Stenasellus* Dollfus, 1897, with 38 nominal species, is by far the most species-rich and widely distributed genus within the family Stenasellidae (see Fig. 1). *Stenasellus* is distributed from east Asia (Thailand, Cambodia, Java and Sumatra in Indonesia, Malaysia) through central Asia (Turkmenistan), western Asia (Iran, Oman), eastern Africa (Kenya, Somalia, Socotra Island) and in the west to southern Europe (France, Italy, Portugal, Spain) (Magniez & Rahmadi 2006; Malard *et al.* 2014; Khalaji-Pirbalouty *et al.* 2018). Seven species of *Stenasellus* have been known from central and western Asia. *Stenasellus asiaticus* Birstein & Starostin, 1949 was first described from a thermal spring in southern Turkmenistan. Magniez & Stock (2000) diagnosed four species from alluvial groundwater of Oman: *S. henry*, *S. grafi*, *S. messanai* and *S. vermeuleni*. More

recently, Khalaji-Pirbalouty *et al.* (2018) described *S. tashanicus* from Tashan Cave, the first species of stenassellid reported from Iran; later, Messana *et al.* (2019) described *S. taitii* from Erher Cave in Socotra Island (an island controlled by Yemen, Asia, but geographically part of Africa).

Here, we diagnose and describe *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov., the second species of the genus from Iran, inhabiting the same groundwater aquifer as *S. tashanicus*. We provide morphological comparisons with other species of the genus in central and western Asia, including *S. tashanicus*. We also use molecular data to corroborate the status of *Stenasellus stygopersicus* and document its phylogenetic relationship with *S. tashanicus*.

Material and methods

Sampling

Specimens were collected by hand and with a small net in a completely dark area of Chah Kabootari Cave near Sarjowshar Village, Tashan City, Behbahan County, Khuzestan Province, southwestern Iran (cave coordinates: 30°52'17.75" N, 50°10'06.61" E, altitude 600 m a.s.l.) and preserved in 96% ethanol (Fig. 1; for photos of Chah Kabootari Cave, see Malek-Hosseini *et al.* 2023a: fig. 2). Access to Chah Kabootari Cave is via a 15 m-deep shaft and the cave is 100 m long. It is located only 1 km north-west of Tashan Cave (cave coordinates: 30°51'54" N, 50°10'29" E, altitude 559 m a.s.l.), the type locality of *S. tashanicus*, in which we collected specimens for comparison with the new species. The water in both caves was rich in hydrogen sulfide.

Morphological description

When necessary, pereopods I–VII, antennae I and II, pleopods, and uropods from one side of the body (preferentially left, if possible), together with pleotelson, were dissected and mounted on slides in glycerin. Specimens and their body parts were photographed and measured using a Sony DXC390P



Fig. 1. Occurrence of genera of Stenasellidae Dudich, 1924 in Europe, Africa and Asia (occurrence data extracted from the World Asellidae Database, Saclier *et al.* 2024). The inset shows the location of Chah Kabootari Cave and Tashan Cave in which *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. and *S. tashanicus* Khalaji-Pirbalouty, Fatemi, Malek-Hosseini & Kuntner, 2018 were collected, respectively. Linear distance between the two caves is 1 km.

digital camera mounted on a stereo microscope or microscope (depending on the size of the structure), and measured with Leica Application Suite – LAS EZ. The remains of dissected specimens were then transferred to 70% ethanol for storage. Vector drawings were made from microphotographs using a graphics tablet (Wacom, Cintiq 13HD Creative Pen Display) and the free software KRITA ver. 4.1.1 (<https://krita.org/>). We described and measured the same structures as in the description of *S. tashanicus* (Khalaji-Pirbalouty *et al.* 2018) to allow comparison between the two species from Iran. In pereopods, the length of the coxa was not included in the total pereopod length because its basal article is inseparably connected to the animal body. Throughout the ensuing description, we provide a single measurement value for the holotype, together with a range of values (in brackets) referring to the males (♂♂) from the type material. Females (♀♀) from the type material were also inspected and we provided remarks on differences with males.

We quantified sexual body length dimorphism (SBLD) using the body length dimorphism index (SDI) of Lovich & Gibbons (1992), as follows:

$$SDI = \frac{\text{Body length (largest sex)}}{\text{Body length (smallest sex)}} - 1$$

SDI equals zero when the two sexes have the same body length, a negative sign is arbitrarily given when males are longer than females, and a positive sign when females are longer. We measured body length as the distance between the anterior margin of the cephalon and the posterior margin of the pleotelson. To avoid including immature specimens and allow comparison with literature data (Saclier *et al.* 2024), we calculated SDI using maximum body length of sexually mature specimens rather than mean body length of all specimens available. Maximum body length provides an estimator of the size of full-grown specimens and is often the only measurement provided in species description articles. We computed SDI in previously described species of stenasellids using literature data.

Molecular taxonomy and phylogenetic analyses

We used molecular data and phylogenetic analyses performed as part of a recent worldwide phylogenetic study of Aselloidea Latreille, 1802 (Asellidae and Stenasellidae) published by Saclier *et al.* (2024) to ascertain the species status of *Stenasellus stygopersicus* sp. nov. and document its phylogenetic relationships to other species of stenasellids for which molecular data were available. We refer the reader to Saclier *et al.* (2024) for details about methods used to perform DNA extraction, gene fragment amplification and sequencing, delimit putative species, and build phylogenetic trees. We used fragments of the following four genes: the mitochondrial cytochrome oxidase subunit I (COI) gene, the 16S mitochondrial rDNA gene, the *FASTKD4* nuclear gene and the 28S nuclear rDNA gene. We used the term morphospecies to refer to species, either formally described or undescribed (i.e., pending a formal description), that were identified based on morphological criteria and the term molecular operational taxonomic unit (MOTU) to refer to putative species delimited based on molecular criteria.

Molecular species delimitation was based on a phylogeny constructed in maximum likelihood using a COI alignment of 1385 haplotypes, which were defined from the sequences obtained from 2093 specimens belonging to 299 morphospecies of Aselloidea (see Saclier *et al.* 2024: supp. inf. tables 1, 4). This COI alignment included 108 haplotypes of Stenasellidae obtained from the sequences of 138 specimens belonging to 21 morphospecies. MOTUs were delimited using the fixed COI threshold method implemented by Lefébure *et al.* (2006) for crustaceans.

Of the 466 MOTUs delimited with the fixed COI threshold method, fragments of three additional genes – the 16S mitochondrial rDNA gene, the *FASTKD4* nuclear gene and the 28S nuclear rDNA gene – were obtained for 424 MOTUs of Aselloidea, including 40 MOTUs of Stenasellidae representing 13 morphospecies (see Saclier *et al.* 2024: supp. inf. tables 5–9). Saclier *et al.* (2024) produced a four-gene dated phylogeny of these 424 MOTUs with PhyloBayes (Lartillot *et al.* 2009), using palaeobiogeographic calibration points to constrain the age of 17 nodes in the phylogeny (see Supp. file 1 for a detailed description of paleobiogeographic events). In this article, we used the four-gene dated phylogeny of these 424 MOTUs provided by Saclier *et al.* (2024) to document the phylogenetic relationship of the new species to other species of stenasellids, specifically *Stenasellus tashanicus*.

Accession numbers of DNA sequences deposited to NCBI for the two species of *Stenasellus* of Iran are as follows. *Stenasellus stygopersicus* sp. nov. Adult ♂ 2012.11.24.81: OR255830 (16S), OR292138 (COI), OR341975 (*FASTKD4*), OR505840 (28S); adult ♂ 2012.11.24.84: OR255831 (16S), OR341311 (COI), OR341976 (*FASTKD4*), OR505841 (28S); adult ♀ 2012.11.24.90: OR255832 (16S). *Stenasellus tashanicus*. Specimen 1ID: OR255880 (16S), OR292135 (COI), OR341989 (*FASTKD4*), OR505818 (28S); specimen 2: OR255881 (16S), OR341990 (*FASTKD4*), OR505819 (28S); specimen 3: OR255882 (16S), OR292136 (COI).

Abbreviations

bl	=	body length
DNA vc	=	DNA voucher
UCBLZ	=	University Claude Bernard Lyon-Zoology, Lyon
vc	=	voucher

Results

Taxonomy

Order Isopoda Latreille, 1816
Superfamily Aselloidea Latreille, 1802
Family Stenasellidae Dudich, 1924

Genus *Stenasellus* Dollfus, 1897

Type species

Stenasellus virei Dollfus 1897, by monotypy.

Stenasellus stygopersicus Jugovic, Malek-Hosseini & Issartel sp. nov.
urn:lsid:zoobank.org:act:34465D91-1AB2-4241-9A5E-63A149997A98
Figs 2–5

Diagnosis

Body dorsal smooth, pleotelson being barely longer than its width (about 1.1 its width), short antennula (in males with only up to 34 segments in flagellum), barely overreaching antennal peduncle (Fig. 3). Antenna with minute squama, ultimate segment of mandible palp without setae (Fig. 3). Short and wide (length < width) protopodite of pleopod I, setae only along mesiodistal margin of pleopod I exopodite (Fig. 5). Pleopod II protopodite subequal in length and width, exopodite segment II with only about 10 (9–11) plumose setae; endopod of pleopods III–V in males distally deeply bifurcated (i.e. bifurcation overreaches half of endopodite III–V length). A species with strongly female-biased sexual dimorphism in body size.

Etymology

The name of the new species is formed from the prefix 'stygo' (from ancient Greek 'stýx'), a common prefix used to refer to groundwater dwelling animals, and the Latin word '*persicus*' referring to Persia.

Type material

Holotype

IRAN • adult ♂ (bl 11.8 mm, vc 2012.11.24.80); Khuzestan Province, Behbahan County, Tashan City, near Sarjowshar Village, Chah Kabootari Cave; 30°52'17.75" N, 50°10'06.61" E; 600 m a.s.l.: 17 Mar. 2018; M.J. Malek-Hosseini and Y. Fatemi leg.; UCBLZ.

Paratypes

IRAN • 1 adult ♂ (bl 11.6 mm, vc 2012.11.24.84, DNA vc 2012.11.24.85); same data as for holotype; UCBLZ • 1 adult ♂ (bl 10.8 mm, pleopods vc 2012.11.24.81, DNA vc 2012.11.24.82, and body vc 2012.11.24.83); same data as for holotype; UCBLZ • 6 adult non-ovigerous ♀♀ (bl 18.2 mm, vc 2012.11.24.86; bl 22.5 mm, vc 2012.11.24.87; bl 19.5 mm, vc 2012.11.24.88; bl 19.9 mm, vc 2012.11.24.89; bl 11.9 mm, vc 2012.11.24.90, DNA vc 2012.11.24.91; bl 11.9 mm, vc 2012.11.24.92); same data as for holotype; UCBLZ • 1 adult ovigerous ♀ (bl 11.7 mm, vc 2012.11.24.93) with a brood pouch containing 22 pulli (1.86 ± 0.13 [standard deviation] mm, minimum body size: 1.65 mm; maximum body size: 2.21 mm); same data as for holotype; 8 Dec. 2018; M.J. Malek-Hosseini and Y. Fatemi leg.; UCBLZ • 3 juvs ♂♂ (bl 10.2 mm, vc 2012.11.24.94; bl 9.5 mm, vc 2012.11.24.95; bl 10.5 mm, vc 2012.11.24.96); same data as for preceding; UCBLZ • 4 juvs and/or subadult ♀♀ (bl 10.8 mm, vc 2012.11.24.97; bl 11.1 mm, vc 2012.11.24.98; bl 10.1 mm, bl 10.0 mm); same data as for holotype; UCBLZ.

All material examined was from Chah Kabootari Cave (30°52'17.75" N, 50°10'06.61" E; 600 m a.s.l.) near Sarjowshar Village, Tashan City, Behbahan County, Khuzestan Province, Iran, and was preserved in 96% ethanol and deposited in the UCBLZ collections (<https://ucblz.univ-lyon1.fr/>).

Description

Males (based on holotype, values in brackets – ♂♂: range of adult males)

BODY (Figs 2, 3A). Body of live specimens completely coral pink. Body length 4.0 times (♂♂: 3.9–4.0) as long as wide (width measured at greatest width, i.e., pereonite IV), head trapezoidal, with slightly concave frontal margin and black-pigmented organs of Bellonci in anterolateral corners of the head, dorsal surface smooth. Pereonites II–IV subequal in length, with rounded lateral margins, pereonites V–VII with posterolateral margins projected posteriorly, pereonites VI and VII sub-equal, longest. Pleonites I–II subequal in length, with projected posterolateral corner. Pleotelson (Figs 3A, 4D) slightly elongated, 1.07 (♂♂: 1.06–1.07) times as long as broad, posterior margin with two slight excavations; with scattered marginal spiniform setae.

ANTENNULA (Fig. 3B). Short, reaching the middle of pereonite I, slightly longer than the peduncle of antenna, flagellum with 12 (♂♂: 12–14) segments, segments 3–11 (♂♂: 3–11) each bearing one or two aesthetascs.

ANTENNA (Fig. 3C). Peduncle segments I and II shortest; the four others longer, the sixth is the longest (in percentages of antennal length: 2.8%:2.6%:8.8%:5.0%:8.8%:12.0%), and the flagellum occupying 60.0% of the total antennal length. Article VI about 1.4 (♂♂: 1.4–1.7) times the length of article V, with long simple setae distally; article III with minute squama bearing two long robust setae, flagellum reaching to pereonite IV anterior margin, with 31 articles in the holotype (♂♂: 31–34).

LEFT MANDIBLE (Fig. 3D). Incisor process and lacinia mobilis with three and five cusps, respectively; spine row of 11 serrated spines; molar process with a row of long, tiny, simple setae. Palp article II longer than I, bearing 6 serrate spines at distal corner; article III distolateral margins without well-developed setae.

LEFT MAXILLULA (Fig. 3E). Lateral endite apical margin with 5 serrated robust setae and 6 tiny serrated smaller setae; mesial endite with three long, robust, combs and two short simple setae.

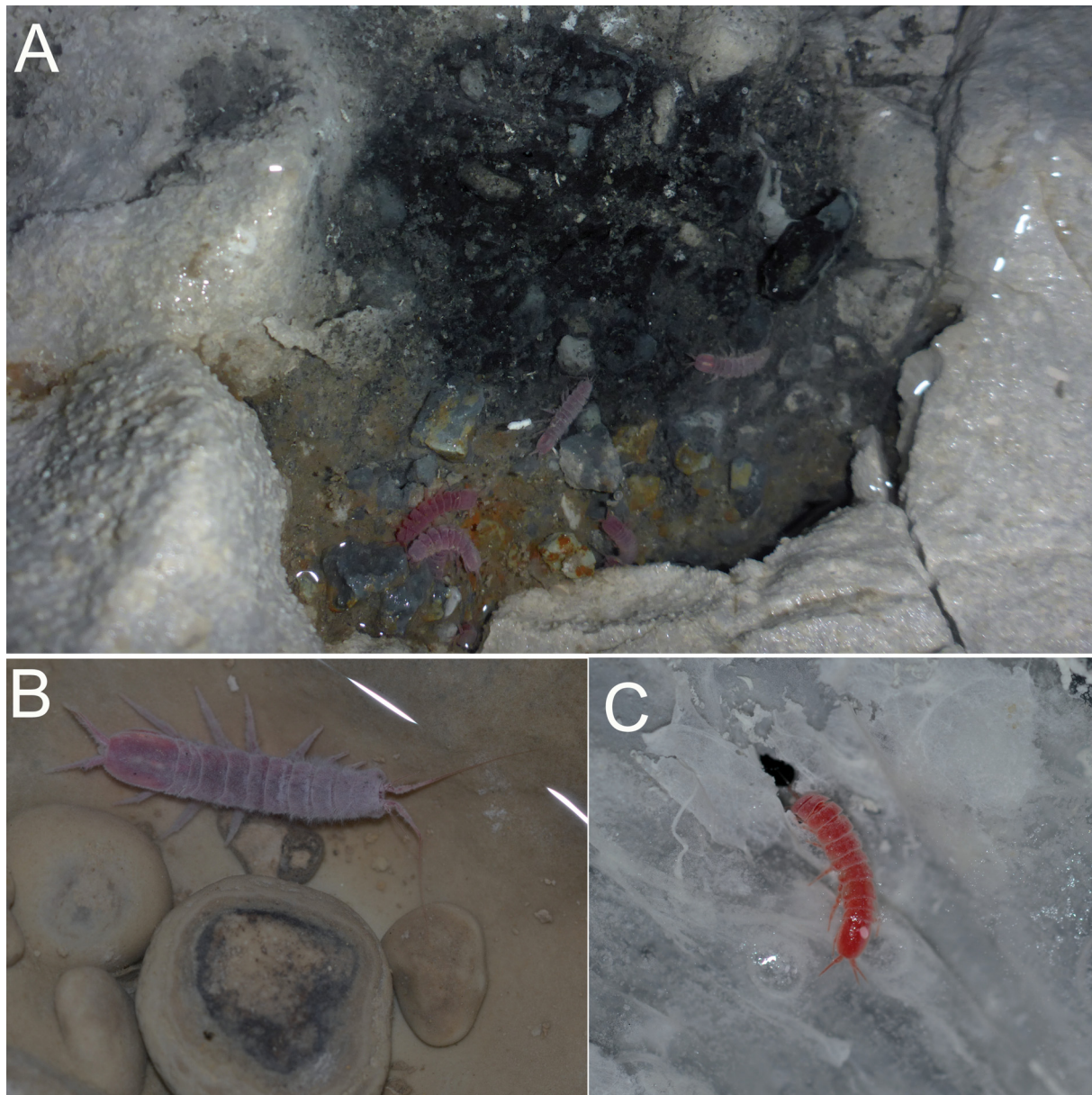


Fig. 2. **A.** Five specimens of *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. in sulfidic water of Chah Kabootari Cave, Iran. **B.** A specimen of *S. tashanicus* Khalaji-Pirbalouty, Fatemi, Malek-Hosseini & Kuntner, 2018 in Tashan Cave, Iran. **C.** Another specimen of *S. tashanicus*, hanging on the white biofilm floating at the surface of sulfidic water in Tashan Cave, Iran.

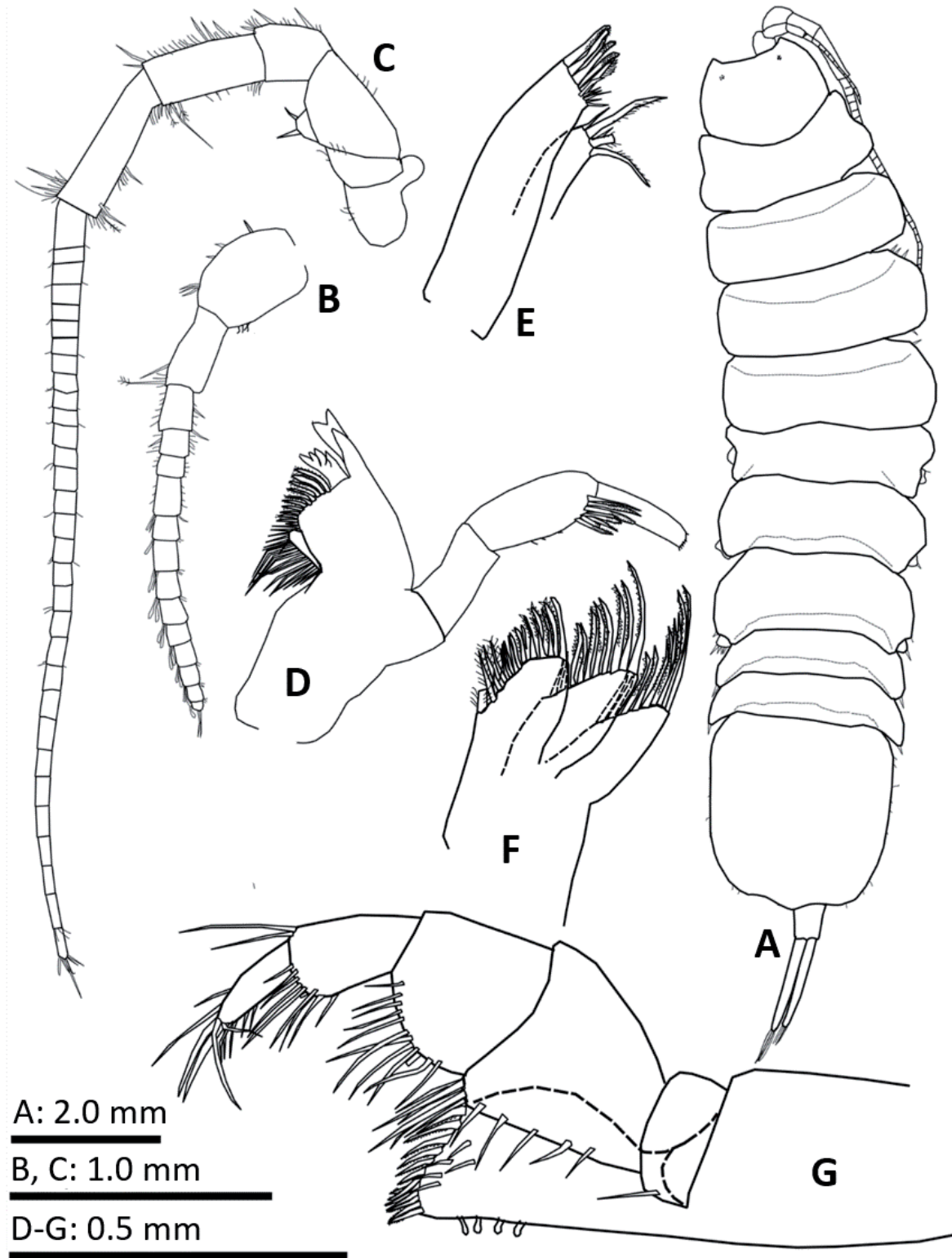


Fig. 3. *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov., holotype, ♂ (UCBLZ 2012.11.24.80, body length = 11.8 mm). **A.** Body. **B.** Antennula. **C.** Antenna. **D.** Left mandible. **E.** Left maxillula. **F.** Left maxilla. **G.** Left maxilliped.

LEFT MAXILLA (Fig. 3F). Lateral and middle endites each with 10 curved pectinate robust setae; mesial endite with 4 strong scarcely plumose, long robust combs, and 11 curved pectinate robust setae.

LEFT MAXILLIPED (Fig. 3G). Endite mesial margin with four coupling hooks, distal margin with 13 serrated and rarely plumose robust setae; palp article I with single robust seta on the inner margin, palp articles II–V with several long simple setae on the inner margin.

PEREOPOD I (Fig. 4A). Basis length 1.66 (♂♂: 1.58–1.66) times its width, ischium anterior margin with one robust seta on distal corner and five small robust setae on the medial projection; merus anterodistal angle with two robust setae, posterior margin with two short robust setae and 4 long slender setae; carpus triangular, posterior margin covered with several long and short simple robust seta, among them with two short robust setae along distal part; propodus almost two times as long as wide (♂♂: 1.86–1.88), its posterior margin covered with 9 stout short simple robust setae set in amongst ten simple slender long setae; dactylus around 9 times as long as basal width, posterior margin with a row of 9 contiguous scale-like flattened setae, main unguis elongate.

PEREOPOD II (Fig. 4B). Basis about 1.6 (♂♂: 1.60–1.67) times as long as the greatest width, anterior margin with approximately seven long distally plumose setae; ischium anterior margin with five long robust setae and one long distally plumose seta, and three strong robust setae along its distal margin; merus anterior margin with one robust seta and its anterodistal angle with three long robust setae, posterior margin with four strong and simple setae and four long distally plumose setae; carpus anterior margin with five strong and a group of weak simple setae, posterior margin covered with 11 strong and more weak long and short simple robust setae; propodus posterior margin bearing five short, simple, acute setae, anterior margin with two simple setae, anterodistal angle with two long simple and single sensory palmate setae; dactylus subequal in length to the main unguis, with two secondary unguis and one sensory plumose seta.

PEREOPOD III (Fig. 4C). Similar to pereopod II as illustrated. Walking pereopods II–VII similar, but progressively larger and longer.

PEREOPOD VII (Fig. 4E). Basis almost two times as long as the greatest width, anterior margin with five simple setae; ischium length two times its width, with 7 robust setae along its anterior margin and two simple setae along posterior margin; merus supradistal angle with two long robust setae; carpus length 4.7 times as long as width, posterior margin covered with several long and short simple robust setae, anterior margin bearing 3 simple spiniform setae, supradistal angle with three simple spiniform setae; propodus length 6 times its width, posterior margin bearing 7 simple acute setae, and superior margins bearing five acute distally plumose setae; dactylus with elongated unguis, bearing two secondary spines at posterior margin and two distally plumose setae at its anterior margin.

PENIAL PROCESSES (Fig. 5A). Elongated, cylindrical, about 5.3 times as long as the greatest width.

PLEOPOD I (Fig. 5B). Protopod shorter than its width (length/width ratio ≈ 0.8), mesial margin with a single coupling hook, exopodite elongated (length/width ratio = 2.1; ♂♂: 2.1–2.4), mesial margin without seta (or few at its distal end), a row of about 10 (♂♂: 10–13) plumose marginal setae and 5 (♂♂: 4–5) simple fine setae at mesio-apical and apical margins, lateral margin concave, bearing two setae (♂♂: 0–2).

PLEOPOD II (Fig. 5C). Protopod subequal in length and width (width/length ratio = 1.1; ♂♂: 1.1–1.2), exopodite article I small, without seta, article II oval, with 9 (♂♂: 9–11) plumose marginal setae; appendix masculina article II length 1.4 (♂♂: 1.35–1.40) times of article I length, tapering to curve acute apex.

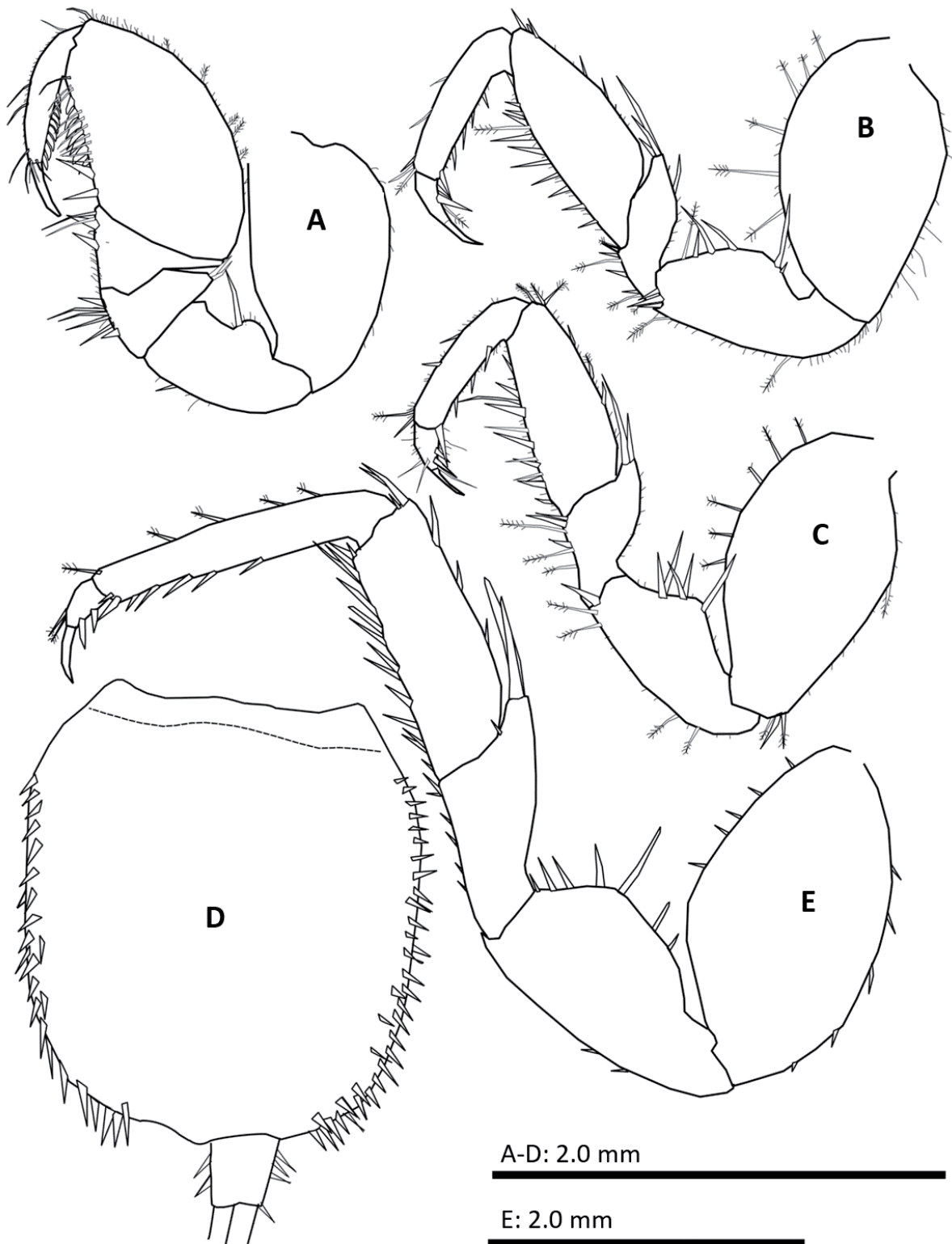


Fig. 4. *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. **A–D.** Holotype, ♂ (UCBLZ 2012.11.24.80, body length = 11.8 mm). **A.** First left pereopod. **B.** Second left pereopod. **C.** Third left pereopod. **D.** Pleotelson. **E.** Paratype, ♂ (UCBLZ 2012.11.24.84, body length = 11.6 mm), seventh right pereopod.

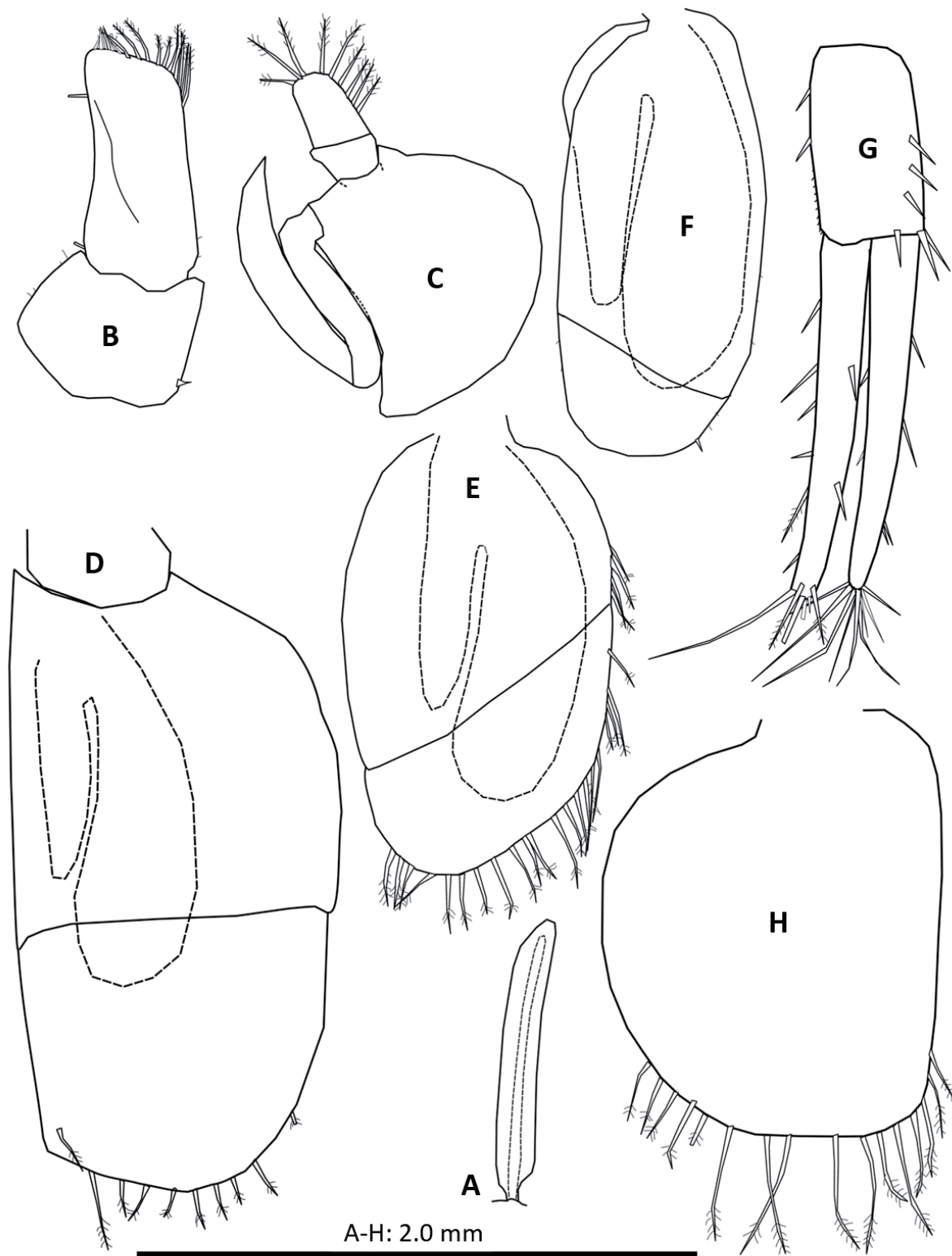


Fig. 5. *Stenasellus stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. **A–G.** Holotype, ♂ (UCBLZ 2012.11.24.80, body length = 11.8 mm). **A.** Penial processus. **B.** First left pleopod. **C.** Second left pleopod. **D.** Third left pleopod. **E.** Fourth left pleopod. **F.** Fifth left pleopod. **G.** Left uropod. **H.** Paratype, ♀ (UCBLZ 2012.11.24.87, body length = 22.5 mm), left second pleopod.

PLEOPOD III (Fig. 5D). Exopodite with transverse suture, apical margin with 10 slender plumose setae; endopodite about 0.65 times as long as exopodite, deeply bifurcated distally.

PLEOPOD IV (Fig. 5E). Exopodite with transverse suture, distolateral margin with 25 slender plumose setae; endopodite about 0.8 times as long as exopodite, deeply bifurcated distally.

PLEOPOD V (Fig. 5F). Exopodite with transverse suture, apical margin with one slender simple seta, endopodite almost 0.9 times as long as exopodite, deeply bifurcated distally.

UROPOD (Fig. 5G). Protopodite and rami covered with scattered acute simple setae with few plumose setae; endopodite longer than exopodite, both rami with distal tuft of mostly simple setae and few plumose setae set among them.

Females

In the sample containing 3 adult males and 6 adult females, the body size of the longest female (22.5 mm) is almost two times that of the longest male (11.8 mm). Except from female-biased body size dimorphism (SDI = 0.91) and differences in pleopods 1–2 (females are without pleopods 1), female is mostly similar to male. Pleotelson is relatively broader, and antenna is relatively longer than in males. Pleopod 2 (Fig. 5H), distolateral margin bearing ca. 16 plumose setae.

Habitat

The new species was discovered in Chah Kabootari Cave or in local language Chal Kabootari (Fig. 2), which means “nest of pigeons”. Aquatic habitats consist of a stream running through the cave and water pools, some of which are rich in hydrogen sulfide content. At certain periods of the year, a thick white biofilm develops at the water surface of pools, as in Tashan Cave (see Fig. 2C). Specimens of *Stenasellus stygopersicus* sp. nov. were observed mostly crawling on the bottom in stinky sulfidic water of Chah Kabootari Cave. An obligate groundwater melitid amphipod, *Tegano tashanensis* Malek-Hosseini, Brad, Fatemi, Kuntner & Fišer, 2023, was described from this cave in syntopy with *S. stygopersicus*. Water temperature was 25.6°C throughout the year and pH was 7.1. Air temperature was 25.3°C, relative humidity was 99.8%, and the air contained 768 ppm CO₂ (see Malek-Hosseini *et al.* 2023a).

Morphological comparison with other species

The new species is a large-sized species (bl: 22.5 mm), similar to *S. tashanicus* (bl: 20 mm), and both species are considerably longer than all other species known from Central and Western Asia: *S. asiaticus* (bl: 11.5 mm) from Turkmenistan, *S. vermeuleni* (bl: 11.4 mm), *S. messanai* (bl: 7.7 mm), *S. henryi* (bl: 4.9 mm), *S. grafi* (bl: 2.5 mm) (all four from Oman) and *S. taitii* (bl: 13.7 mm) from the island of Socotra (Yemen) (Birstein & Starostin 1949; Magniez & Stock 2000; Bakhshi *et al.* 2018; Khalaji-Pirbalouty *et al.* 2018) (Supp. file 2). All species of *Stenasellus* from Central and Western Asia are either monomorphic for body size (SDI = 0; *S. asiaticus*, *S. henryi*) or exhibit a moderate female-biased sexual size dimorphism (*S. grafi*, SDI = 0.04; *S. tashanicus*, SDI = 0.05; *S. messanai*, SDI = 0.08; *S. taitii*, SDI = 0.12; *S. vermeuleni*, SDI = 0.18) (Supp. file 2). However, *Stenasellus stygopersicus* sp. nov. exhibits a more extreme female-biased SBLD (SDI = 0.91). All the above-mentioned Asian species, including *S. stygopersicus* but excluding *S. asiaticus* from Central Asia, showed black-pigmented Bellonci's organs at anterior lateral angles of cephalon. Although these organs were not mentioned in the description of *S. tashanicus* by Khalaji-Pirbalouty *et al.* (2018), they did appear in the description of *S. tashanensis* Bakhshi & Messana, 2018, a junior synonym of *S. tashanicus*. *Stenasellus stygopersicus* have in common with *S. tashanicus*, *S. taitii* and *S. vermeuleni* that all have an acute apex of the appendix masculina, and bifurcated endopodites of pleopods III–V. The bifurcation however is the deepest in the new species and more than half of the endopodite lengths. We provide below a key to Central and Western Asian species of *Stenasellus*.

Key to Central and Western Asian species of *Stenasellus*

1. Body dorsal surface setose; pleopod III–V endopods distally monolobate *S. asiaticus* Birstein & Starostin, 1949 (Turkmenistan)
 – Body dorsal surface smooth; pleopod III–V endopods distally bilobate 2
2. Male pleopod II exopod segment II small, with less than five marginal setae, appendix masculina flat and swollen 3
 – Male pleopod II exopod segment II large, with more than eight marginal setae, appendix masculina elongate and distally acute 4
3. Male pleopod II protopodite heart-shaped *S. grafi* Magniez & Stock, 2000 (Oman)
 – Male pleopod II protopodite trapezoid *S. henryi* Magniez & Stock, 2000 (Oman)
4. Appendix masculina distolateral margin fringed with tiny setae *S. messanai* Magniez & Stock, 2000 (Oman)
 – Appendix masculina distolateral margin without setae 5
5. Antenna squama with three robust setae, male exopodite of pleopod I apical margin with a row of ~6 simple fine setae; pleopod II exopodite about 1.4 times as long as maximum width; pleopods III–V endopodite bilobed (<< half of their lengths) *S. vermeuleni* Magniez & Stock, 2000 (Oman)
 – Antenna squama with two robust setae 6
6. Male pleopod I protopodite longer than its width, with 1–2 coupling hooks on its mesial margin, setae on exopodite of male pleopod I along mesial and apical margins, apical margin with a row of $\geq \sim 8$ simple fine setae; male pleopod II exopodite ≥ 1.5 times as long as its greatest width; pleopods III–V endopodite bilobed (<< half of their lengths) 7
 – Male pleopod I protopodite shorter than its width, with a single coupling hook on its mesial margin, setae on exopodite of male pleopod I only along apical margin with a row of ~5 simple fine setae; male pleopod II exopodite subequal in length and greatest width; pleopods III–V endopodite bilobed (>> half of their lengths) *S. stygopersicus* Jugovic, Malek-Hosseini & Issartel sp. nov. (Iran)
7. Male pleopod I protopodite with a single coupling hook on its mesial margin, apical margin of pleopod I exopodite with a row of ~18 simple fine setae; male pleopod II exopodite > 2 (~2.4) times as long as greatest width *S. tashanicus* Khalaji-Pirbalouty, Fatemi, Malek-Hosseini & Kuntner, 2018 (Iran)
 – Male pleopod I protopodite with a pair of coupling hooks on its mesial margin, apical margin of pleopod I exopodite with a row of ~8 simple fine setae; male pleopod II exopodite about 1.5 times as long as greatest width *S. taitii* Messana & Argano, 2019 (Socotra, Yemen)

Molecular taxonomy and phylogenetic position

Of the 13 morphospecies of Stenasellidae included in the phylogeny of the Aselloidea (Fig. 6, Saclier *et al.* 2024), the fixed COI threshold method delimited 40 MOTUs, including one MOTU corresponding to *S. stygopersicus* sp. nov. The patristic distance for the COI gene between *S. stygopersicus* and any other MOTUs was > 0.9023 (uncorrected p-distance > 0.16 ; K2P > 0.18), thereby largely exceeding the 0.16 threshold value of patristic distance above which two clades have been considered to belong to distinct species (Lefébure *et al.* 2006).

The four gene Bayesian phylogeny supported a sister relationship (posterior probability = 1) between *S. stygopersicus* sp. nov. and *S. tashanicus* (Fig. 6, Saclier *et al.* 2024). The two species might have diverged in Late Eocene–Oligocene with a divergence time estimate ranging from 23 to 39.8 Ma.

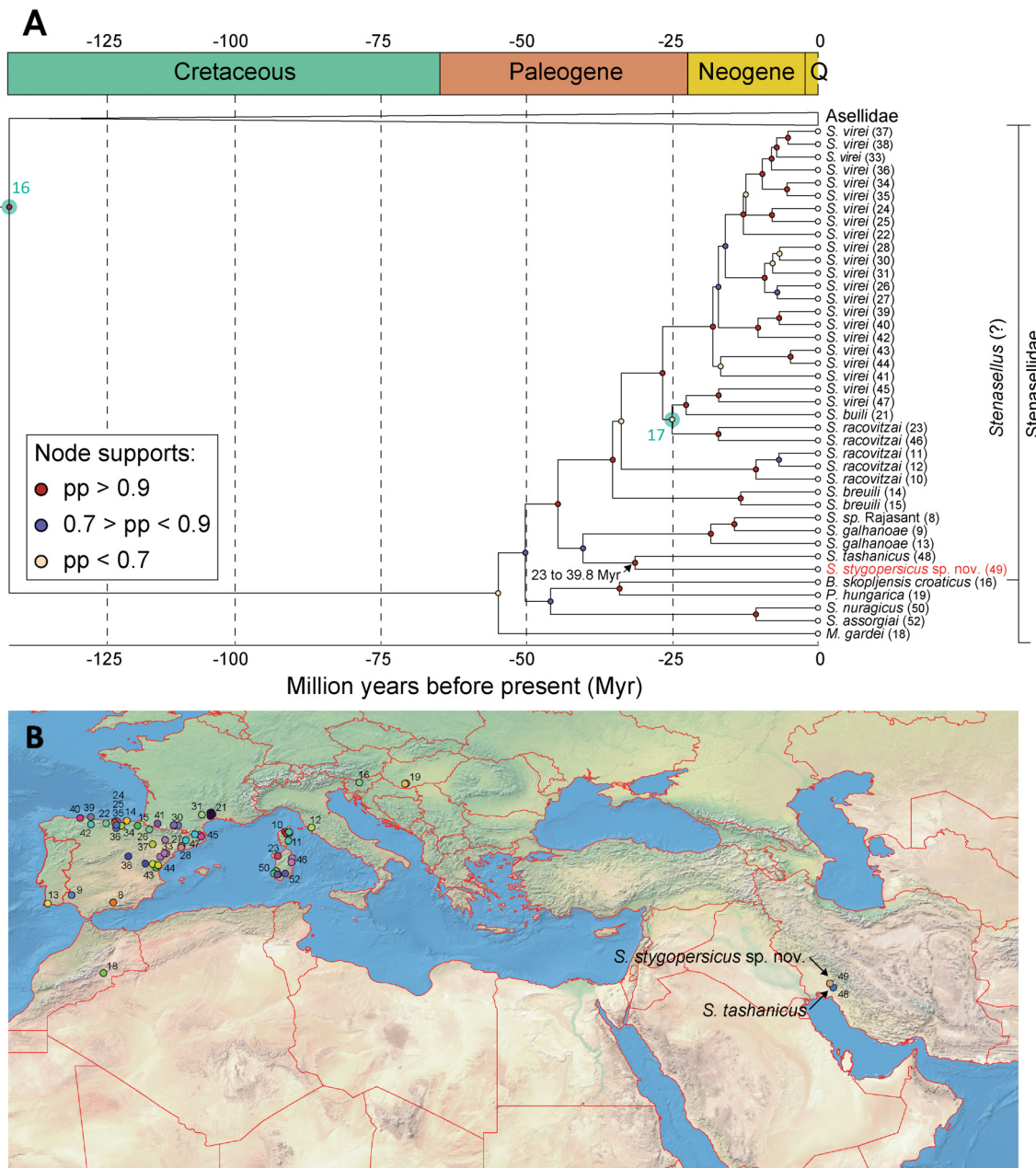


Fig. 6. A. A four-gene (COI, 16S, 28S and *FASTKD4*) dated phylogeny of Stenasellidae Dudich, 1924 extracted from the World Aselloidea Phylogeny of Saclier *et al.* (2024). Terminal nodes are molecular operational taxonomic units (MOTUs) as delimited with the fixed COI threshold method implemented by Lefébure *et al.* (2006). MOTU numbers are given in parenthesis. Names of genera as follows: B: *Balkanstenasellus* Cvetkov, 1975; M: *Magniezia* Lanza, 1966; P: *Protelsonia* Méhely, 1924; S: *Stenasellus* Dollfus, 1897. All branches leading to Aselloidea Latreille, 1802 (i.e., 384 MOTUs) were collapsed. Blue dots show two of the 17 paleobiogeographic calibration points used to obtain a dated phylogeny of Aselloidea Latreille, 1802. Point 16: divergence time between Stenasellidae and Aselloidea (139 Ma; 95% credibility interval: 174–106 Ma); point 17: divergence time between Sardinian species of the *S. racovitzae* species complex (MOTUs 23 and 46) and their continental relatives in France (25 Ma; 95% credibility interval: 31–19 Ma) (15 other calibration points within Aselloidea are not shown). pp are posterior probabilities. **B.** Map showing the distribution of MOTU occurrence. MOTU numbers as in panel A.

Discussion

The present study provides morphological and molecular evidence supporting the species status of *Stenasellus stygopersicus* sp. nov., which is morphologically and genetically distinct from its sister species *S. tashanicus*. Although *S. stygopersicus* and *S. tashanicus* are sister species in the phylogeny, they show marked genetic distances with their estimated divergence in Late Eocene or Oligocene (23 to 39.8 Ma). We can only speculate on the events leading to their speciation. The two species might have diverged within the aquifer. The Gachsaran Formation, Zagros Mountains, the constituent rock of the Tashan-Chah Kabootari aquifer is generally considered to be from lower Miocene (23 Ma) (James & Wynd 1965), but other studies dated the base of the geological formation to Oligocene (34 Ma) or even Eocene (56 Ma) (Bahroudi & Koyi 2004). However, karstification of the Gachsaran Formation and, hence, the presence of karst groundwater habitats likely occurred more recently, during Miocene (23 Ma). Also, we cannot exclude that the two species might have diverged prior to their colonization of the Tashan-Chah Kabootari aquifer. Messana *et al.* (2019) emphasized morphological similarities between species of *Stenasellus* from Oman and Socotra Island (Yemen) and *S. tashanicus* and Magniez & Stock (1999) hypothesized that dispersal might have occurred between Oman and Iran during Pleistocene, when the Persian Gulf was reduced to a series of small lakes and the Strait of Hormuz was emerged.

Aside from the fact that *Stenasellus stygopersicus* sp. nov. is closely related to *S. tashanicus*, its phylogenetic position within Stenasellidae and more especially within *Stenasellus* remains to be determined. The molecular systematics of the Stenasellidae is in its infancy and the monophyly of *Stenasellus* is still to be tested since most of their constituent species have not yet been sequenced. The phylogenetic tree in Fig. 6 contains only nine of the 38 species of *Stenasellus* currently described, but it suggests that *Stenasellus* may indeed represent a widely distributed clade comprising species from Europe to Iran, except *Stenasellus assorgiai* Argano, 1968 and *Stenasellus nuragicus* Argano, 1968 from Sardinia Island, Italy. Although Magniez (1982, 2005) emphasized morphological similarities of male pleopods II among species of *Stenasellus* distributed from southern Europe to eastern Africa and Asia, he acknowledged that “the taxonomic status of the genus *Stenasellus* auct. needs to be reconsidered in the future” (Magniez & Stock 1999: 173). Thus, we recommend that new species as well as specimens of already described *Stenasellus* be systematically sequenced upon sampling, including the four genes examined in this study.

The two species from Iran share a number of morphological characters that are worth to be mentioned. First, *Stenasellus stygopersicus* sp. nov. and *S. tashanicus* are large-sized species reaching a maximum body size of 22.5 and 20 mm, respectively. Maximum body size among Stenasellidae varies from 2.5 mm in *Stenasellus grafi* Magniez & Stock, 2000 to 26 mm in *Stenasellus costai* Lanza, Chelazzi & Messana, 1970 but only two species out of 72 are larger than 20 mm (i.e., *S. costai* and *S. agiuranicus* Chelazzi & Messana, 1987). Body size in groundwater metazoans is constrained by the size of habitat or pore volume available to species (Pipan & Culver 2017; Saclier *et al.* 2024), with food availability likely another important factor. Sulfidic caves may harbor large-sized species because they offer both large-sized habitats and abundant food composed of microbial biofilm for primary consumers and abundant prey for top predators such as *Stenasellus*. Preliminary investigations of groundwater metazoans in the Tashan-Chah Kabootari aquifer have revealed a diverse fauna including the fish *Garra tashanesis* Mousavi-Sabet, Vatandoust, Fatemi & Eagderi, 2016 and *Garra rufa* (Heckel, 1843), the melitid amphipod *Tegano tashanensis* and the gastropod *Trogloiranica tashanica* Fatemi, Malek-Hosseini, Falniowski, Hofman, Kuntner & Grego 2019 (Mousavi-Sabet *et al.* 2016; Khalaji-Pirbalouty *et al.* 2018; Fatemi *et al.* 2019; Malek-Hosseini *et al.* 2023a, 2023b).

Second, *Stenasellus stygopersicus* sp. nov. and *S. tashanicus* exhibit female-biased SBLD. This appears to be a common characteristic among Stenasellidae (Magniez 1975, 1976). Of 65 species of Stenasellidae for which maximum body size data were available for males and females, we found that 50

exhibited female-biased SBLD, 11 exhibited male-biased SBLD and 4 were monomorphic for body size (Supp. file 2). SBLD is an evolutionary outcome affected by numerous opposing selective forces related to natural and sexual selection (Kuntner & Coddington 2020). As in groundwater Asellidae Latreille, 1802 (see Saclier *et al.* 2024), we suggest that competition for rare receptive females may have selected for smaller, more agile males in Stenasellidae, while fecundity selection has probably favored large-bodied females with large brood sizes.

Third, *Stenasellus stygopersicus* sp. nov. and *S. tashanicus* show distinct black-pigmented Bellonci's organs on the anterior part of head. In Stenasellidae, the ultrastructure of the organ of Bellonci was first described by Pitzalis & Juberthie (1992) in *Stenasellus virei boui* Magniez, 1968. Although this sensory organ with an unknown function is typical of many crustaceans (Chaigneau 1994), it is not systematically reported in species descriptions of Stenasellidae. This is probably because the two small cavities of this organ (about 30 µm in diameter) located in anterolateral corners of head are conspicuous with a light microscope only when they contain brown or black pigments. Pigmented Bellonci's organ has most exclusively been reported in stenasellids from Asia and eastern Africa.

The first discovery in 2018 of *S. tashanicus* from Tashan Cave in Iran confirmed the circumglobal feature of the distribution of Stenasellidae. Our discovery of a second species at a nearby site suggests the Zagros Mountains, Iran, may harbor many more species of stenasellids. At present, regional hotspots of stenasellid diversity include the Cantabrian Range, Spain (11 MOTUs; this study), the eastern coast of Mexico (9 morphospecies; Bowman 1982; Álvarez & Guillén-Servent 2016), Benin (11 MOTUs; Lagnika *et al.* 2024), the northern region of Oman (4 morphospecies; Magniez & Stock 2000) and Sumatra, Indonesia (5 morphospecies; Magniez 2001).

Acknowledgments

We are grateful to Fazel Baroononezhad and his family from Sarjowshar Village, Shahab Azizi and Saatad Rahideh for their assistance with caving and their hospitality during field work. Mohammad Javad Malek-Hosseini was supported by the Fonds de la Recherche Scientifique (F.R.S.-FNRS) via an incoming mobility grant in the frame of PDR T.0078.23 (PI: Jean-François Flot), and a 2024 research stipend from ZRC SAZU. Matjaž Kuntner was supported in part by the Slovenian Research and Innovation Agency (P1-0255 and J1-9163). Colin Issartel, L. Konecny-Dupré, C.J. Douady and F. Malard were supported by EUR H20'Lyon project (ANR-17-EURE-0018) and Biodiversa+ DarCo project (Grant/Award Number: GAN°101052342).

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Manuscript received: 28 March 2024

Manuscript accepted: 4 July 2024

Published on: 15 November 2024

Topic editor: Magalie Castelin

Section editor: Fabio Stoch

Desk editor: Pepe Fernández

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Supplementary files

Supp. file 1. Paleobiogeographic events used to constrain the age of 17 nodes in the phylogeny of the Aselloidea Latreille, 1802. <https://doi.org/10.5852/ejt.2024.968.2733.12545>

Supp. file 2. Maximum body length and sexual body length dimorphism in Stenasellidae Dudich, 1924 (Pancrustacea, Isopoda). <https://doi.org/10.5852/ejt.2024.968.2733.12547>

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Digitale Literatur/Digital Literature

Zeitschrift/Journal: [European Journal of Taxonomy](#)

Jahr/Year: 2024

Band/Volume: [0968](#)

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