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Description of two new species of freshwater *Gammarus* Fabricius, 1775 (Amphipoda: Gammaridae) from the Middle Atlas of Morocco

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Abstract. This study describes, both morphologically and molecularly, two new species, *Gammarus latispinus* sp. nov. and *G. tazekkaensis* sp. nov. from the Middle Atlas of Morocco. Both species are similar to *Gammarus acalceolatus*, but differ by having setae as long as, or longer than, the diameter of the article on the second antenna, lacking calceoli, and by the absence of long setae on merus and carpus of pereopods 5–7. *Gammarus latispinus* sp. nov. is characterized by the presence of spinules on the outer face of epimeral plates 2 and 3, a pereopod 5 much shorter than pereopods 6 and 7, and telson lobes with dorsal setae but without lateral spines. *Gammarus tazekkaensis* sp. nov. is also characterized by the presence of a single lateral spine on telson lobes. Full descriptions of the new species are provided in this paper together with molecular data (genes COI and 28S) that corroborate the molecular delimitation. The two new species are phylogenetically close to *G. acalceolatus*, followed by *G. marmouchensis* and *G. rifatlensis*, all of which inhabit the Middle Atlas Mountains in Morocco.

Keywords. Amphipoda, integrative taxonomy, *Gammarus latispinus* sp. nov., *Gammarus tazekkaensis* sp. nov., North Africa.

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Introduction

The Mediterranean Basin harbours 35% of the Palearctic freshwater fauna and more than 6% of the world freshwater biodiversity with a very high rate of endemic species (Tierno de Figueroa *et al.* 2013;

Maasri & Bonada 2024). This is particularly true for freshwater Malacostraca Latreille, 1802 for which the Mediterranean species represent 18% of the world freshwater species known and up to one-third of the world known species of almost all orders (Piscart *et al.* 2024).

Among Mediterranean Malacostraca, Amphipoda Latreille, 1816 is the most diversified order with 581 species, most of them being known from the northern part of the Mediterranean Sea. A first evident explanation to consider in studying the diversity of aquatic fauna in Northern Africa is the limitation of the water resources during the last 6000 years (Schneider *et al.* 2017). Indeed, unlike insects, which have a flying adult stage that allows them to escape drought events, crustaceans have an entirely aquatic life cycle, and they are also particularly threatened by climate change (Dehedin *et al.* 2013a, 2013b; Aspin *et al.* 2019).

Another important factor contributing to the lower species richness in North Africa may be the lack of knowledge on amphipods (Tuekam Kayo *et al.* 2012; Ayati *et al.* 2019). Africa remains largely unexplored with respect to the aquatic fauna, especially crustaceans, and Amphipoda is one of the least known taxonomic groups, with 20% of the currently known species described in the last 15 years (Arfianti *et al.* 2018). As a consequence, knowledge on freshwater amphipods is rather limited in Northern Africa, with only 23 epigean freshwater species currently known (Ayati *et al.* 2019; Hadjab *et al.* 2021). Half of the species are known from Morocco, which harbours the seven species of the genus *Gammarus* Fabricius, 1775, all of them, except *G. gauthieri* (Karaman, 1935), being endemic (Ayati *et al.* 2019).

Samplings in the northern part of Morocco yielded gammarid populations morphologically close to *G. acalceolatus* Pinkster, 1970, a species already known from the Northern part of Morocco (Karaman & Pinkster 1977). However, several morphological traits did not fully match, and molecular analyses confirmed their evolutionary divergence. Both of these species are described in this paper.

Material and methods

Field surveys and animal collection

Several locations were sampled in the northern part of Morocco, including the Atlas Massif. Invertebrate fauna, including Gammaridae Latreille, 1802, was collected at 31 sites using a handnet and a Surber sampler (20 × 25 cm surface area, 400 µm mesh) during several seasons between 2019 and 2023 (Fig. 1). Samples were preserved in 96% ethanol until identification. In addition, some samples were collected at type localities / area of several species of *Gammarus* in Morocco for molecular analyses. DNA extracts from specimens collected at each sampling site were stored in the private collection of Christophe Piscart, University of Rennes (France).

Conductivity, pH, dissolved oxygen, and temperature were measured in situ with a multiparametric measuring device (WTW, MultiLine P4). Biological oxygen demand after 5 days (BOD_5) and ammonium ($N\text{-}NH_4$) were measured in the laboratory.

Institutional abbreviations

MNHN = Muséum national d'Histoire naturelle, Paris, France

Molecular analyses

Total genomic DNA was extracted from individuals using NucleoSpin Tissue Kits (Macherey-Nagel™) following the manufacturer’s instructions (Düren, Germany). DNA was amplified with primers targeting the mitochondrial cytochrome oxidase subunit I (COI) and nuclear 28S genes. We used the primer set LCO1490 and HCO2198 (Folmer *et al.* 1994) to amplify the COI gene; NIPH15 / NIPH16 (Verovnik *et al.* 2005) and 28F / 28R (Hou *et al.* 2007) to amplify a fragment of the 28S gene. PCR were performed in a final volume of 27 µl containing 12 µl of PCR water, 10 µl of Type-it PCR Master Mix (©Qiagen, Germany), and 1.5 µl of each primer (5 µM) and 2 µL of DNA extracts.

The success of the PCR reactions was checked by gel electrophoresis. The PCR products were then purified and sequenced in both directions by the Eurofins sequencing facility or with an Applied Biosystem 3130 XL sequencer in the DNA sequencing facility of the Institute of Genetics and Development of the University of Rennes (https://igdr.univ-rennes.fr/en). Sequences of the new species were submitted to GenBank with Additional DNA sequences of closely related species of Morocco (accession number in Table 1). Then, all sequences were aligned with MUSCLE (Edgar 2004) as implemented in Seaview ver. 5.05 (Gouy *et al.* 2010). Alignments were then checked by eye and minor editing was done manually.

To assess divergence from other previously described and sequenced species of *Gammarus*, we calculated corrected genetic distances using the Kimura two-parameter (K2P) model and used the Assemble Species by Automatic Partitioning (ASAP) method to check species delimitation (Puillandre *et al.* 2021) implemented in iTAXOTOOLS ver. 0.1 (Vences *et al.* 2024), for COI with a transition/transversion ratio (R) of 0.592 calculated in SeaView software. ASAP was run using p-distances as well as both the Jukes-Cantor (JC69) and the Kimura 2-parameter (K2P) substitution models to compute the distances, allowing us to investigate the possible impact of different distance models on the partitioning.

In addition, we used the Bayesian Poisson Tree Processes (Zhang *et al.* 2013). Current approaches either rely on simple sequence similarity thresholds (OTU-picking as a tree-based method to identify the Molecular Operational Taxonomic Units (MOTUs) based on the COI dataset for each species. The appropriate nucleotide substitution models were selected on the www.phylogeny.fr webserver under a HKY85 model of evolution. A neighbour-joining (NJ) tree was then constructed with HKY85 node

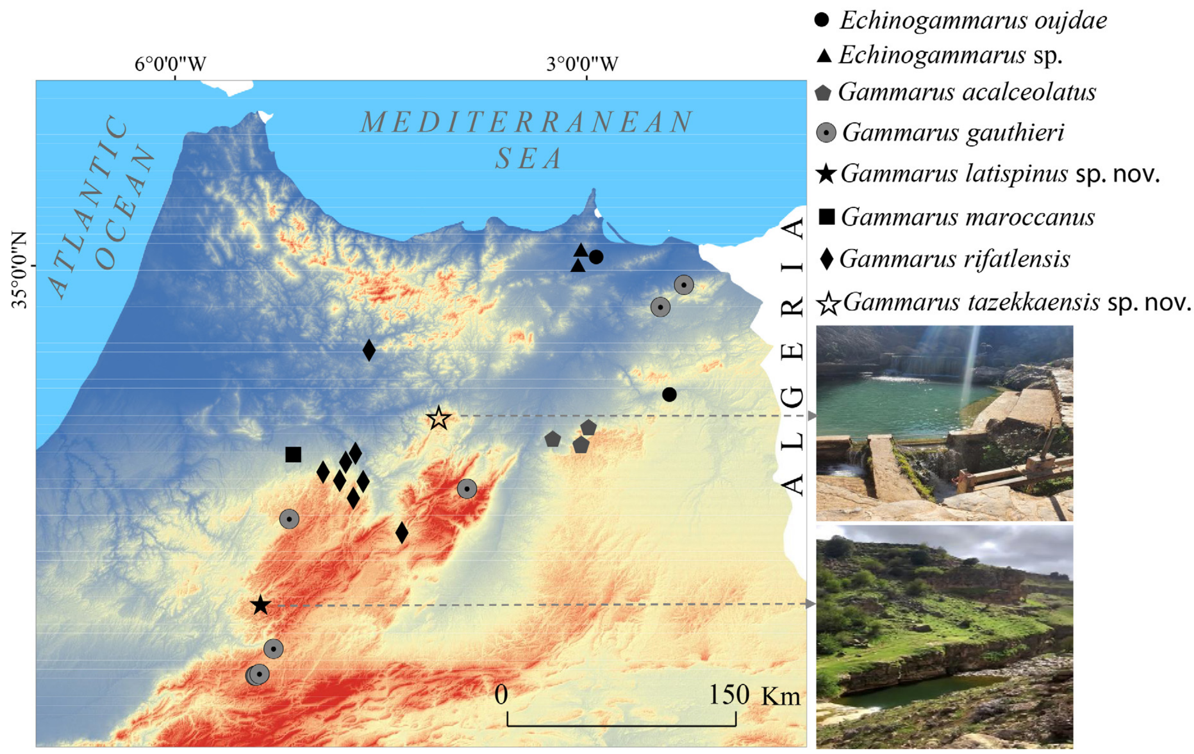

Fig. 1. Location of the species of *Gammarus* Fabricius, 1775 sampled in the study area in Morocco.

Table 1. Information about data on the species of *Gammarus* Fabricius, 1775 used in molecular analyses. Abbreviations: Fr = France; Mo = Morocco; * = type locality.

Species	Locality	Assession numbers		References
		COI	28S	
G. gauthieri (S. Karaman, 1935)	Fès (Mo)	JF965899.1	JF965710.1	Hou *et al.* 2011
G. cf iberic us Margalef, 1951	Lascaux (Fr)	JF965901.1	JF965713.1	Hou *et al.* 2011
G. acalceolatus Pinkster, 1970	Timahdite (Mo)	JF965831.1	JF965636.1	Hou *et al.* 2011
G. acalceolatus	Debdou (Mo)	PV657838	PV658258	this study
*G. marmouchensis** Fadil & Dakki, 2006	Imouzzer (Mo)	PV657834	PV658255	this study
*G. marmouchensis**	Imouzzer (Mo)	PV657835	PV658256	this study
*G. maroccanus** Fadil & Dakki, 2006	Ain Chkef (Mo)	PV657841	PV658261	this study
*G. maroccanus**	Ain Chkef (Mo)	PV657842	PV658262	this study
*G. latispinus** sp. nov.	Sidi El Makhfi (Mo)	PV657836	PV658257	this study
*G. latispinus** sp. nov.	Sidi El Makhfi (Mo)	PV657837	–	this study
*G. rifatlensis** Fadil & Dakki, 2006	Bouadel (Mo)	PV657832	PV658253	this study
*G. rifatlensis**	Bouadel (Mo)	PV657833	PV658254	this study
G. tazekkaensis sp. nov.*	Bab Boudir (Mo)	PV657839	PV658259	this study
G. tazekkaensis sp. nov.*	Bab Boudir (Mo)	PV657840	PV658260	this study

support, which was calculated (Hasegawa *et al.* 1985) using 1000 bootstrap pseudo-replicates. The resulting tree was analysed using the iTAXOTOOLS executable.

A Neighbour-Joining (NJ) tree of all sequences was built in Seaview ver. 5.05 based on the K2P-distance matrix with both transitions and transversions included and all positions with gaps or missing data removed (Saitou & Nei 1987). The node support was inferred with a bootstrap analysis using 1000 bootstrap pseudo-replicates (Felsenstein 1985). The molecular sequences of another *G. maroccanus* Fadil & Dakki, 2001, also present in Morocco but member of a sister clade of other species used in the tree, were used as outgroup.

Morphological description

The habitus of the amphipods was studied in glycerine under a stereo microscope and slides were prepared using Reyne's permanent mounting medium (Stock & Von Vaupel Klein 1996) after maceration of the material in lactic acid (4 h) and a digestion in KOH (10%) overnight before staining with pink lignin (4 h). Body parts were carefully dissected and were drawn using a Wacom tablet and the Illustrator software package (Adobe™).

Results

Molecular analysis

Whether ASAP or bPTP, both approaches delineated 8 MOTUs that correspond to singletons in the NJ tree (Fig. 2A). ASAP analyses consistently suggested the same partitioning into 8 different MOTUs (p-values > 0.1), regardless of the distance estimation method (p-distances, JC69, K2P). K2P distances between MOTUs ranged from 12.9% (between MOTUs associated to the two species *Gammarus acalceolatus* and *G. tazekkaensis* sp. nov.) to 26.5% (between *Gammarus* cf. *ibericus* Margalef, 1951 and *G. maroccanus*). The new MOTUs are close to the MOTU associated with *G. acalceolatus,* with a distance of 12.9% for *G. tazekkaensis* sp. nov. and 14.9% with *G. latispinus* sp. nov. This partition was also strongly supported by the bPTP delimitation method applied to the COI phylogeny.

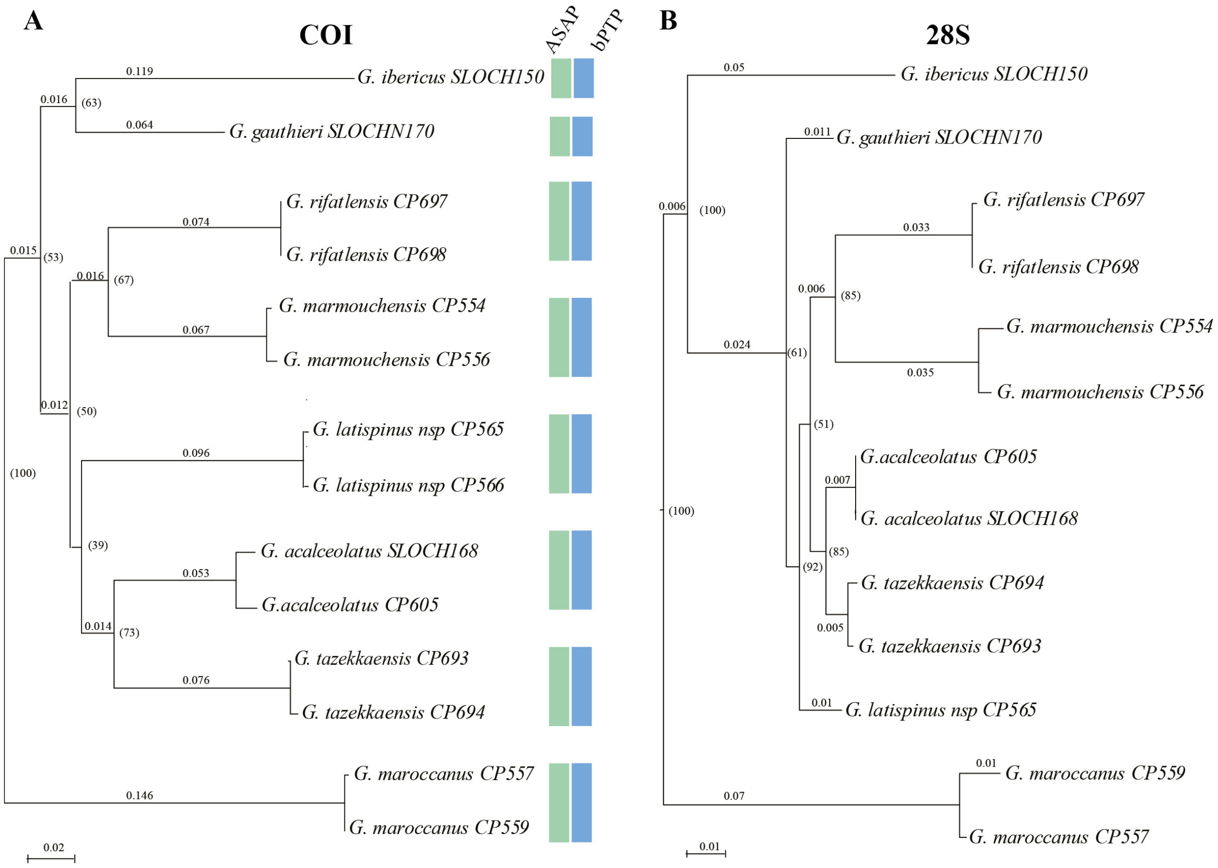

Fig. 2. Phylogenetic relationships of some species of *Gammarus* Fabricius, 1775. **A**. Reconstructed with the NJ method based on COI. **B**. Reconstructed with the NJ method based on 28S genes. Numbers between brackets indicate the bootstrap result and other numbers indicate the K2P distances. Green and blue boxes highlight the optimal species partitions identified with ASAP and bPTP delimitation methods applied to the COI gene.

In addition, results obtained with the COI gene were confirmed using the 28S gene, for which the K2P distances between *Gammarus acalceolatus* and *Gammarus tazekkaensis* sp. nov. was 1.3%, and between *G. acalceolatus* and *G. latispinus* sp. nov. was 2.4% (Fig 2B).

Taxonomy

Order Amphipoda Latreille, 1816
Family Gammaridae Latreille, 1802
Genus *Gammarus* Fabricius, 1775

Gammarus latispinus sp. nov.
urn:lsid:zoobank.org:act:56EBA8F0-07F7-49CE-99B7-E724D9CF8F01
Figs 1–8, Tables 1–2

Diagnosis

A relatively large-sized species of the *Gammarus* with epimeral plate 2 with 1–3 spinules on the outer face in addition to spinules on the ventral margin. Pereopods 5–7 have no long setae on the anterior margin of the merus and carpus, a relatively short endopodite of uropod 3 that never exceeds 60% of the exopodite. Antenna 2 with setae as long as or longer than the diameter of the article, without calceoli

Etymology

The specific epithet '*latispinus*' refers to the presence of spinules on the lateral surface of epimeral plate 2, which is unique in North African freshwater *Gammarus*.

Type material

Holotype

MOROCCO • ♂ (19.8 mm); Bakrit waterfall; 33°02′59.7″ N, 5°16′21.2″ W; alt. 1645 m; 16 May 2021; pond at the foot of the waterfall, collected by handnet; MNHN-IU-2025-2611.

Paratypes

MOROCCO • 3 ♂♂; same data as for holotype; MNHN-IU-2025-2612 • 1 ♀; same data as for holotype; MNHN-IU-2025-2613.

Other material examined (used for molecular analysis)

MOROCCO • 5 incomplete specs (♂♂, ♂♂ or juvs); same data as for holotype; DNA extracts stored in the personal collection of Christophe Piscart, University of Rennes (France); CP564 to CP566, CP609 to CP610.

Description

Male

Habitus robust, up to 19.8 mm length (Fig. 3A). Head with truncated lateral cephalic lobe, eyes relatively small, always less than 2 × as long as wide and widely separated from mid-dorsal line, inferior antennal sinus deep (Fig. 4C). First antenna longer than half body length, with few setae (Fig. 4A). First article of peduncle longer than second, itself longer than third. Flagellum more than 2 × as long as peduncle, with 35 relatively long articles. Accessory flagellum with 3 articles. Second antenna longer than ½ of first antenna (Fig. 4B). Gland cone 0.75 2 × as long as third article of peduncle. Peduncle article 4 armed with 4 groups of setae on all sides, as long as diameter of article. Peduncle article 5 as long as, but thinner than, peduncle article 4 and armed with 5 groups of setae as long as or slightly longer than diameter

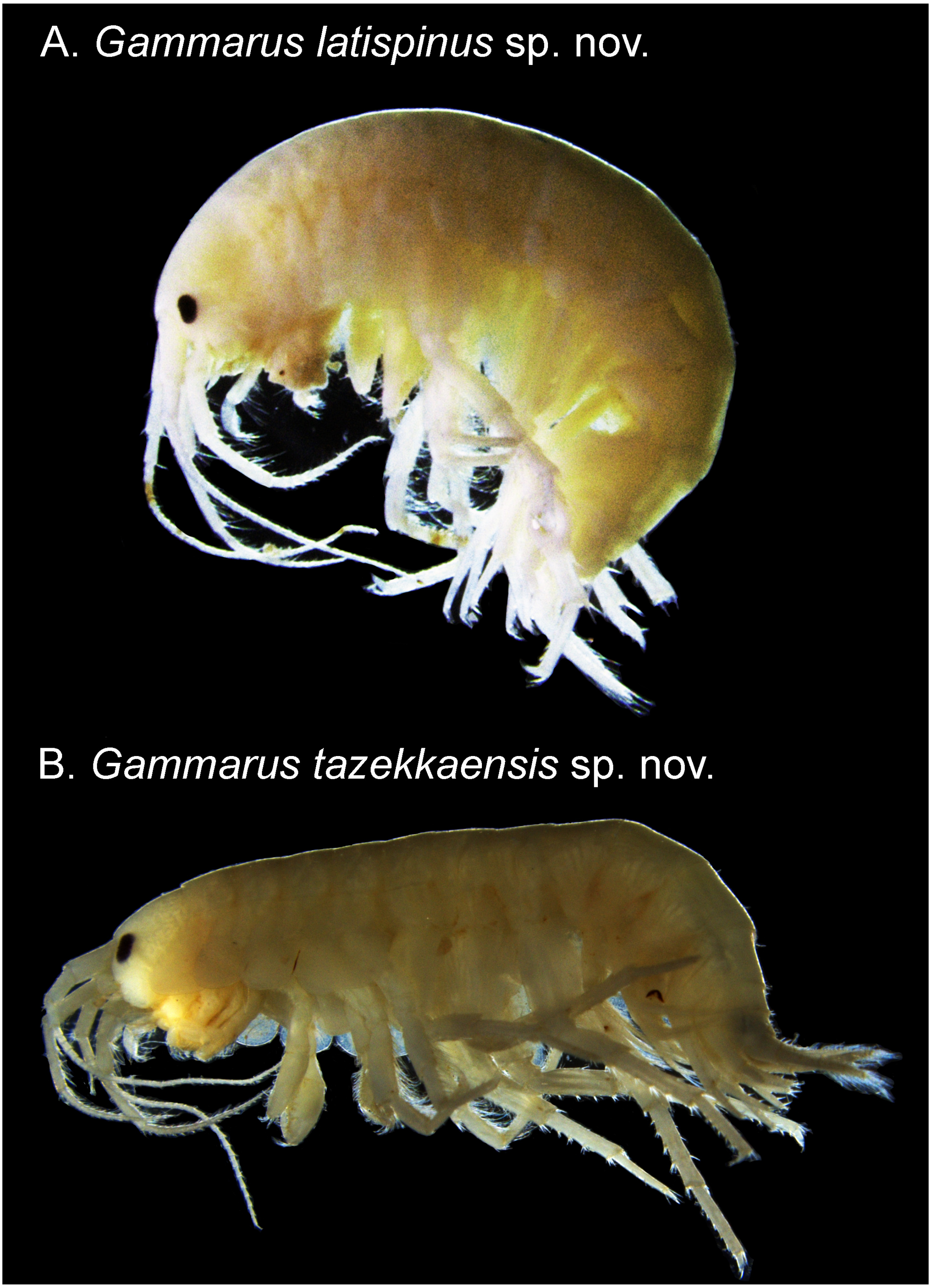

Fig. 3. A. Habitus of *Gammarus latispinus* sp. nov., paratype, ♂ (MNHN-IU-2025-2612), 19.8 mm. **B**. Habitus of *G. tazekkaensis* sp. nov., paratype, ♂ (MNHN-IU-2025-2614), 17 mm.

of article. Flagellum with 12 articles and armed with transverse rows of setae longer than articles and decreasing in length distally. Calceoli absent.

Mouthparts similar to those of other species of *Gammarus* (Fig. 5). Mandible incisor 4-toothed, lacinia mobilis 4-toothed, followed by row of plumose setae. Molar robust, triturative, with one plumose seta (Fig. 5A). Three articles of mandibular palp well developed (Fig. 5B). First article unarmed, second armed with 12–15 long ventral setae. Third article with two rows of A-setae and B-setae, row of more

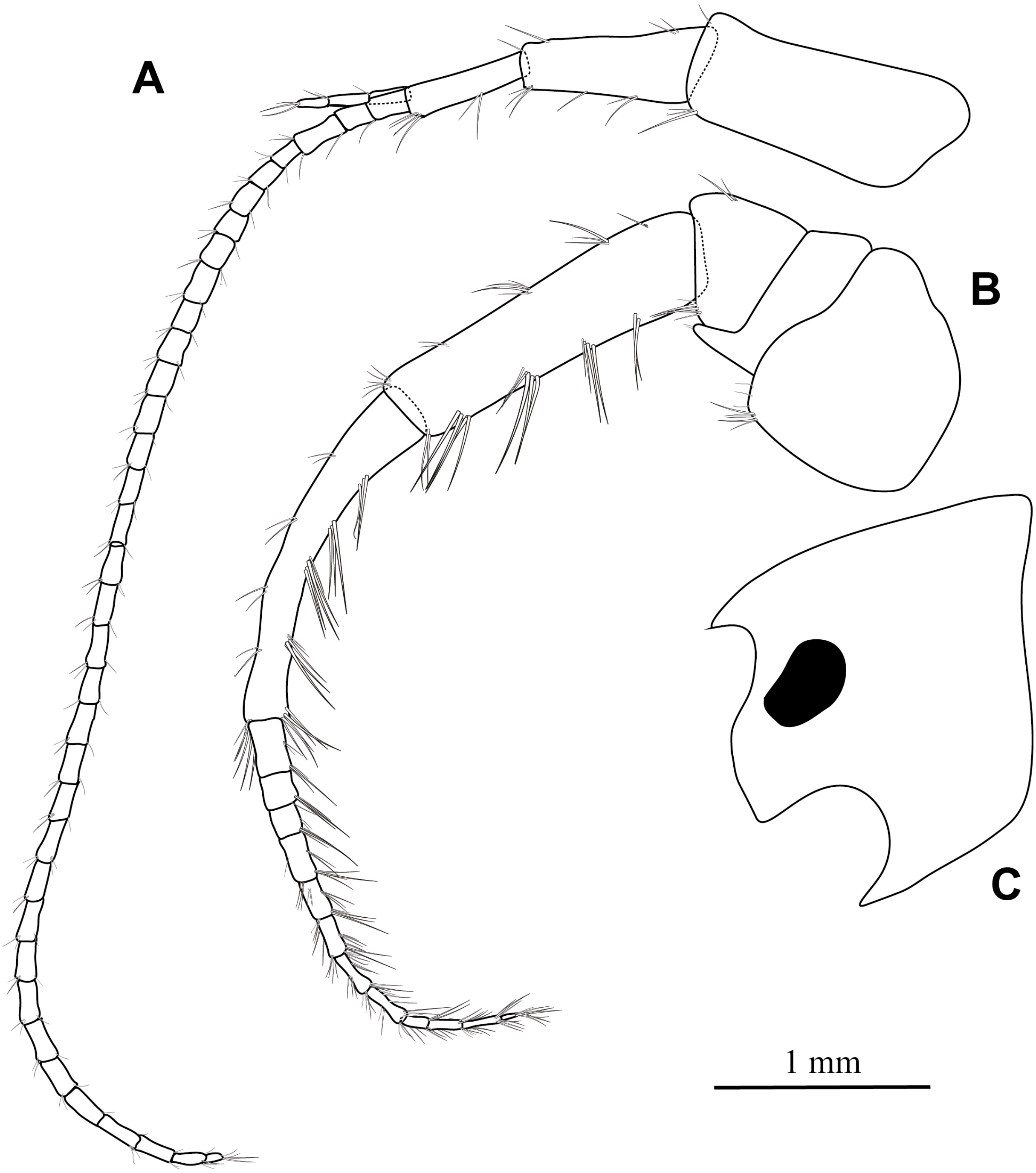

Fig. 4. *Gammarus latispinus* sp. nov., holotype, ♂ (MNHN-IU-2025-2611), 19.8 mm. **A**. Antenna 1. **B**. Antenna 2. **C**. Head.

than 30 regular D-setae, and 5 long apical E-setae. Right maxilla 1 asymmetric relative to left (Fig. 5C). Inner plate triangular, longer than wide, with plumose apical setae. Outer lobe bears 11 pectinate setae. Palp longer than outer lobe, with relatively long apical setae. Palps two-articulate, fine, and curved, with 8 thin terminal spines for right maxilla 1 and enlarged with 5 stout terminal spines for left maxilla 1. Maxilla 2, inner and outer lobes with one row of apical and subapical simple setae; outer lobe slightly larger than inner lobe (Fig. 5D). Lateral row of setae ends with simple setae on external face of inner

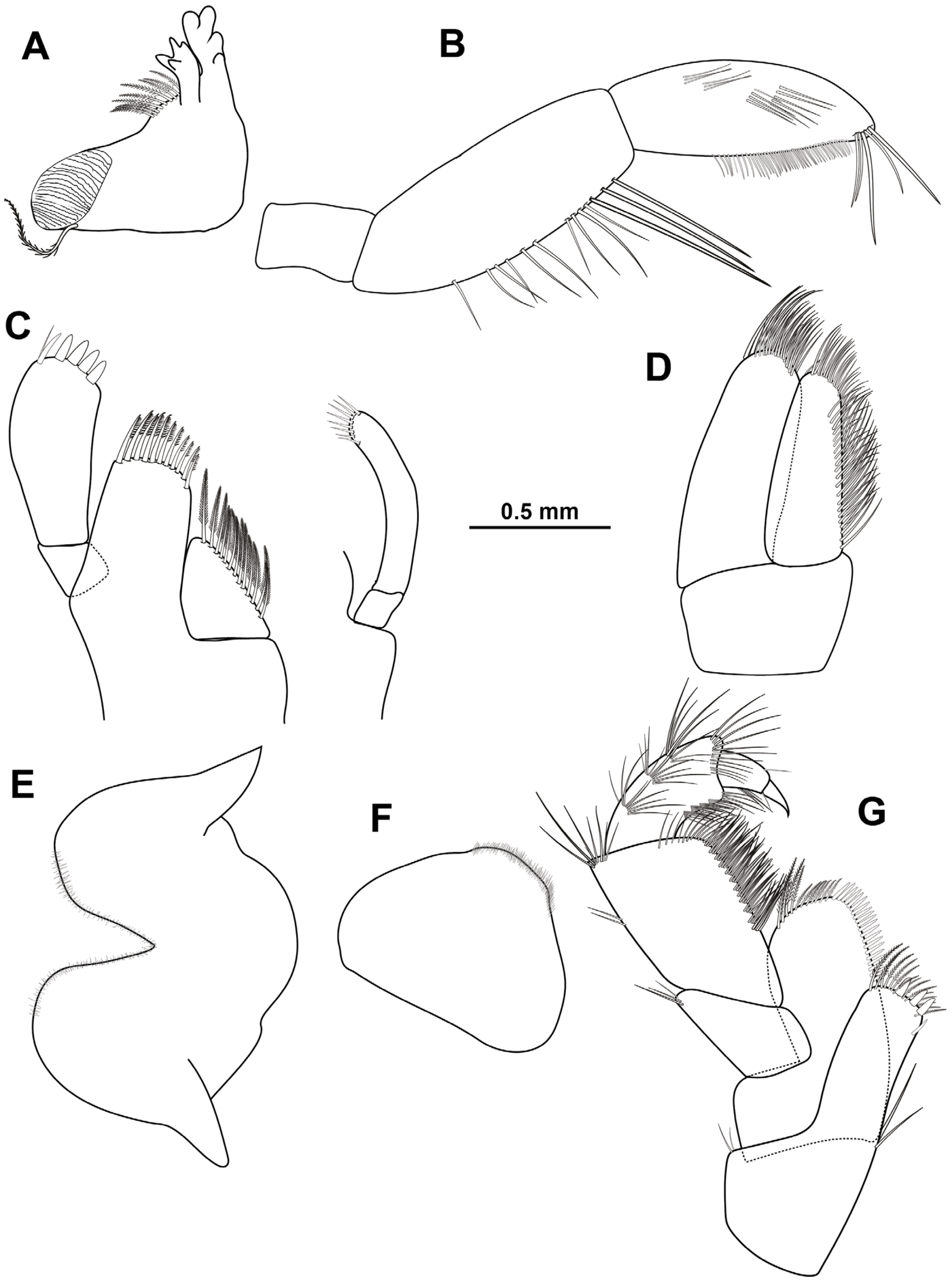

Fig. 5. *Gammarus latispinus* sp. nov., holotype, ♂ (MNHN-IU-2025-2611), 19.8 mm. **A**. Right mandible. **B**. Mandibular palp. **C**. Left maxilla 1 and palp of the right maxilla 1. **D**. Maxilla 2. **E**. Lower lip. **F**. Upper lip. **G**. Maxilliped.

lobe. Lower and upper lips similar to those of *Gammarus*, with setose inner surface and without inner lobe (Fig. 5E–F).

Maxilliped inner lobe ~3 × as long as wide, distal margin with 3 stout teeth and long sub-apical spine (Fig. 5G); distal part of lobe covered with fine setules and bearing lateral simple setae on outer margin. Outer lobe with lateral margin evenly rounded, distomedial margin fringed with ~20 knife-like teeth; teeth progressively thinner towards distal part; apex with 5–6 plumose setae. Rows of teeth on inner and

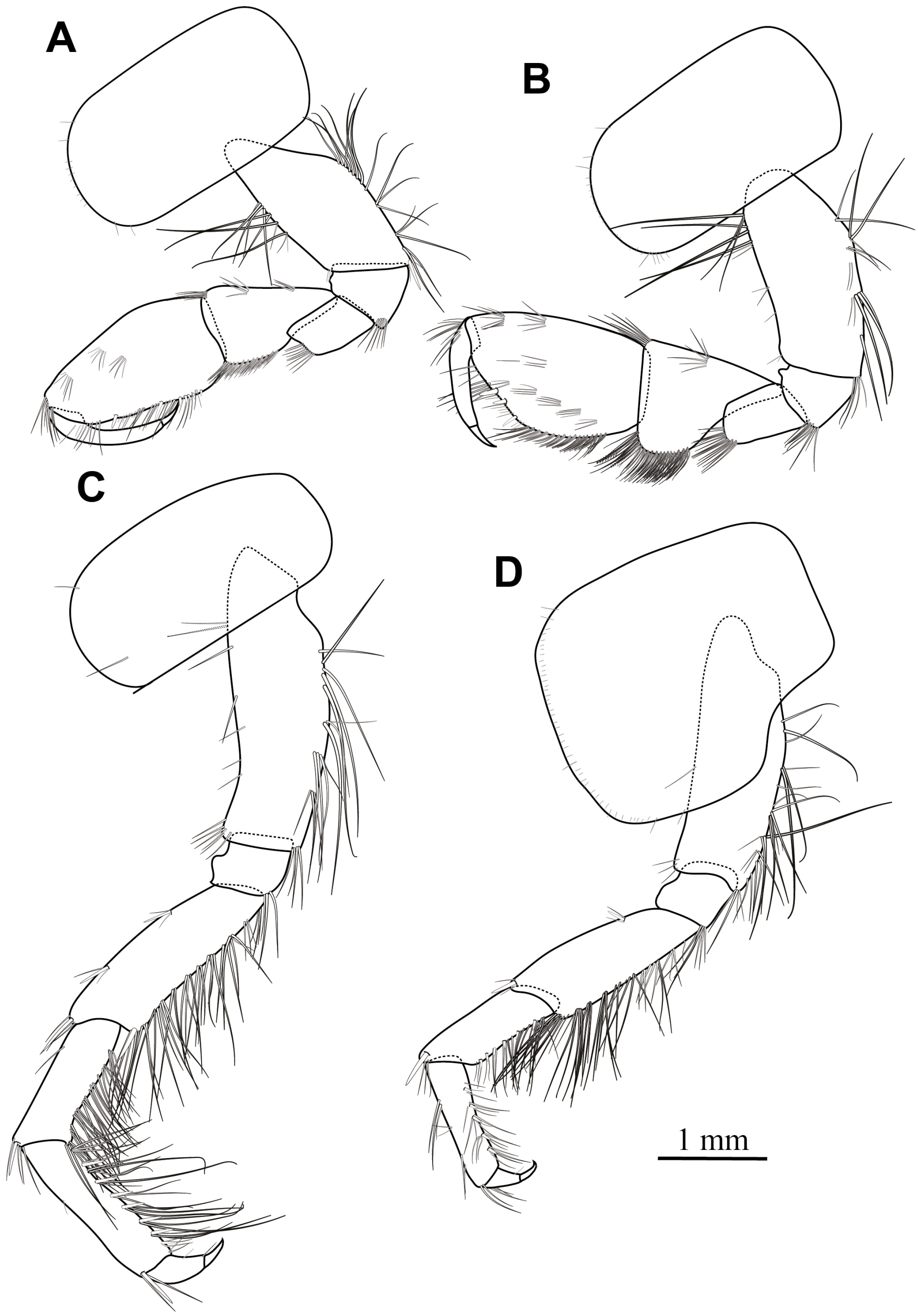

Fig. 6. *Gammarus latispinus* sp. nov., holotype, ♂ (MNHN-IU-2025-2611), 19.8 mm. **A**. Gnathopod 1. **B**. Gnathopod 2. **C**. Pereopod 3. **D**. Pereopod 4.

outer lobes continue with plumose setae proximally and distally. First segment of palp short, trapezoidal and bearing few distal simple setae on distomedial angle; segment 2 long, bearing numerous setae (>20) on inner margin and 3–4 groups of simple setae on outer margin. Segment 3 slightly expanded distally, with numerous facial and marginal setae. Dactylus with few setae; unguis shorter than dactylus.

Gnathopod 1 more slender and slightly shorter than gnathopod 2, subchelate (Fig 6A); basis longer than depth of coxa 1; carpus shorter than propodus, with hind margin furnished with setae and several rows of

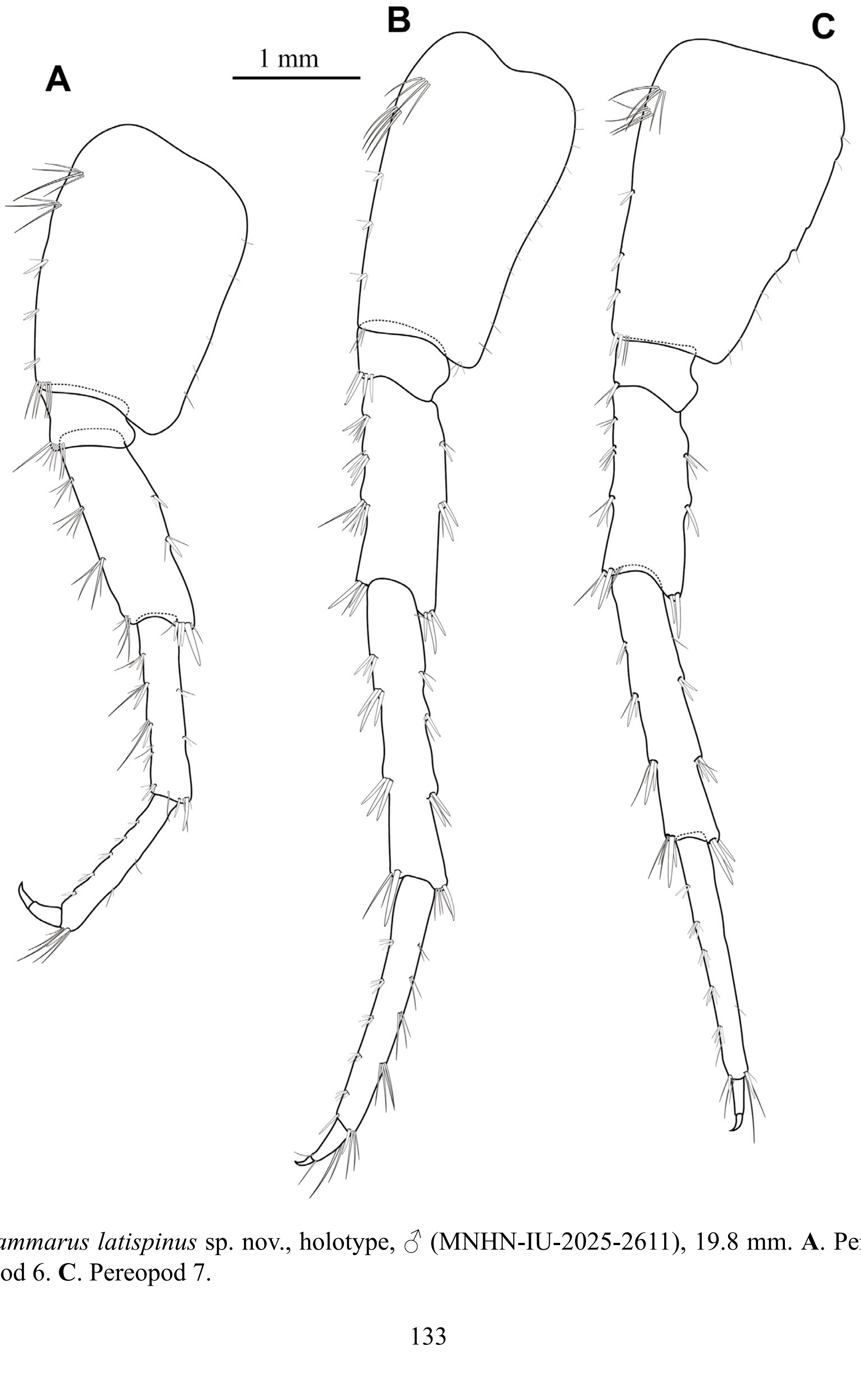

Fig. 7. *Gammarus latispinus* sp. nov., holotype, ♂ (MNHN-IU-2025-2611), 19.8 mm. **A**. Pereopod 5. **B**. Pereopod 6. **C**. Pereopod 7.

setae on outer face. Propodus pyriform, with few groups of simple dorsal setae and many ventral setae. Palm armed with strong medial palmar spine, variable number of palmar angle spines, and few smaller spines along posterior margin, dactylus shorter than palm width.

Gnathopod 2, carpus shorter than propodus (Fig. 6B). Palm more transverse and stronger than for first gnathopod, with more groups of longer dorsal and ventral setae and 5–6 rows of lateral setae on outer

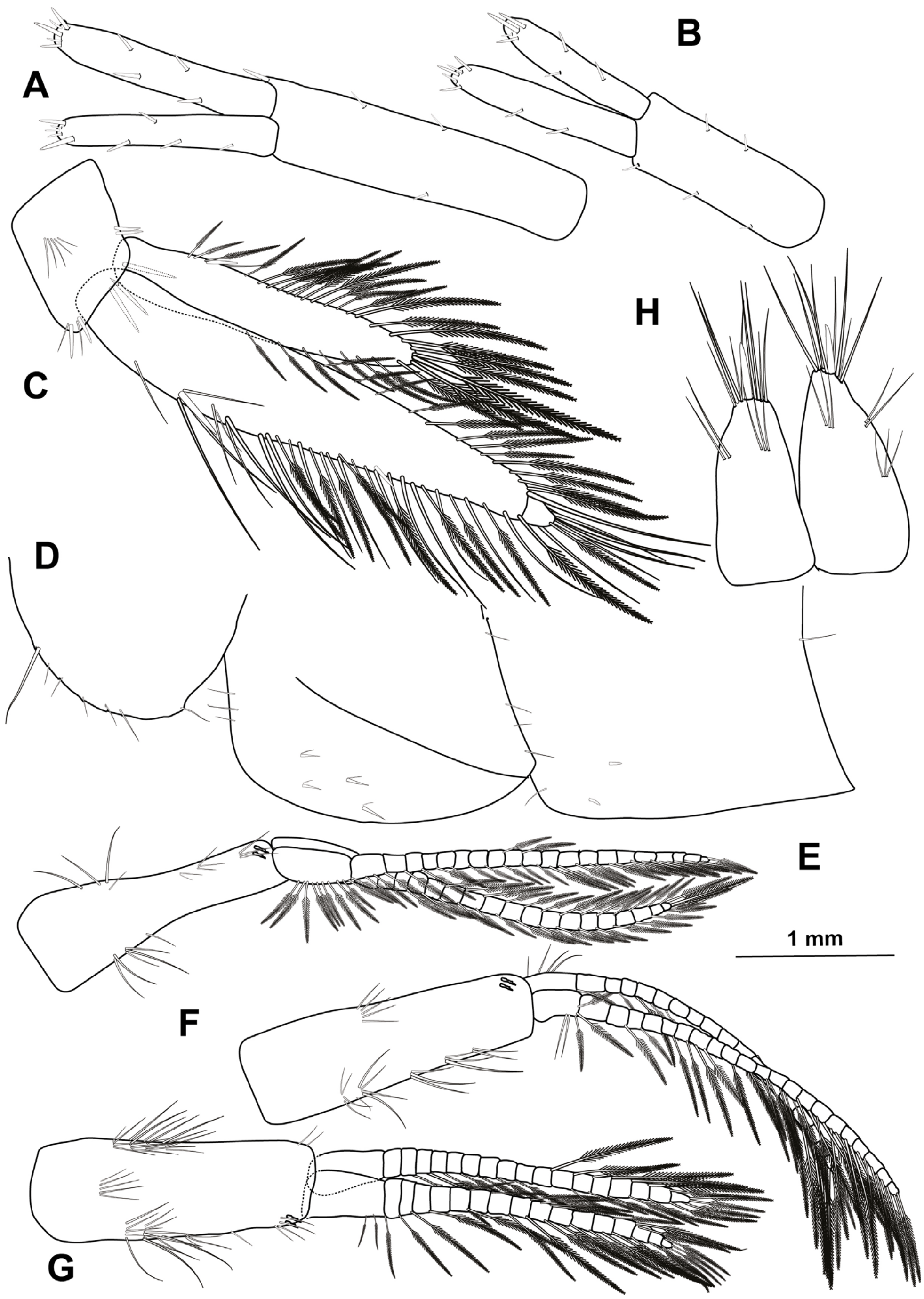

Fig. 8. *Gammarus latispinus* sp. nov., holotype, ♂ (MNHN-IU-2025-2611), 19.8 mm. **A**. Uropod 1. **B**. Uropod 2. **C**. Uropod 3. **D**. Epimeral plates 1–3. **E**. Pleopod 1. **F**. Pleopod 2. **G**. Pleopod 3. **H**. Telson.

face. Palm also with thin medial palmar spine and several strong and small spines toward palmar angle; dactylus as long as palm width.

Pereopod 3 longer than pereopod 4 (Fig. 6C). All segments armed with many groups of setae longer than segment diameter on posterior margin and few spines on anterior margin. Propodus with 5–7 spines on posterior margin and one long distal spine anteriorly. Dactylus relatively short with one single seta. Pereopod 4 similar to pereopod 3, but setation, especially of propodus, reduced in both density and size (Fig. 6D).

Coxal plates 1–4 with rounded ventral corners, set with short ventral and lateral setules (Fig 6). Coxal plate 4 wide and deep, reaching almost length of basis.

Pereopods 5–7 similar in shape but pereopod 5 25% as short as pereopods 6 and 7 (Fig 7); basis with 2 proximal rows of 4–5 setae on external margins, meri, carpi and propodi with very few setae as long as or shorter than spines along anterior margin, especially on pereopod 5. Pereopod 5 with short subrectangular basis less than 1.5 × as long as wide (Fig. 7A). Pereopods 6 and 7 bases are 2 × as long as wide (Fig. 7B–C). Pereopod 7 similar to pereopod 6 but basis different and constricted near distal end.

Uropod 1 almost as long as uropod 3; basis with 1 or 2 short marginal and 4–5 terminal spines (Fig. 8A). Endopodite and exopodite subequal in length and armed with 2–3 lateral spines. Uropod 2 similar to uropod 1 but shorter (Fig. 8B). Uropod 3 relatively long; basis with long distal spines (Fig. 8C); endopodite length 0.5–0.6 × that of exopodite; exopodite with mainly simple and plumose setae on inner and outer margins and few spines on outer margin; endopodite only with plumose setae.

Dorsal surface of metasome unarmed, except for few setules on distal margin of last segment. Urosome segments with rare dorsal setae, always shorter than spines. Urosomites 1 and 2 armed with 2 pairs of spines on each side, and urosomite 3 with only one spine on each side, longer than spines on urosomites 1 and 2. Epimeral plates with postero-inferior corner rounded on plate 1 and subrectangular on plates 2 and 3 (Fig. 8D). Epimeral plate 1 with relatively long setae along ventral margin. Epimeral plates 2 and 3 exhibit main discriminating morphological trait, with 1–3 spinules on outer face and 2–3 spinules on ventral margin; epimeral plate 2 with diagonal ridge. Pleopods 1–3 similar in shape, with 2 coupling hooks and several groups of setae on basis, and very long plumose setae on the flagellum (Fig. 8E–G).

Telson lobes elongate, each lobe about 2 × as long as wide (Fig. 8H). Armature of lobes consisting of one apical spine and several long dorsal, distal, and lateral simple setae longer than apical spine.

Female

Females slightly shorter than males, maximum size observed 14 mm. Characteristic lateral spinules on outer face of epimeral plates 2 and 3 not present in females.

Ecology and distribution

Despite additional samplings in the study area, the species was never been found outside the type locality in Oued Fellat. The analysis of the physicochemical parameters of the water (ammonium and BOD_5) showed a good environmental quality of the water, according to the Moroccan surface water guidelines of good quality (Table 2).

Differential diagnosis

Gammarus latispinus sp. nov. is characterized by the presence of spinules on the outer margin of epimeral plates 2 and 3. Among North African members of *Gammarus*, no species has spinules on the outer face of the epimeral plates. *Gammarus latispinus* resembles *G. gauthieri*, *G. rifatlensis* Fadil & Dakki, 2006, and

G. marmouchensis Fadil & Dakki, 2006, in the absence of long setae on pereopods 5–7, but differs from these species in the presence of long setae on antenna 2. Due to the lack of calceoli, the new species is morphologically close to *G. acalceolatus* and *G. marmouchensis* but differs from *G. acalceolatus* by the setation of antenna 2 and pereopods 5–7, and from *G. marmouchensis* by a flat urosome, the presence of two rows of B-setae on the mandibular palp, the subrectangular epimeral plates 2 and 3, and the armature of the telson (long dorsal setae and only one terminal spine for *G. latispinus*).

Gammarus tazekkaensis sp. nov.
urn:lsid:zoobank.org:act:C9121497-71F5-4D6B-8324-67ACAF7A4D48
Figs 1–3, 9–13, Tables 1–2

Diagnosis

A relatively large species of freshwater *Gammarus* with long setae on Antenna 2 but no calceoli. Epimeral plate 2 with spinules only on the ventral margin, pereopods 5–7 without setae on the anterior margin of the merus and carpus, pereopod 5 being shorter than the others. The endopodite of uropod 3 is relatively short, never exceeding 60% of the exopodite, and the telson has a lateral spine on each lobe.

Etymology

The specific epithet refers to Tazekka National Park, where the new species was discovered.

Holotype

MOROCCO • ♂ (15.4 mm); Raz el Oued or Ras El Ma waterfalls near Taza, 34°08′51.2″ N, 4°00′36.2″ W; alt. 880 m; 20 Dec. 2022; small stream, collected by handnet; MNHN-IU-2025-2613.

Paratypes

MOROCCO • 5 ♂♂; same data as for holotype; MNHN-IU-2025-2614 • 3 ♀♀; same data as for holotype; MNHN-IU-2025-2615.

Other material examined (used for molecular analysis)

MOROCCO • 5 incomplete specs (♂♂, ♀♀ or juvs); same data as for holotype; DNA extracts stored in the personal collection of Christophe Piscart, University of Rennes (France); CP690, CP693 to CP696.

Description

Male

Habitus slender, up to 17 mm length (Fig. 3B). Head with truncated lateral cephalic lobe; eyes relatively small, always less than 2 × as long as wide; inferior antennal sinus deep (Fig. 9A). First antenna as long as half body length, with few setae (Fig. 9B). First article of peduncle is longer than second, itself longer than third. Flagellum more than 2 × as long as peduncle, with 31 relatively long articles and accessory flagellum of 3 articles. Second antenna as long as ½ of first antenna (Fig. 9C). Gland cone about ⅔ × as long as third article of peduncle. Peduncle article 4 armed with simple setae on all sides, longer than or as long as diameter of article. Peduncle article 5 as long as, but thinner than, peduncle article 4 and armed with 4–5 groups of setae as long as or slightly longer than diameter of article. Flagellum with 13 articles and armed with transverse rows of setae longer than articles and decreasing in length distally. Calceoli absent.

Mouthpart not showing distinctive characteristics (Fig. 10). Mandible incisor 5-toothed, lacinia mobilis 4-toothed (Fig 10A). Mandibular palp with three developed articles (Fig. 10B). First article unarmed; second armed with ~10–12 long ventral setae. Third article with one row of A-setae and B-setae, row of more than 40 regular D-setae, and 4–5 long apical E-setae. Right maxilla 1 asymmetric relative to left

(Fig. 10C). Inner plate triangular and longer than wide, with simple apical setae on right maxilla and plumose setae on left. Outer lobe bearing 11 pectinate setae. Palp longer than outer lobe with relatively long apical setae. Palps two articulate, fine, and curved, with 5 thin terminal spines for right maxilla 1 and enlarged, with 6 stout terminal spines, for left maxilla 1. Maxilla 2 inner and outer lobes with one row of apical and subapical simple setae; outer lobe slightly larger than inner lobe (Fig. 10D). Lower and upper lips similar to those of *Gammarus,* with setose inner surface and without inner lobe (Fig. 10E–F). Maxilliped similar to that of *G. latispinus* (Fig. 10G). Maxilliped inner lobe ~3 × as long as wide, distal

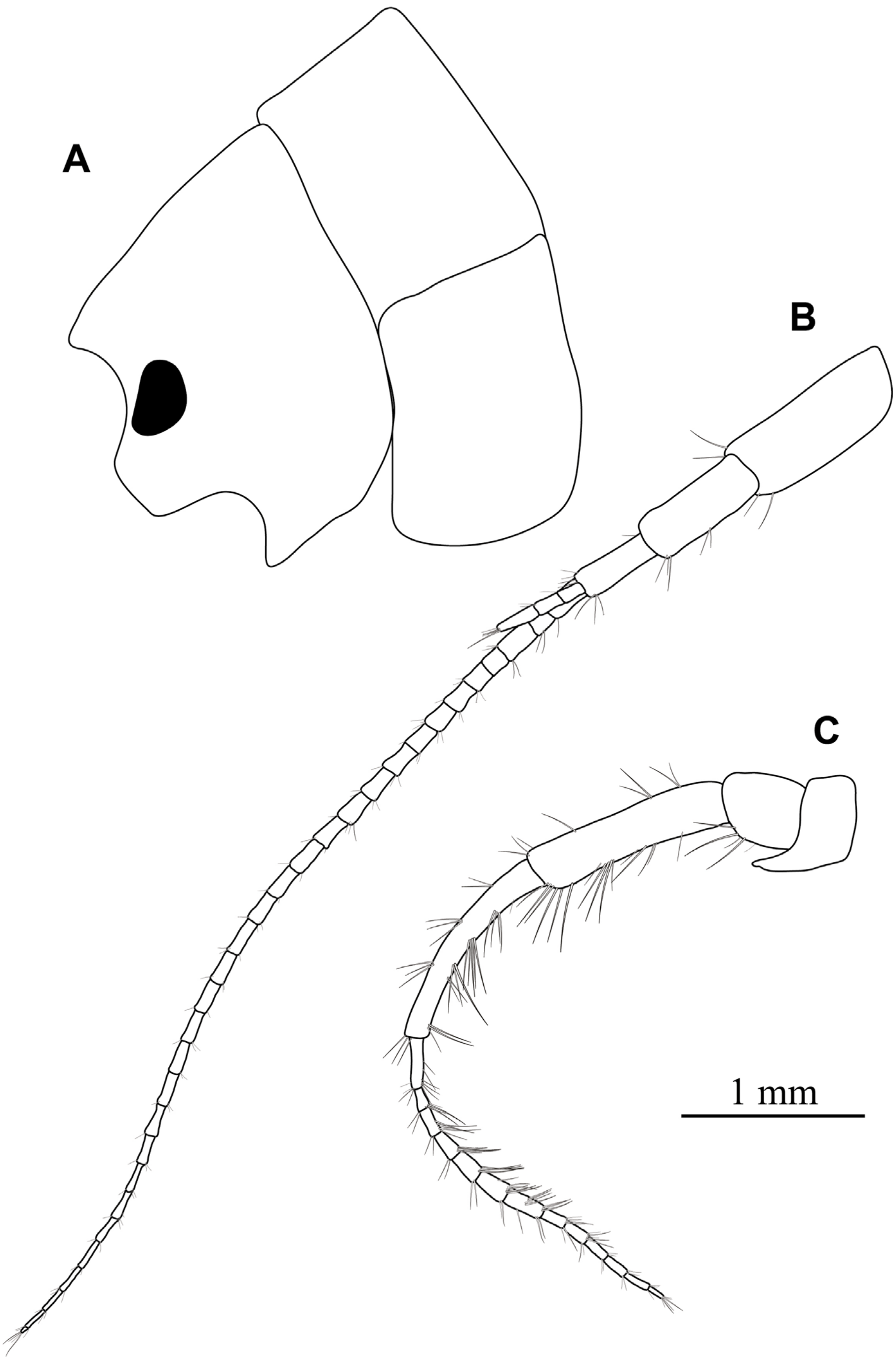

Fig. 9. *Gammarus tazekkaensis* sp. nov., holotype, ♂ (MNHN-IU-2025-2613), 17 mm. **A**. Antenna 1. **B**. Antenna 2. **C**. Head.

margin with 3 stout teeth and long subapical spine; distal part of lobe covered with few fine setules and bearing lateral simple setae on outer margin. Outer lobe with lateral margin evenly rounded, distomedial margin fringed with ~20 knife-like teeth; teeth progressively thinner towards distal part, apex with 7–8 plumose setae. First segment of palp short, trapezoidal and bearing few distal robust setae on distomedial angle; segment 2 long, bearing numerous setae (> 20) on inner margin and 2–3 groups of simple setae on outer margin. Segment 3 slightly expanded distally, with many groups of facial and marginal setae. Dactylus with few setae; unguis shorter than dactylus.

Gnathopod 1 more slender and slightly shorter than gnathopod 2, subchelate (Fig. 11A); basis longer than depth of coxa 1; carpus shorter than propodus, with hind margin furnished with setae and several rows of

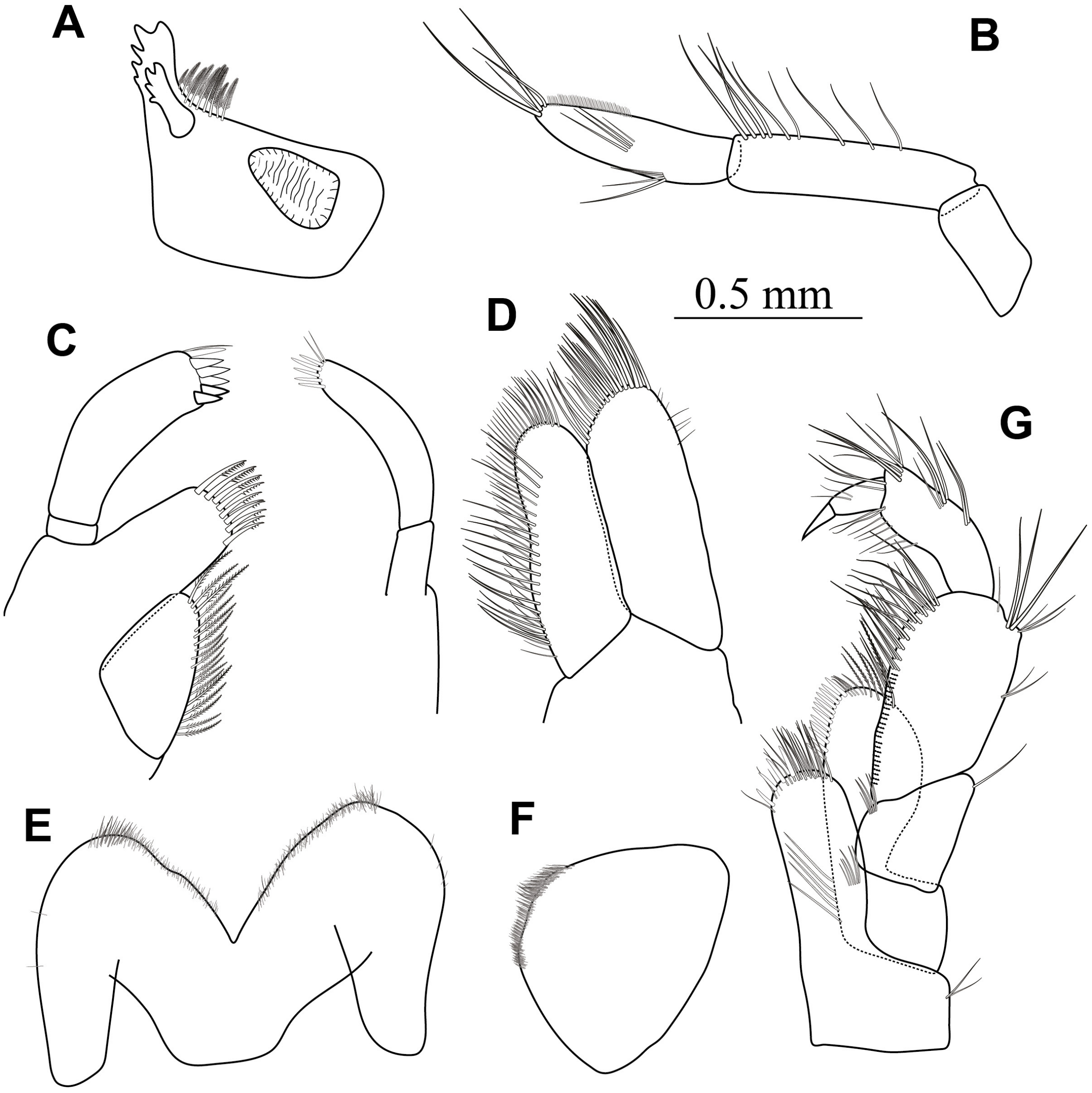

Fig. 10. *Gammarus tazekkaensis* sp. nov., holotype, ♂ (MNHN-IU-2025-2613), 17 mm. **A**. Right mandible. **B**. Mandibular palp. **C**. Left maxilla 1 and palp of the right maxilla 1. **D**. Maxilla 2. **E**. Lower lip. **F**. Upper lip. **G**. Maxilliped.

setae on outer face. Propodus pyriform, with 2–3 groups of simple dorsal setae and many ventral setae. Palm armed with medial palmar spine, variable number of palmar angle spines and few smaller spines along posterior margin; dactylus shorter than palm width.

Gnathopod 2 carpus shorter than propodus (Fig. 11B). Palm more transverse and stronger than in first gnathopod, with more groups of longer dorsal and ventral setae and only 2–3 rows of lateral setae on outer face. Palm also with thin medial palmar spine and several strong and small spines toward palmar angle; dactylus as long as or slightly longer than palm width.

Pereopod 3 slightly longer than pereopod 4 (Fig. 11C). All segments armed with many groups of long setae on posterior margin and few spines on anterior margin. Propodus with 4–5 spines on posterior

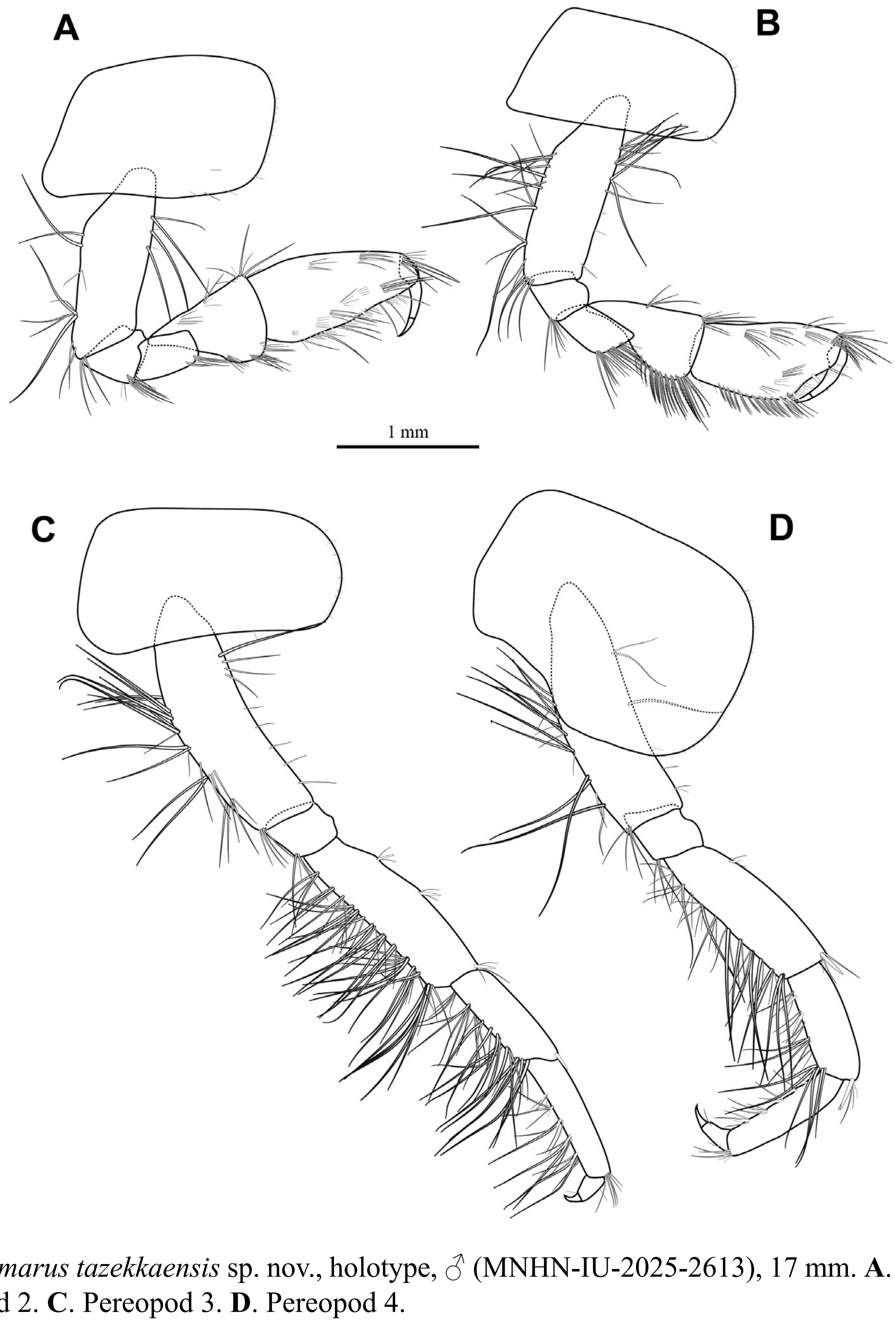

Fig. 11. *Gammarus tazekkaensis* sp. nov., holotype, ♂ (MNHN-IU-2025-2613), 17 mm. **A**. Gnathopod 1. **B**. Gnathopod 2. **C**. Pereopod 3. **D**. Pereopod 4.

margin. Dactylus relatively short with one distal seta. Pereopod 4 similar to pereopod 3, but setation reduced in both density and size (Fig. 11D).

Coxal plates 1–4 with rounded ventral corners, set with short ventral and lateral setules (Fig. 11). Coxal plate 4 wide and deep reaching ~0.75 × the length of basis.

Pereopods 5–7 similar in shape, but pereopod 5 15% shorter than pereopods 6 and 7 (Fig. 12); meri, carpi and propodi with very few setae, sometimes longer than spines along anterior margin, especially on pereopod 5. Pereopod 5 with short subrectangular basis less than 1.7 × as long as wide (Fig. 12A). Pereopods 6 and 7 bases 2 × as long as wide (Fig. 12B–C). Pereopod 7 similar to pereopod 6, but basis different and constricted near distal end.

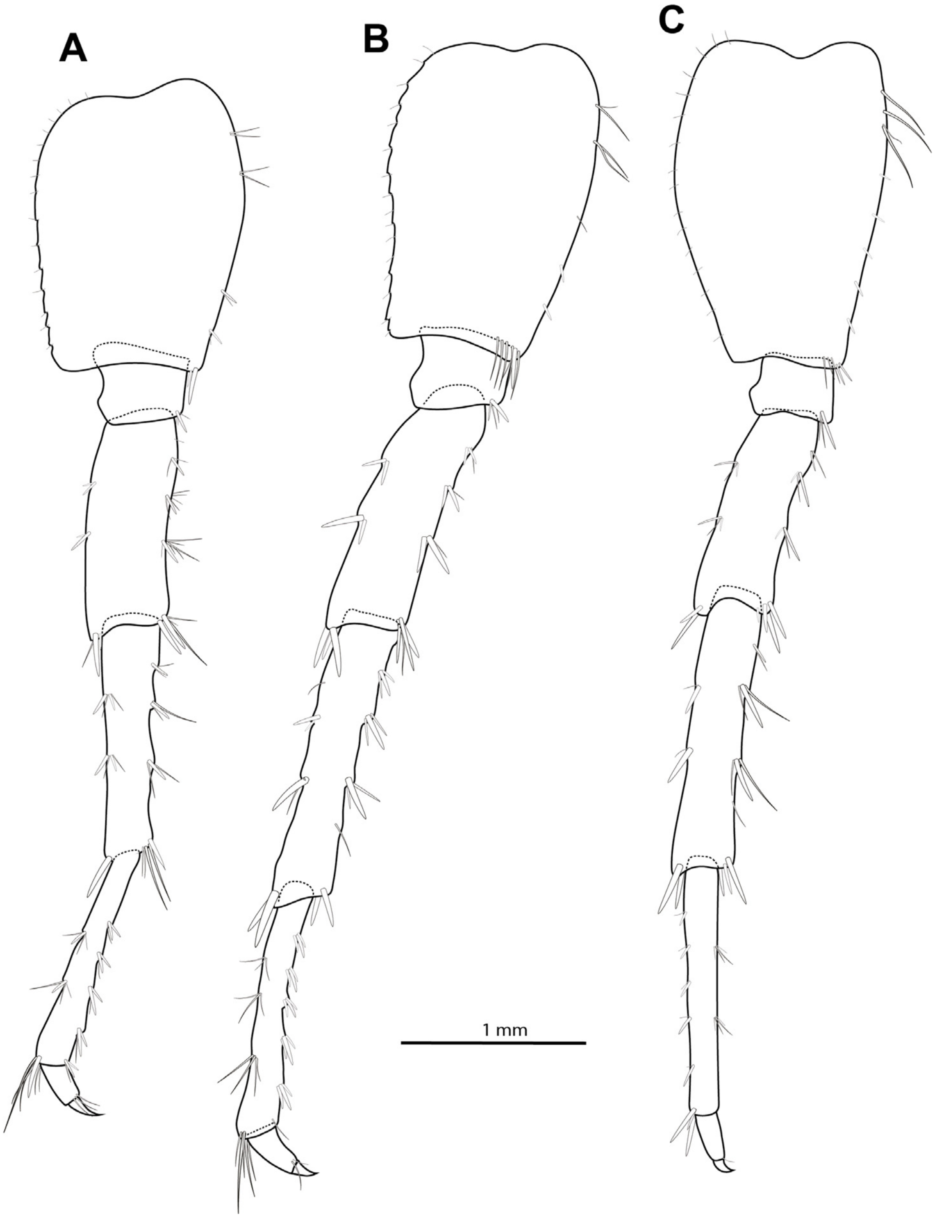

Fig. 12. *Gammarus tazekkaensis* sp. nov., holotype, ♂ (MNHN-IU-2025-2613), 17 mm. **A**. Pereopod 5. **B**. Pereopod 6. **C**. Pereopod 7.

Uropod 1 longer than uropod 2; basis with 3 lateral spines on each side and few terminal spines (Fig. 13A). Endopodite as long as exopodite, armed with 1–3 lateral spines and 3 terminal spines. Uropod 2 similar to uropod 1 but much shorter (Fig. 13B), endopodite and exopodite with one lateral spine on each side. Uropod 3 basis with long distal spines (Fig. 13C); endopodite length 0.5–0.6 × that of exopodite, both bearing mainly plumose setae on inner and outer margins and few spines on outer margins.

Dorsal surface of metasome unarmed, except for few setules on distal margin of last segment. Urosome segments with rare dorsal setae, as long as spines; each urosomite armed with 2 pairs of spines on each side. Epimeral plates postero-inferior corner rounded on plate 1 and subrectangular on plates 2 and 3 (Fig. 13D). Epimeral plate 1 with relatively long setae along anterior part. Epimeral plates 2 and 3 armed

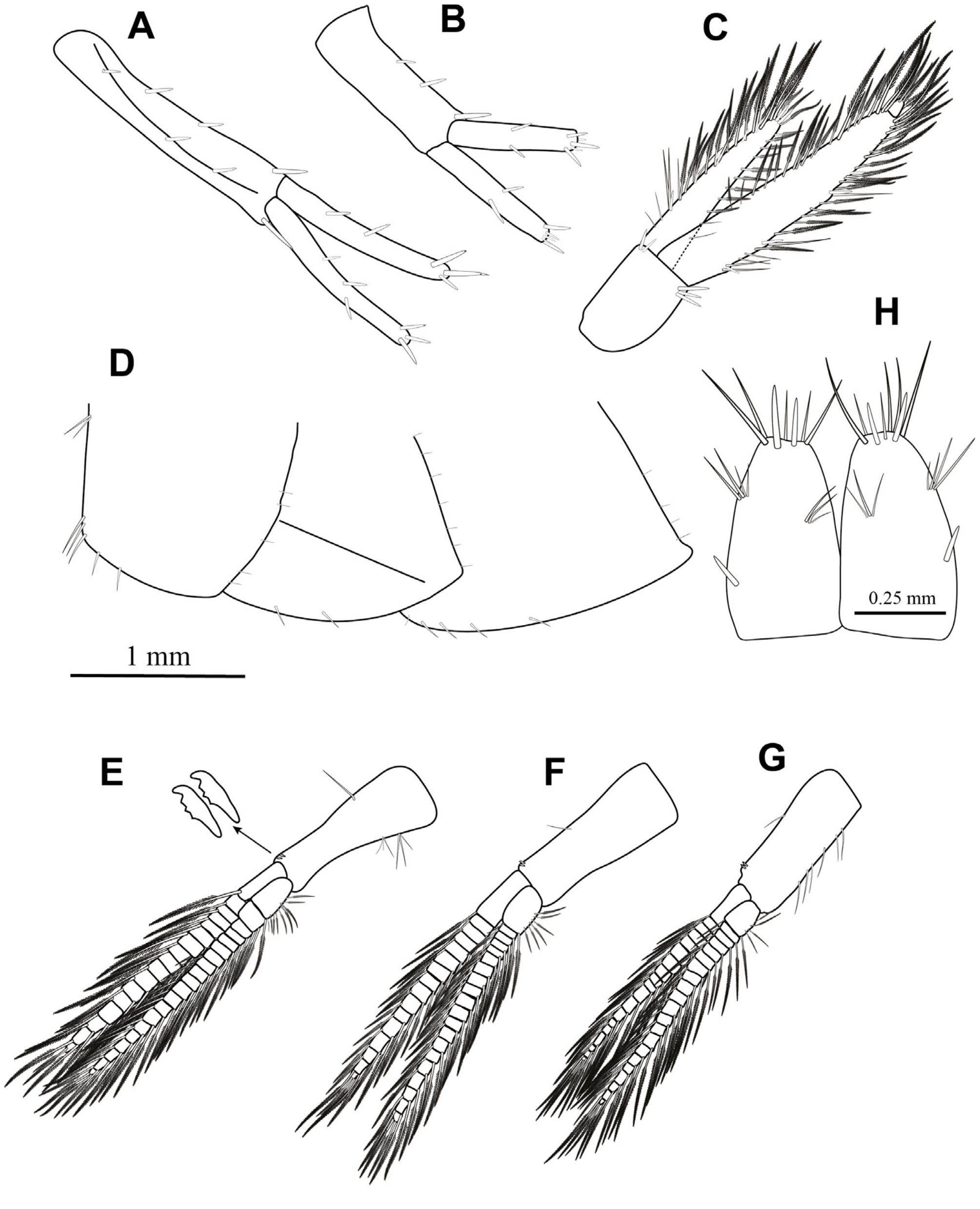

Fig. 13. *Gammarus tazekkaensis* sp. nov., holotype, ♂ (MNHN-IU-2025-2613), 17 mm. **A**. Uropod 1. **B**. Uropod 2. **C**. Uropod 3. **D**. Epimeral plates 1–3. **E**. Pleopod 1. **F**. Pleopod 2. **G**. Pleopod 3. **H**. Telson.

Table 2. Mean values of the physical and chemical water parameters measured at the type localities of *Gammarus latispinus* sp. nov. (Sidi El Makhfi) and *G. tazekkaensis* sp. nov. (Bab Boudir). Added are the Moroccan surface water guidelines of good quality (MSWG).

Sampling sites	Temperature (°C)	pH	Electrical conductivity ($mg \cdot l^{-1}$)	Dissolved oxygen ($mg \cdot l^{-1}$)	Ammonium ($mg\ N \cdot l^{-1}$)	BOD_5 ($mg \cdot l^{-1}$)
Sidi El Makhfi	19°C	7.5	282	10.6	0.01	2.5
Bab Boudir	17°C	7.2	485	9.4	0.01	3.4
MSWG	**–**	**6.5–8.5**	**< 1300**	**> 5**	**< 0.5**	**< 5**

with 2–3 spinules on ventral margin; epimeral plate 2 with diagonal ridge. Pleopods 1–3 similar in shape with 2 coupling hooks on basis and very long plumose setae on flagellum (Fig. 13E–G).

Telson lobes elongate, each lobe about 2 × as long as wide (Fig. 13H). Armature of lobes consisting of two apical spines, one lateral spine and several long dorsal and lateral simple setae.

Female

Females shorter than males, maximal observed size 12 mm. Antenna 2 with more and sometimes longer setae than in males. Telson lobes similar to those of males, with lateral spines and several lateral and dorsal setae. Exopodite of uropod 3 shorter but similar in structure to that of males.

Ecology and distribution

Despite additional sampling in the study area, the species has never been found outside the type locality in the Ras El Oued River, located in Tazekka National Park. *Gammarus tazekkaensis* sp. nov. seems to require habitats with good water quality and relatively high ionic concentration (Table 2).

Differential diagnosis

Gammarus tazekkaensis sp. nov. is characterized by the presence of long setae and by the lack of calceoli on antenna 2, the lack of long setae on pereopod 7 and a telson with a lateral spine on each lobe. Among members of the North African *Gammarus*, few species share these characteristics. *Gammarus tazekkaensis* resembles *G. acalceolatus, G. latispinus* sp. nov. and *G. marmouchensis* in lacking calceoli, but it differs from these species in several characters. It differs from *G. acalceolatus* by having long setation on antenna 2 and short setation on pereopods 5–7. It differs from *G. latispinus* in the absence of lateral spinules on epimeral plate 2, a pereopod 5 that is slightly shorter than pereopods 6 and 7, the presence of a lateral spine on the telson, and the number of A- and B-setae rows on the mandibular palp. Finally, it differs from *G. marmouchensis* in having a flat urosome, subrectangular epimeral plates 2 and 3, and telson armature bearing a lateral spine on each lobe. It resembles *G. gauthieri*, *G. rifatlensis* and *G. marmouchensis* in lacking long setae on pereopods 5–7, but differs from these species by the presence of long setae on antenna 2.

Discussion

The consensus of the morphological and molecular results showed that the two investigated *Gammarus* populations from Morocco are distinct from their congeners and should be recognized as two new species. Both species belong to the *G. pulex*-group because of the characteristic setation of pereopods 3 and 4, the lack of long setae on pereopods 5–7, and the relative size of the uropod 3 endopodite, not overreaching 0.6 × the exopodite (Karaman & Pinkster 1977). At first glance, the newly identified species are morphologically close to *G. acalceolatus* and *G. marmouchensis* due to the absence of calceoli on antenna 2, already recorded in Morocco (Karaman & Pinkster 1977; Fadil & Dakki 2006). However, they are clearly distinguished from these species morphologically by the setation of pereopods 5–7, the armature of epimeral plates 2–3, and the telson. The two new species also differ from each other in several stable morphological characteristics and are geographically separated. Finally, molecular data on the COI and 28S genes (genetic distance, delimitation methods and phylogeny) strongly support the distinction between the two species and the other species found in this region.

The distribution of both species is limited to their type localities: near Taza for *G. tazekkaensis* sp. nov. and south of Azrou (Bakrit Waterfalls) for *G. latispinus* sp. nov. In these localities, the two species do not co-occur with other amphipod species. The two new species can easily be confused with species related to *G. gauthieri*, which underlines the need to continue the taxonomic revision of *G. gauthieri* across its vast distribution area between Spain and Algeria (Ayati *et al.* 2019), where other species probably remain to be described. This region is characterised by a remarkable diversity of wetland habitats, supporting rich and original biodiversity, with numerous endemic taxa described recently. These taxa belong to different classes of benthic invertebrate communities such as Mollusca Cuvier, 1797 (Glöer *et al.* 2020; Taybi *et al.* 2022; Bespalaya *et al.* 2024), Trichoptera Kirby, 1813 (Ibrahimi *et al.* 2021), and Diptera Linnaeus, 1758 (Mabrouki *et al.* 2023).

The high level of endemicity in the Middle Atlas makes aquatic communities vulnerable to biological invasions, which represent a major threat to aquatic biodiversity in Morocco. In fact, the Middle Atlas is one of the main hotspots for biological invasions in the country's freshwater systems (Taybi *et al.* 2023) Ramsar Site and SIBE. Numerous invasive vertebrate and invertebrate species have been documented as established in the area, and their populations are increasing (Taybi *et al.* 2024; Mabrouki *et al.* 2025; El Caidi *et al.* 2025). Conservation problems are further exacerbated by the significant rainfall deficit linked to climate change, which is causing severe droughts with substantial consequences for water resources. As a result, many freshwater ecosystems in the Middle Atlas massif are drying out more frequently (el Morabet *et al.* 2021). In addition to stepping up hydrobiological and taxonomic studies, drastic measures are needed to protect the freshwater wetlands of the Middle Atlas and North Africa in general.

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