



## The genus *Stammericaris* Jakobi (Copepoda: Harpacticoida: Parastenocarididae) in the Nearctic subregion: description of *Stammericaris remotaepatriae* sp. nov., proposal of *Stammericaris palmerae* (Reid 1992) comb. nov., and remarks on other North American Parastenocarididae

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### Abstract

We describe a new harpacticoid, *Stammericaris remotaepatriae* sp. nov., collected from the hyporheic habitat of a stream in Nantucket, MA, USA. The new species is characterized by the size of the caudal rami of both sexes, which are shorter than the anal somite, by the morphology and armature of the P3 and, mainly, by the P4 endopod of males, represented by a curved plate with a strongly bifid tip, the distal proximal outgrowth of the distal margin spiniform and denticled, the proximal outgrowth missing. The study of the new species allowed us to review the systematic position of *Parastenocaris palmerae* Reid, 1992, which we transferred to *Stammericaris* Jakobi, 1972 as *Stammericaris palmerae* (Reid, 1992) **comb. nov.**, based mainly on the structure of the male P4 endopod complex and the setation of the caudal rami. We also discussed the taxonomic position and affinities of *Parastenocaris trichelata* Reid, 1955, suggesting that this species is related to the two former ones for a set of diagnostic features, but can not be attributed to the genus due to the peculiar morphology of the male P4 endopod complex; *P. trichelata* is therefore considered *species inquirenda*. We also discussed *Parastenocaris* sp. 1 and *Parastenocaris* sp. 3, two taxa only partially described and drawn in Strayer (1988). In fact, *Parastenocaris* sp. 1 can be related to *Stammericaris* and might represent a third species of the genus in the Nearctic region. Remarkably, the structure of the male P4 endopod of *Parastenocaris* sp. 3 is typical of *Proserpinicaris* Jakobi, 1972; this hypothetical assignment of the species to *Proserpinicaris*, if confirmed, would be of relevant taxonomic and biogeographic value. Finally, we provide an updated distribution map of the genus *Stammericaris* and brief remarks on the faunistic and ecological characteristics of the taxa presented and discussed in this paper.

**Key words:** North American dwelling fauna, hyporheic, Parastenocaridinae, copepod taxonomy

### Introduction

In the vast territory of the United States, research on groundwater copepod fauna has a long tradition, but in this country, as in many other countries, the studies certainly cannot be considered completed (Galassi *et al.* 2009). Hence, in order to provide more information on North American Parastenocarididae, a previously undescribed species of *Stammericaris* Jakobi, 1972 from a sample of interstitial fauna collected in Nantucket Island, Massachusetts, and given to one of us (VC) for determination, is described herein.

The genus *Stammericaris* (subfamily Parastenocaridinae Chappuis, 1940) was originally described by Jakobi (1972), and later on revised and redefined by Schminke (2013). Bruno *et al.* (2017) slightly emended Schminke's (2013) diagnosis of the genus, based on a taxonomic and molecular study of some species of *Stammericaris*. The genus currently includes the following species: the type-taxon *S. stammeri stammeri* (Chappuis, 1937); *S. acherusia* (Noodt, 1954); *S. amyclaea* (Cottarelli, 1969); *S. destillans* Bruno and Cottarelli in Bruno *et al.*, 2017; *S. diversitatis* (Cottarelli and Bruno in Cottarelli *et al.*, 2012); *S. lorenzae* (Pesce, Galassi and Cottarelli, 1995); *S. orcina* (Chappuis, 1938); *S. pasquinii* (Cottarelli, 1972); *S. phreatica* (Chappuis, 1936); *S. trinacriae* (Pesce, Galassi and

Cottarelli, 1988); *S. vincentimariae* Bruno and Cottarelli in Bruno *et al.*, 2020; plus two species from Italy (one from the epikarst in Sicily, and one from the psammal in Northern Italy) and one from Anatolic Turkey (hyporheic), presently being studied.

Interestingly, as already discussed by Schminke (2013), some of the diagnostic characters of the genera *Stammericaris* and *Cottarellicaris* are similar, and these two genera can be considered sister taxa (Bruno *et al.* 2017, 2020), their synapomorphy being the structure of the endopod P4 of the male, i.e., a complex two-branched hyaline structure, with a modified distal outgrowth. The outgrowth is an elongate lamella in *Cottarellicaris* and a pointed inner tip in *Stammericaris* (not a seta, as wrongly reported in Bruno *et al.*, 2017, pag. 272). Our recent molecular and morphological analyses (Bruno *et al.* 2020) confirmed that the genera *Cottarellicaris* and *Stammericaris*, belonging respectively to the two subfamilies Parastenocaridinae and Fontinalicaridinae, are well-defined and valid genera, as they form two monophyletic and distinct clades in the phylogenetic analysis based on the mitochondrial COI and ribosomal 18S sequences.

In this work, we therefore aim to: 1) describe and discuss *Stammericaris remotaepatriae* **sp. nov.**, the first recorded species of *Stammericaris* for the Nearctic subregion; 2) propose and justify the transfer of *Parastenocaris palmerae* Reid, 1992 to *Stammericaris* as *S. palmerae* (Reid, 1992) **comb. nov.**, a hyporheic species known from the sandy bed of Goose Creek, a stream in northern Virginia (Reid 1992); 3) review the uncertain taxonomic status and affinities of *Parastenocaris trichelata* Reid, 1995, a second species from Goose Creek (Reid 1995), related to *S. remotaepatriae* **sp. nov.** and *S. palmerae* **comb. nov.**; 4) discuss the affinities and taxonomic position of *Parastenocaris* sp. 1 and *Parastenocaris* sp. 3, collected from the hyporheic habitat of a creek in southeastern New York State by Strayer (1988); 5) underline the faunistic and biogeographic relevance of these new representatives of the interstitial harpacticoid fauna of North America, and their ecological peculiarities.

## Materials and methods

Specimens were collected using the Karaman-Chappuis method (Delamare-Deboutteville 1960), by filtering the water from holes dug in sandy soil. Samples were fixed in 5% buffered formalin solution, sorted in the laboratory and mounted in Faure's medium under a stereoscope. Illustrations were made at different magnifications up to a maximum of 1250 x, using drawing tubes mounted on a Zeiss Axioskop® phase-contrast microscope and a Polyvar Reichert-Jung® interferential-contrast microscope. Specimens of the type series are deposited at La Specola Museum of Natural History, Zoology Section Florence, Italy (MZUF).

The following abbreviations are used throughout the text and figures: enp: endopod; exp: exopod; A1: antennule; A2: antenna; ae = aesthetasc; enp = endopod; exp = exopod; mdb = mandible; mx1 = maxillule; mx2 = maxilla; mxp = maxilliped; P1–P5 = first to fifth pereopod; P6 = rudimentary sixth pereopod. The nomenclature and descriptive terminology follow Huys and Boxshall (1991), terminology and homologisation of maxillary and maxillipedal structures follow Ferrari and Ivanenko (2008).

## Taxonomy

### Family Parastenocarididae Chappuis, 1940

#### Subfamily Parastenocaridinae Chappuis, 1940

#### Genus *Stammericaris* Jakobi, 1972

**Type species.** *Stammericaris stammeri stammeri* (Chappuis, 1937).

**Other species.** *Stammericaris acherusia* (Noodt, 1954); *Stammericaris amyclaea* (Cottarelli, 1969); *Stammericaris destillans* Bruno & Cottarelli 2017; *Stammericaris diversitatis* (Cottarelli & Bruno 2012); *Stammericaris lorenzae* (Pesce, Galassi & Cottarelli, 1995); *Stammericaris orcina* (Chappuis, 1938); *Stammericaris pasquinii* (Cottarelli, 1972); *Stammericaris phreatica* (Chappuis, 1936); *Stammericaris trinacriae* (Pesce, Galassi & Cottarelli, 1988); *Stammericaris vincentimariae* Bruno & Cottarelli, 2020.

***Stammericaris remotaepatriae* sp. nov.**

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(Figs. 1–4)

**Type locality.** Interstitial habitat on a sandy beach, Abrams's Point, near the mouth of the Abrams Creek, Nantucket Island, MA; USA. Approximate coordinates: 41°17'44.48" N, 70°03'46.43" W.

**Type material.** Holotype: undissected male mounted on slide labelled "*Stammericaris remotaepatriae* holotype, male, Nantucket, MA, USA, 20/III/1981" (MZUF 665). Paratypes: three undissected males, mounted each on one slide labelled: "*Stammericaris remotaepatriae* paratype, male, Nantucket, MA, USA, 20/III/1981" (MZUF 666, 667, 668); three undissected females mounted each on one slide labelled: "*Stammericaris remotaepatriae* paratype, female, Nantucket, MA, USA, 20/III/1981" (MZUF 669, 670, 671). All material collected by Prof. Roberto Argano (Biology and Biotechnology Department "Charles Darwin", Sapienza University of Rome).

**Diagnosis.** The male of *Stammericaris remotaepatriae* is characterized by: i) P1: lamellar hook with a curved tip on the outer margin of the basis; ii) P3: exp-1 with two rows of two spinules on the inner margin; endopod represented by a thin seta; iii) P4: inner margin of basis with only one strong spinule; exp-1 enlarged and strongly curved inwards, enp a curved plate with tip deeply incised (bifid) instead of pointy. The female of *Stammericaris remotaepatriae* Bruno and Cottarelli **sp. nov.** is characterized by: i) genital field: broader than long, occupying anterior ventral 1/3 of genital double-somite; ii) P3: enp spiniform and shorter than the corresponding exp-1; iii) P4: enp represented by a short cylindrical segment with 3–4 spinules and one spiniform apical setula. Both sexes are characterized by caudal rami shorter than last urosomite; the P5 is slightly dimorphic, being larger in the females, and with a stronger inner spiniform process.

**Etymology.** The species epithet is the genitive of the Latin adjective *remota* (meaning "distant, far"), and the name *patria* (meaning "country, land"); it refers to the collection of the new species in a land distant from the core of diversity of the genus, i.e., Europe. The epithet also refers to the name of the island Nantucket, where the species was collected which, according to some scholars, is a name derived from the Algonquian (a widespread North American native language) name for the island, possibly meaning "faraway land or island".

**Description.** Adult male. Body unpigmented, nauplius eye absent. Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae) from 398 to 430 µm, mean 407 µm (n = 4). Habitus (Fig. 1A) cylindrical and slender, without any demarcation between prosome and urosome; prosome/urosome = 0.78. Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodistal membranes. Integument weakly sclerotized, without cuticular pits, ornamented with sensilla on all somites except preanal one. Sensillar pattern as in Fig. 1A. Cephalothorax with rounded dorsal integumental window (Fig. 1A), urosomites 2–5 with dorsal elliptical integumental window of different sizes: smallest window on urosomite 3, largest on urosomite 5 (Fig. 1A). Anal somite (Figs 1A, 2A) with pair of large dorsal sensilla at base of anal operculum, anal sinus wide open, with two diagonal rows of small proctodeal spines. Anal operculum (Fig. 2A) well-developed, with convex distal margin, transverse row of ventral spinules discernible through transparent operculum.

Caudal rami (Figs. 1A, 2A). Diverging, approximately cylindrical, tapering distally, shorter than anal somite, anal somite length/caudal ramus length = 1.76; length/width = 2.0; small pore on outer surface, above seta IV. Anterolateral accessory seta (I) slightly longer than anterolateral seta (II), posterolateral seta (III) short, all setae inserted together distally at 3/4 length of caudal ramus. Outer terminal seta (IV) long and unipinnate (length seta/length caudal rami = 1.2), inserted subapically; inner terminal seta (V) without fracture plane. Terminal accessory seta (VI) short (length seta/length caudal ramus = 0.7) and bare. Dorsal seta (VII) bare, articulated, inserted distally at 3/4 length of the caudal ramus.

Rostrum (marked with asterisk in Fig. 1B) small, not demarcated at base, almost reaching distal margin of first antennular segment, ornamented with two dorsal sensilla.

A1 (Figs 1B, 1C). Prehensile, eight-segmented; seventh segment sickle-shaped, folded back onto the fifth segment, with eighth segment pointing medially, i.e., pocket-knife type *sensu* Schminke (2010). First segment short and bare; second segment longest, with nine setae, longest seta unipinnate; third segment with four distal bare setae; fourth segment reduced to small sclerite with one seta. Fifth segment enlarged with inner triangular expansion (arrowed in Fig. 1B), distal tubercle with one basal short seta, two long subequal distal setae and large apical aesthetasc, reaching distal margin of eighth segment. Sixth segment bare, small and cylindrical, partially fused to previous one. Seventh segment bare, sickle-shaped, with distal anterior corner protruding as curved apophysis ending in tip

(arrowed in Fig. 1C). Eight segment with eight setae and apical acrothek represented by one seta and slender long aesthetasc. Armature formula: 1-[0], 2-[1 uniplumose + 8 bare], 3-[4 bare], 4-[1 bare], 5-[2 bare +(1+ ae)], 6-[0], 7-[0], 8-[8 bare + (1 bare + ae)].

A2 (Fig. 1D). Coxa unarmed; allobasis with two abexopodal transverse row of spinules. Exp represented by small segment merged with allobasis, with bipinnate apical seta. Enp bearing along inner margin from proximal to distal: two spinules, two bare and one unipinnate spines of the same length; apically: two geniculate, two spiniform, and one transformed setae of different lengths, the transformed seta is smooth in the first half, curved and one-side pinnate in the second half. Some long and thin spinules along the distal margin, near the insertions of apical setae.

Mandible (Fig. 1E): coxal gnathobase with lateral pinnate short seta, cutting edge with apical teeth. Palp one-segmented, with two distal setae of subequal lengths.

Maxillule (Fig. 1F): praecoxal arthrite with three apical curved robust spines apically denticled, one lateral curved seta. Coxal endite long, with apical pinnate seta. Basis cylindrical, with two distal bipinnate setae of subequal lengths. Endopod and exopod absent (fused to basis without trace).

Maxilla (Fig. 1G): syncoxa with two endites, proximal endite short, with one seta; distal endite cylindrical, armed apically with two subequal thin bare setae and one transformed, leaf-like pinnate seta; proximal endopodal segment drawn into apical unipinnate claw; vestige of distal endopod represented by two long setae of equal length.

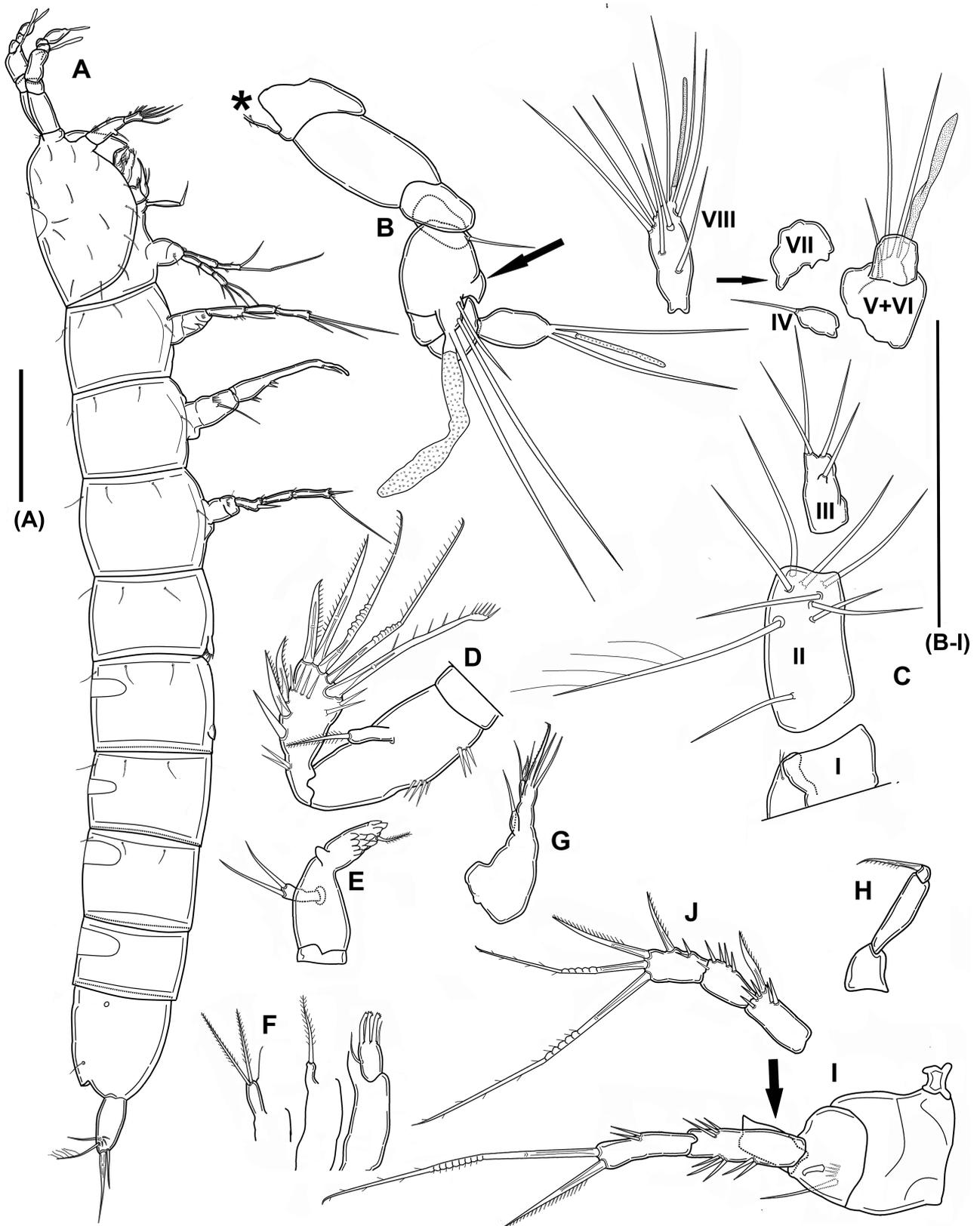
Maxilliped (Fig. 1H): prehensile. Syncoxa small and unarmed; basis slim and elongate, unarmed; endopod represented by distally unipinnate claw.

P1 (Figs 1I, 1J). With smooth and small intercoxal sclerite; coxa bare. Basis large, armed with single slender seta and row of four spinules on outer margin, and lamellar, apically-curved hook on inner margin near enp insertion. Exp three-segmented, slightly shorter than enp; exp-1 with thin unipinnate spine on outer distal corner; exp-2 shortest and unarmed; exp-3 with two apical geniculate setae, bipinnate in the distal half, one spiniform unipinnate apical seta, one subapical unipinnate spiniform seta. Enp two-segmented; enp-1 as long as first two segments of corresponding exp, with one distal row of spinules on inner margin and two rows of spinules on outer margin; enp-2 shorter and thinner than enp-1, with two spinules at 2/3 of inner margin; apical margin with long geniculate bipinnate seta and shorter unipinnate spiniform seta.

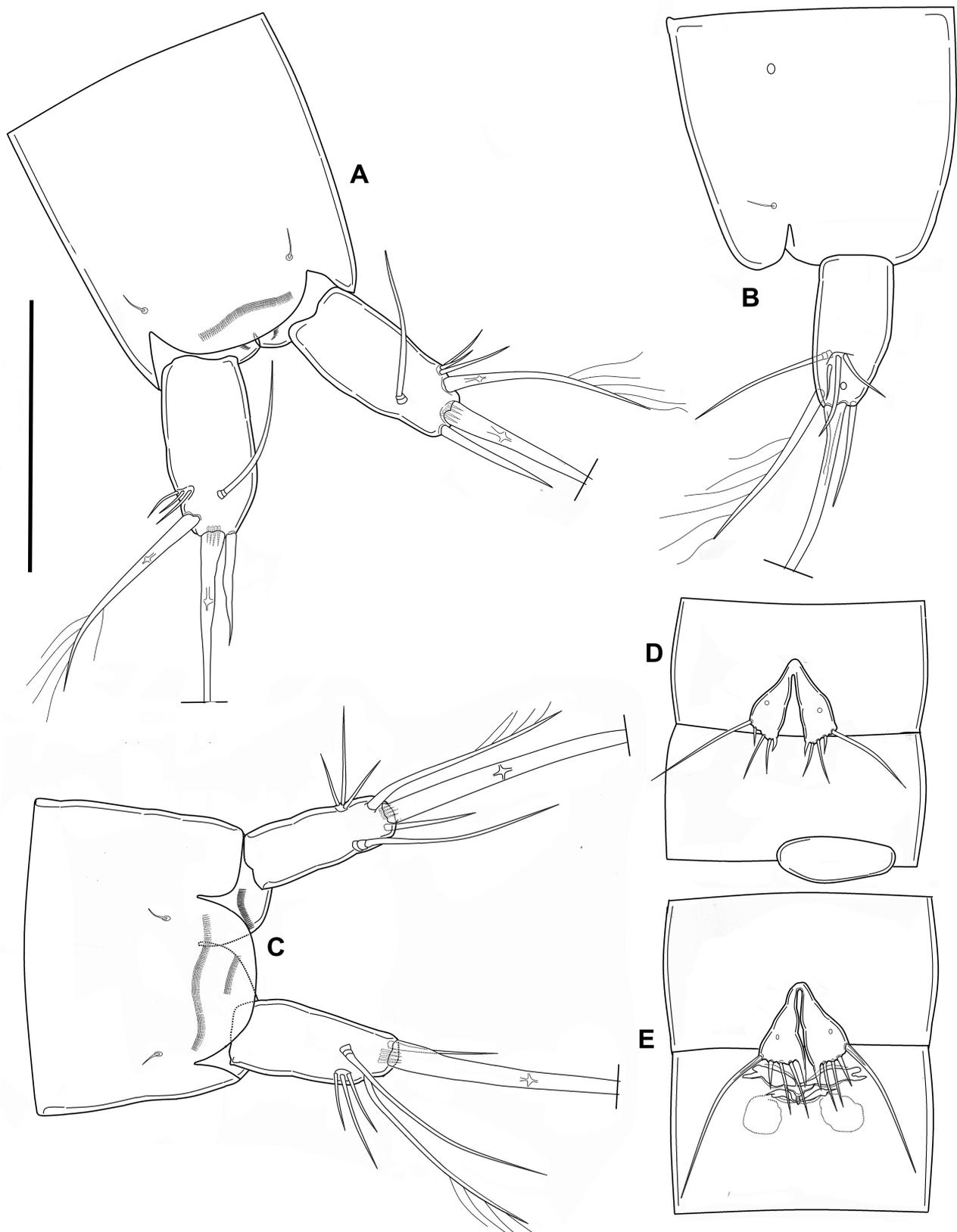
P2 (Fig. 3A). Quadrangular and smooth intercoxal sclerite with concave distal margin. Coxa smooth. Basis unarmed, with row of five spinules and small pore on outer margin. Exp three-segmented, exp-1 longest, with transversal row of spinules at 1/3 of the outer margin, two longitudinal spinules proximal to strong distolateral bipinnate spine. Second and third segments of same length, exp-2 unarmed, with distal row of spinules; exp-3 with inner hyaline frill, armed with subapical outer bipinnate spiniform seta, apical bipinnate seta and bipinnate spiniform seta; ornamented with distal row of spinules. Enp one-segmented, slightly longer than half length of corresponding exp-1, cylindrical, with bare apical seta about as long as half of the segment, and three apical spinules.

P3 (Fig. 3B). Intercoxal sclerite narrow and long, trapezoidal, unornamented, with concave distal margin. Coxa smooth. Basis robust, with long, slender, smooth outer seta, transverse spinular row and row of chitinous denticles along the inner margin; pore at midlength of the segment on the dorsal surface. Enp reduced to short and thin seta. Exp-1 distally slender, two groups of two spinules each (distalmost being largest) on the outer margin in the first 1/2 of the segment; rounded tubercle (arrowed in Fig. 3B) on the inner margin, approximately at 1/3 of the segment. Exp-2 fused with exp-1, without ornamentation, prolonged into long finger-like apophysis, slightly bent inwards, with rounded tip. Distal thumb represented by a leaf-like, thin and pointed process, reaching to half-length of the apophysis.

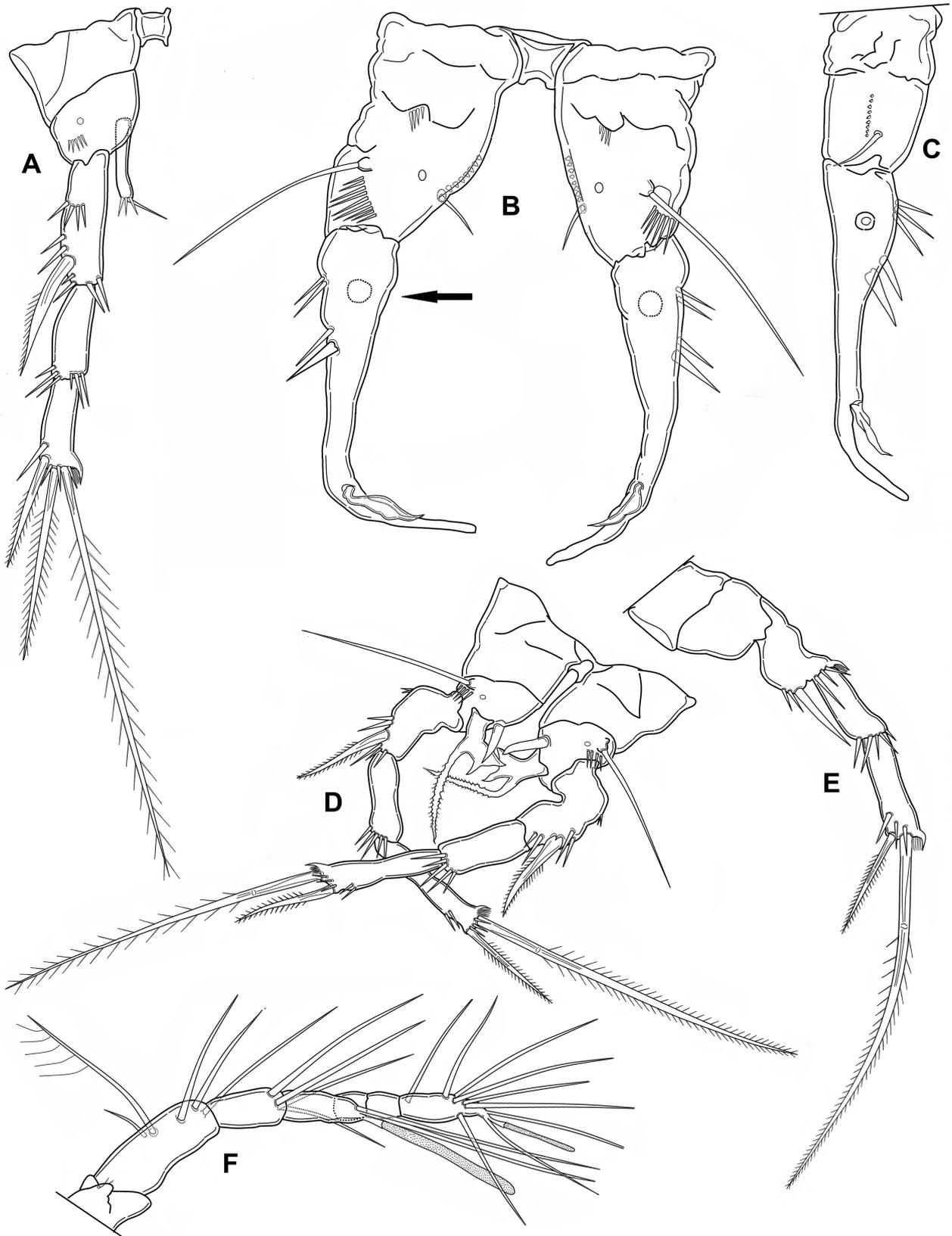
P4 (Figs 3D, 3E). Intercoxal sclerite smaller than in P1– P3, with concave, smooth distal margin. Coxa smooth. Basis armed with single slender seta on outer margin; ornamented with row of spinules at base of outer seta and pore, with large, inwardly-curved spinule on the inner margin. Exp three-segmented, first segment strongest, third longest; exp-1 enlarged, strongly bent inwards (unusual shape for the genus), armed with outer distal unipinnate spiniform seta and inner hyaline frill; with transversal row of two spinules at 1/3 of outer margin and below insertion of spiniform seta, and with spinular row along distal margin. Exp-2 unarmed, with row of five spinules along outer distal margin; exp-3 armed with outer unipinnate spiniform seta and long apical bipinnate seta, spiniform seta less than 1/3 the length of seta; ornamentation represented by row of apical spinules, row of spinules along distal outer margin, and inner hyaline frill. Enp one-segmented, slightly longer than 1/2 the length of the corresponding exp-1, represented by plate curved inwards in an almost L-shape, with strongly bifid tip; enp with long spiniform and denticled outgrowth on outer border, reaching almost to the end of corresponding exp-2.



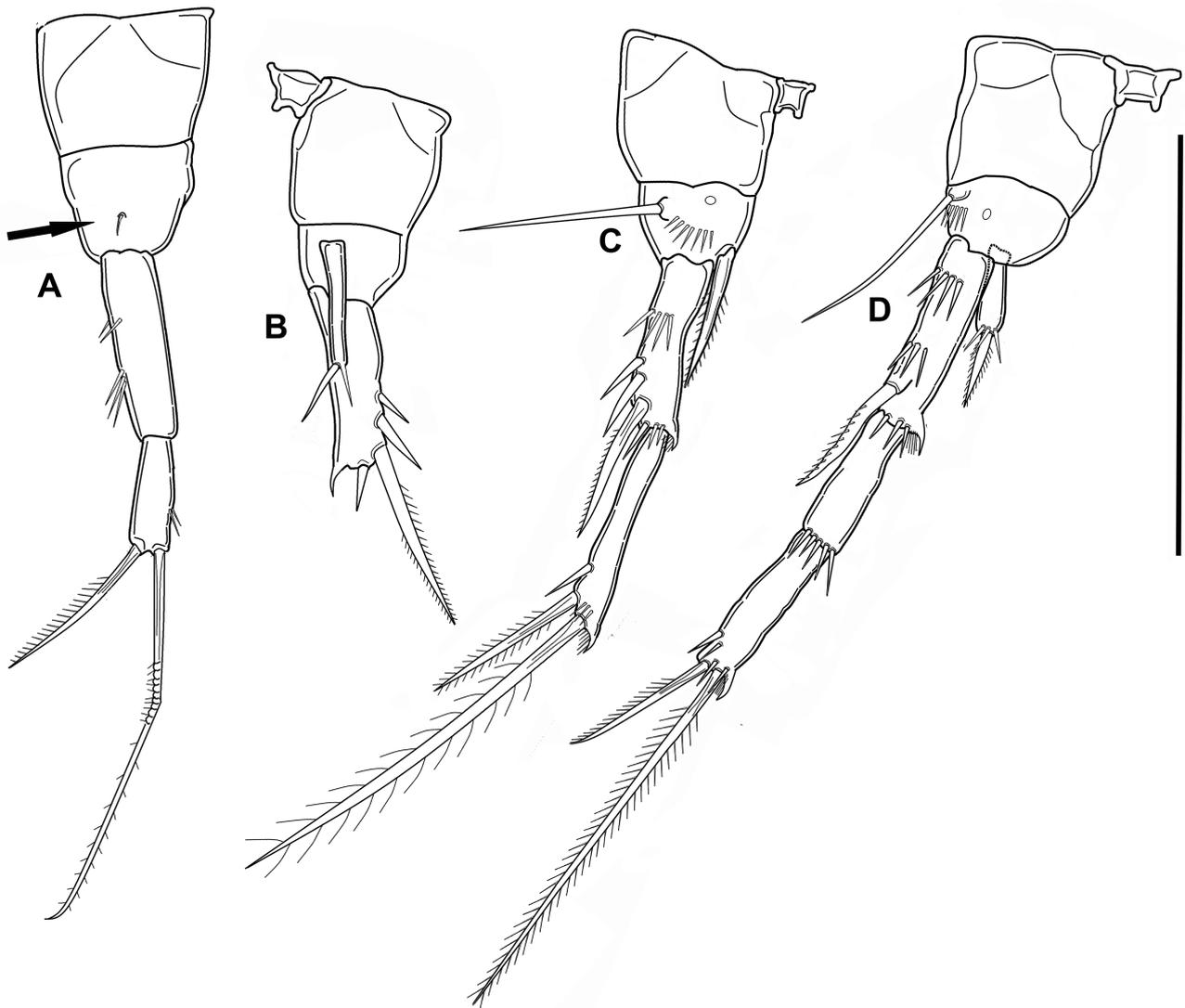
**FIGURE 1.** *Stammericaris remotaepatriae* sp. nov., male. A, habitus, lateral view (MZUF 666); B, rostrum marked with asterisk and antennule, schematic (MZUF 667); C, antennule, disarticulated (antennular segments marked with Roman numerals) (MZUF 665); D, antenna (MZUF 665); E, mandible (MZUF 665); F, maxillule, disarticulated (MZUF 665); G, maxilla (MZUF 665); H, maxilliped (MZUF 665); I, P1 coxa, basis and endopod, inner view (MZUF 665); J, P1 exopod, inner view (MZUF 665). Scale bar: 50 micrometers.



**FIGURE 2.** *Stammericaris remotaepatriae* sp. nov. A, male, anal somite, anal operculum and caudal rami, dorsal view (MZUF 665); B, female, anal somite, anal operculum and caudal rami, lateral outer view (MZUF 669); C, female, anal somite, anal operculum and caudal rami, dorsal view (MZUF 671); D, male, P5, P6, first and second urosomites, ventral view (MZUF 665); E, female, P5, P6, genital double-somite and genital field, ventral view (MZUF 671). Scale bar: 50 micrometers.



**FIGURE 3.** *Stammericaris remotaepatriae* sp. nov. A, male, P2 (MZUF 665); B, male, P3 (MZUF 665); C, male, P3 (variability) (MZUF 668); D, male, P4 (MZUF 665); E, male, P4 coxa, basis, exopod, outer view (MZUF 666); F, female, antennule (MZUF 669). Scale bar: 50 micrometers.



**FIGURE 4.** *Stammericaris remotaepatriae* sp. nov., female (MZUF 671). A, P1 coxa, basis and endopod, inner view; B, P2 intercoxal sclerite, coxa, basis, endopod; C, P3, D, P4. Scale bar: 50 micrometers.

P5 (Fig. 2D). Pair of P5 fused to intercoxal sclerite; represented by two trapezoidal cuticular plates with proximal pore and long basipodal seta. Armature on free distal margin, from inner to outer: three bare setae, outermost very short and spiniform, remaining two subequal. One spiniform slightly curved process on inner distal corner.

P6 (Fig. 2D). Vestigial, fused into simple cuticular asymmetrical oval plate, unornamented and unarmed.

Adult female. Habitus. Cylindrical, slender, without any demarcation between prosome and urosome. Body length, excluding caudal setae, 418 and 410  $\mu\text{m}$  ( $n=2$ ). Free pedigerous somites without any lateral or dorsal expansions, all connected by well-developed arthrodistal membranes. Cephalothorax and urosomites 2–4 with dorsal elliptical integumental window of different sizes, largest one on genital double somite. Ornamentation of cephalothorax, somites, pigmentation and lack of nauplius eye as in male, except genital and first urosomite fused into double-somite. Prosome/urosome = 0.80. Genital double-somite (Fig. 2E) without any trace of subdivision. Genital field (Fig. 2E) broader than long, occupying anterior ventral  $\frac{1}{3}$  of genital double-somite; single genital aperture covered by fused vestigial sixth legs; copulatory pore located medially at proximal third of double-somite. Anal operculum and anal sinus (Figs 2B, 2C) as in male.

Caudal rami (Figs 2B, 2C). Shape, ornamentation and armature similar to those of male, length/width ratio: 2.5.

Mouthparts, rostrum (Fig. 3F), A2 as in male.

A1 (Fig. 3F). Seven-segmented, aesthetasc on fourth segment, as long as in male but proportionally thinner,

reaching beyond seventh segment. First segment bare, second segment longest. Apical acrothek represented by two setae of subequal lengths and slender aesthetasc. Armature formula: 1-[0], 2-[1 pinnate + 4 bare], 3-[4 bare], 4-[2 bare + ae], 5-[0], 6-[0], 7-[7 bare + (2 bare + ae)].

P1 (Fig. 4A). Intercoxal sclerite and coxa as in male. Basis as in male, but with small inner spiniform seta instead than lamellar hook (arrowed in Fig. 4A); exp and enp similar to those of male.

P2. Intercoxal sclerite, coxa, basis and exp as in male. Enp (Fig. 4B) similar in shape to that of male, but with apical seta and only one distal spinule.

P3 (Fig. 4C). Intercoxal sclerite small, trapezoidal, with concave margin, bare. Coxa bare. Basis armed with single seta, pore and outer spinular row; exp two-segmented: exp-1 shorter and larger than exp-2, with outer distal curved unipinnate spiniform seta and two subdistal spinules, transversal spinular row at  $\frac{1}{3}$  of outer margin and along distal margin, hyaline frill on inner distal corner. Exp-2 with subapical outer unipinnate spiniform seta and longer apical bipinnate seta, subdistal outer spinule, apical spinular row and hyaline frill on inner distal corner. Enp represented by a pointed and bipinnate segment, slightly shorter than the corresponding exp-1.

P4 (Fig. 4D). Intercoxal sclerite and coxa as in male. Basis as in male but without strong spinule on inner margin. Exp-1 straight (not enlarged and bent as it occurs in male), slightly longer than exp-2 and exp-3; with distolateral curved unipinnate spiniform seta and two transversal rows of spinules at  $\frac{1}{3}$  and  $\frac{2}{3}$  of outer margin, distal spinular row, hyaline frill on inner distal corner. Exp-2 with distal spinular row; exp-3 with apical outer unipinnate spiniform seta and longer apical bipinnate seta, with distal spinule on outer margin, apical spinular row and hyaline frill on inner distal corner. Enp represented by thin club-shaped segment shorter than  $\frac{1}{2}$  the length of the corresponding exp-1, ending in spiniform seta with spinules around insertion.

P5 (Fig. 2E). Both legs fused to intercoxal sclerite, represented by cuticular plate with pore; trapezoidal, larger and more elongated than in male, with inner spiniform process stronger than in male, remaining ornamentation as in male but proportionally longer.

P6 (Fig. 2E). Vestigial, fused into simple cuticular plate, covering gonopore, unornamented and unarmed.

Variability. One male paratype (MZUF 668) with proximal row of three spinules on outer margin of P3 Exp-1 (Fig. 3C).

## Discussion

**Taxonomic definition and affinities of the new species.** To properly discuss the taxonomy and affinities of the new species described herein, we examined the drawings and descriptions of other species of *Stammericaris* available in the literature. Additionally, we examined specimens of the following taxa from our collection: *S. amyclaea*, *S. destillans*, *S. diversitatis*, *S. lorenzae*, *S. orcina*, *S. pasquini*, *S. trinacriae*, *S. vincentimariae*, *Stammericaris* sp. 1 (Trento, Northern Italy, unpublished), *Stammericaris* sp. 2 (Siracusa, Sicily, Italy, in preparation), *Stammericaris* sp. 2 (Egridir Lake, Turkey, unpublished). We also examined the published data on other Parastenocarididae, which can be related to the new species (see below).

*Stammericaris remotaepatriae* **sp. nov.** fits fairly well with the emended description of the genus (Bruno *et al.* 2017; but see also Schminke 2013). The male antennule is of the “pocket-knife” type and the basis of P1 has an inner thin seta in females and a hook in males. The outer margin of male P3 exp-1 in males has two groups of two spinules, the distal ones being stronger; all spinules are inserted in the first  $\frac{1}{2}$  of the exp-1; the male P3 apophysis is about twice as long as the thumb. The male P4, being perhaps the most important diagnostic feature of some genera of Parastenocarididae (Bruno *et al.* 2020), is conservative in its general structure, but shows some intergeneric variability, and characterizes the different species. In *S. remotaepatriae* **sp. nov.**, the male P4 endopod fits with the emended diagnosis of Bruno *et al.* (2017): “P4 male endopod a curved plate with a pointed inner tip carrying at its outer border two outgrowths, in most cases the distal one is a feathered or plain seta”, but in *S. remotaepatriae* **sp. nov.**, the curved plate tip is strongly bifid rather than pointy, and the proximal outgrowth of the distal margin is not present. The generic typical endopod structure with a bifid tip, albeit smaller than in *S. remotaepatriae* **sp. nov.**, is also present in some other species of the genus (i.e., *S. diversitatis* and *S. vincentimariae*); the P4 endopod is simplified, lacking the proximal outgrowth on the distal margin in *S. orcina* and in the new species. The P4 basis in *S. remotaepatriae* **sp. nov.** carries only one strong spinule on the inner margin, a rare condition in the genus, which we have so far recorded only in *Stammericaris* sp. 3 from lake Egridir. The morphology of the male P4 exp-1, which

is strongly bent inwards, and much larger than the other segments, is a peculiar character, which is not diagnostic for the genus *Stammericaris*. This peculiar morphology is present in other Parastenocarididae such as, for instance, *Parastenocaris brevipes* Kessler 1913, as reported in Reid (1995), *P. biwae* Miura 1969, *P. koreana* Karanovic and Lee 2012, and in a new genus of Parastenocarididae from Thailand we are presently studying. Apparently, this character has evolved independently in taxa phylogenetically unrelated, and therefore we consider it an autapomorphy for *S. remotaepatriae* **sp. nov.** Similarly, the reduced length of the caudal rami of the new species (shorter than the anal somite), differs from the character which is diagnostic for the genus: “Caudal rami cylindrical almost as long as anal somite, group of lateral setae located at end of rami” (Bruno *et al.* 2017). Also in this case, the reduced length of the caudal rami does not preclude the attribution to the genus *Stammericaris*, because the insertion of the setae I-III and VII corresponds to the diagnostic position, and the caudal rami are shorter than the anal somite also in other species of the genus (specifically, *S. phreatica* and *S. lorenzae*). This character is present also in the females, which, however, display all the remaining diagnostic features of the genus.

The affinities of the new species with the 11 known Palearctic species of *Stammericaris* can be supported by the following morphological features: i) male antennule of the “pocket-knife” type; this peculiar morphology is present in all the species described recently but it is not described in the oldest papers, probably because it was overlooked (Bruno and Cottarelli 2017); ii) cuticular windows on the cephalothorax and urosomites of both sexes are present in the new species and in *S. diversitatis*, *S. lorenzae*, *S. trinacriae*, *S. destillans*, *Stammericaris* sp. 3; all windows are missing in *S. vincentimariae*, *S. pasquinii*, *S. orcina*, *S. amyclaea*, *Stammericaris* sp. 1 and sp.2. Cuticular windows also are apparently lacking in *S. acherusia*, *S. stammeri*, *S. phreatica*, but this feature might have been overlooked in the older descriptions; iii) the P1 basis carries one hook in the male and one seta in the female; this condition is present also in *S. destillans* and *S. trinacriae*; in the other species of the genus the male carries one hook and one seta, and the female only one seta, which therefore is the most common condition in the genus; there is only one small seta in both sexes in *S. lorenzae* (however, the basal ornamentation was probably not recorded or drawn in some of the earlier descriptions); iv) outer margin of male P3 exp-1 with two rows of spinules inserted in the first ½ of the segment, while in the other species the distal row is inserted in the second ½ of the segment, except in *S. destillans*, which has spinules only proximally, and in *S. trinacriae*, which does not have spinules; v) male P3 apophysis long, with a rounded tip curved inwards, twice as long as the thumb or even longer in the new species and all the other species of the genus except *S. stammeri*, where the apophysis is as long as the thumb; vi) inner row of curved spinules on the male P4 basis decreasing in size laterally: there are three spinules in *S. diversitatis*, *S. trinacriae*, *S. lorenzae*, *S. pasquinii*, *S. amyclaea*, *S. stammeri*, *Stammericaris* sp. 1; four in *S. orcina*, *S. phreatica*; two in *S. destillans* and *S. vincentimariae* and *Stammericaris* sp. 2, only one strong spinule in *S. remotaepatriae* **sp. nov.** and *S. acherusia*, and only one thin spinule in *Stammericaris* sp. 3; vii) the male P4 endopod is typically a curved plate, which is strongly bifid in the new species and, in a lesser extent, in *S. diversitatis* and *S. vincentimariae*; the inner tip not is bifid but pointed in the remaining species of *Stammericaris*. Only in *S. destillans* and *Stammericaris* sp. 2, the enp is a cylindrical element distally enlarged in three pointed protrusions, the middle one strongest and apically curved outwards.

*Stammericaris remotaepatriae* **sp. nov.** is therefore characterized by a set of features (e.g., P4-exp1 and P4 enp in males, caudal rami in both sexes); the remaining characters are shared but differently distributed among all other species of *Stammericaris* and, as a consequence, it is not possible to define convincing affinities between the new species and the Palearctic *Stammericaris*, which are “scattered around the Mediterranean” (Schminke 2013). On the contrary, we detected some affinities with other North American Parastenocarididae. *Parastenocaris palmerae* is, in our opinion, the taxon with strongest affinities to *S. remotaepatriae* **sp. nov.** In fact, the analysis of the drawings and description provided by Reid (1992) show that *P. palmerae* and *S. remotaepatriae* **sp. nov.** share the following features: i) cuticular windows are present on the cephalothorax and urosomites in both sexes; ii) female P3 enp of similar morphology; iii) male P3 very similar: the basis is ornamented with a row of chitinous denticles (*S. remotaepatriae* **sp. nov.**) or “proximally directed spines” (*P. palmerae*) along the inner margin, two rows of spinules inserted in the first ½ of the outer margin of exp-1; the endopod reduced to a small seta in both species; iv) male P4: in both species, the basis carries only one strong and slightly curved spine; the exp-1 is enlarged, strongly bent inwards in *S. remotaepatriae* **sp. nov.**, the same segment is slightly enlarged and curved in *P. palmerae*; v) the P5 of both sexes have similar shape and armature; vii) the caudal rami of both sexes have almost identical shape, size and position of the setae. The differences between the two species are the following: i) the dorsal body surface of *P. palmerae* is pitted; this feature is not present in any *Stammericaris*, including the new species; pits of varying depth

and density are present (convergence?) rather randomly within the family in genera which are either phylogenetically close to *Stammericaris*, such as *Cottarellicaris luciae* (Cottarelli Bruno and Berera 2008), or more distant, such as *Kinnecaris variolata* (Chappuis 1952), *Monodicaris cristiani* (Dumont 1981), *Remaneicaris ignotus* (Dussart 1983), *Parastenocaris jane* Karanovic 2006; ii) based on the drawings and the synthetic description provided by Reid (1992), the male antennule of *P. palmerae* is not of the “pocket-knife” type *sensu* Schminke (2010). However, this feature was not described in the older descriptions of species of Parastenocarididae, either because this feature was not taken into account, or because the A1 was not properly oriented (see discussion on this issue in Bruno and Cottarelli 2015); iii) in *P. palmerae*, the inner margin of the P1 basis is without ornamentation in both sexes (this feature might have been overlooked for similar reasons as those listed for the A1 in the earlier descriptions); iv) in *P. palmerae*, the distal seta of the P4-enp of females is fused to the endopod which ends with a spiniform seta in *S. remotaepatriae* **sp. nov.**; v) the male P4-enp of *P. palmerae* is different and more complex than that of *S. remotaepatriae* **sp. nov.** However, a closer examination allows to relate the enp of *P. palmerae* to that of *S. remotaepatriae* **sp. nov.** and of the other *Stammericaris*, since the base structure is the same in the two species: in *Stammericaris*, as already mentioned, the enp is “a curved plate with a pointed inner tip carrying at its outer border two outgrowths, in most cases the distal one is a feathered or plain seta”. In *S. remotaepatriae* the inner tip is bifid, i.e., split into two pointed processes of the same size; in *P. palmerae* the inner tip is split into two pointed inner processes, with a third, small, proximal pointed process; the remaining of the endopod is represented by one long apical process and two further outgrowths on the outer margin. Hence, according to us, the differences can be reduced to the inner tip being divided into three processes (*P. palmerae*) or two (*S. remotaepatriae* **sp. nov.** and most *Stammericaris*, see also Bruno *et al.* 2017) or not split.

**Taxonomic position of some other North American Parastenocarididae.** In the original description, Reid (1991) assigned *Parastenocaris palmerae* to the *brevipes*-group of Lang (1948). Later on, the same author (Reid 1995) remarks how *P. palmerae* belongs to the group of North American *Parastenocaris* that have been loosely considered members of the *brevipes*-group, but which do not belong there. In fact, *P. palmerae* could be considered a member of such species-group based on the structure of the male P4 endopod complex and the long and spinulate female P4 endopod, but other characters (short genital field, male P3, caudal rami setation) are not compatible with the group. Schminke (2013) reinforces this view, criticizing the position of *P. palmerae* in a cluster with other species of the *brevipes*-group in the cladistic analysis of Karanovic and Lee (2012), as not supported by a single clear synapomorphy. In the same paper, Schminke (2013) states that the structure of the male P4 endopod in *P. palmerae* is more complicated than in *Stammericaris*, but could be viewed as a precursor of the condition of *Stammericaris*, where the transformation to a simpler structure could have taken place, and as a consequence also “the setation of the caudal rami of *P. palmerae* would fit better with *Stammericaris* than with the *brevipes*-group”. Schminke (2013) concluded that *P. palmerae* may belong in the vicinity of *Stammericaris* and *Cottarellicaris* Schminke 2013. Corgosinho *et al.* (2017) further reinforced this view, stating that the presence of a seta or lamella inserted distally on the proximally-bifurcated male P4 endopod is a synapomorphy shared by *Stammericaris* and *Cottarellicaris*, but also by *Parastenocaris palmerae*. Corgosinho *et al.* (2017) also agree with Schminke’s (2013) rejection of Karanovic and Lee’s (2012) phylogeny, and the suggestion to remove *P. palmerae* from *Parastenocaris*, based also on the length of the female P4 enp and the caudal rami shape and setation. As a result of the discovery of *S. remotaepatriae* **sp. nov.**, which proves the presence of the genus *Stammericaris* in North America, based on the affinities of *S. remotaepatriae* **sp. nov.** with *P. palmerae*, and in agreement with the remarks of the above-mentioned authors, we deem justified the transfer of *Parastenocaris palmerae* to *Stammericaris* as *Stammericaris palmerae* (Reid, 1992) **comb. nov.**

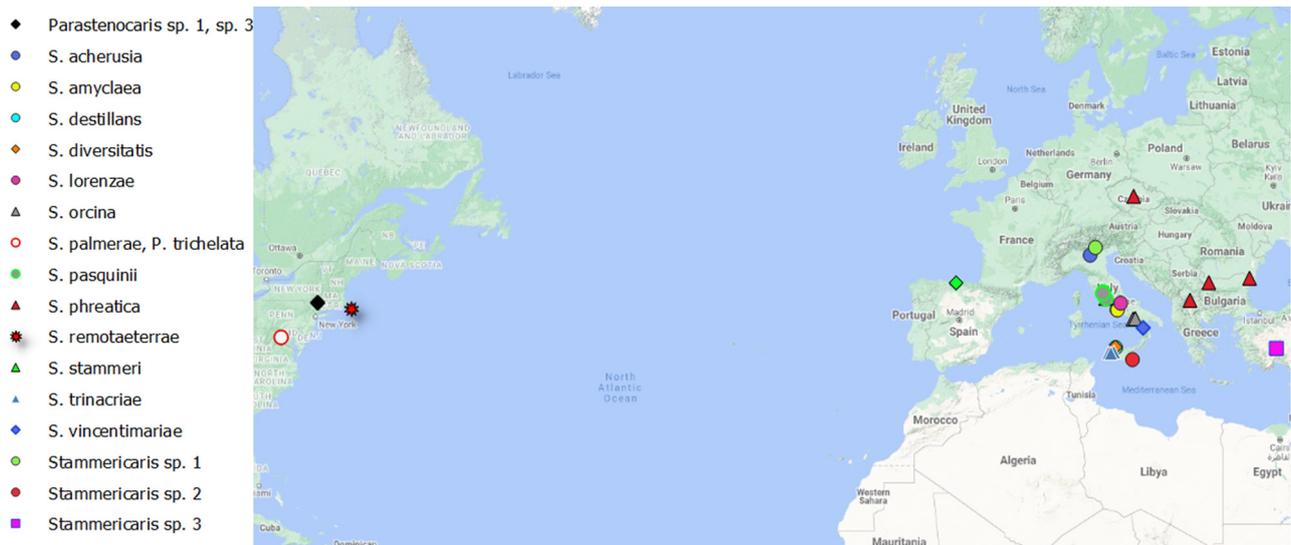
*Parastenocaris trichelata* is a second species of Parastenocaridinae which could be related to *S. remotaepatriae* **sp. nov.** and *S. palmerae* **comb. nov.** In fact, this taxon has windows on the urosomites (but not on the cephalothorax), the male A1 is of the “pocket-knife” type, the P1 basis carries a sclerotized and hooked inner spine in the male and a small seta in the female; the P2 endopod of both sexes, the endopod of P3 and P4, and the P5 of the female are compatible with the generic diagnosis. Moreover, the male P3 of *P. trichelata* is very similar to those of *S. remotaepatriae* **sp. nov.** and *S. palmerae* **comb. nov.**, although the P5 differs. However, in *P. trichelata* the male P4 endopod complex consists of three sclerotized claws and a slender hyaline unsegmented endopodite, longer than claws and inserted posteriorly to them (Reid, 1995). Such structure of the endopod complex is not compatible with the attribution of *P. trichelata* to *Stammericaris*, because it does not correspond to the main apomorphy of the genus (i.e., the presence of the spiniform process with a proximal bifurcation inserted distally on the endopod). Regarding

the presence of other shared characters, "Many of the characteristic features of *Stammericaris* are not exclusive of this genus, but are shared as characters that identify other genera of Parastenocaridinae, such as the pocket-knife type male antennule" (Bruno *et al.* 2017). This is not surprising, considering that convergence phenomena are frequent in the different lineages of this subfamily (Bruno *et al.* 2017). Furthermore, all the above-mentioned characters, male P4 endopod complex included, do not allow the inclusion of *P. palmerae* in the genus *Parastenocaris* as redefined by Reid (1995). Reid (1995) suggested that the species could have been included in the *minuta*-group of Lang (1948). However, this group was split by Jakobi (1972) into several genera, some of which were recently reviewed and confirmed (such as *Stammericaris*), others such as *Minutacaris* Jakobi 1972 still need to be revised. As a consequence, *P. trichelata* should be considered a *species inquirenda*, pending a proper revision of the genera (*Stammericaris* excluded, for the reasons listed above) deriving from the *minuta* group.

In a paper on cyclopoids and harpacticoids from freshwater interstitial habitats in southeastern New York, Strayer (1988) provided the drawings of the male P3 and P4 endopod complex of three species of Parastenocarididae (which he provisionally named *Parastenocaris* sp. 1, *Parastenocaris* sp. 2, and *Parastenocaris* sp. 3) collected together in one sample from the hyporheic of the East Branch of the Wappinger Creek, without providing any taxonomic information on these taxa. Although the collection of new material and more morphological details should be needed, we can remark that both the P3 and P4 endopod complex of *Parastenocaris* sp. 1 are coherent with the diagnostic characters of *Stammericaris*. Moreover, the presence of two groups of spinules on the first half of the outer margin of the P3 exp-1, and of only one curved spine on the P4 basis of *Parastenocaris* sp. 1, suggest a strong relationship of this taxon with *S. remotaepatriae* **sp. nov.** and *S. palmerae* **comb. nov.** Hence, *S. remotaepatriae* **sp. nov.**, *S. palmerae* **comb. nov.** and *Parastenocaris* sp. 1 could represent a phylogenetically-defined group, which further phylogenetic and molecular analyses could define as either a subgenus of *Stammericaris* or a new sibling group of this genus. Copepods are an ancient group (Huys and Boxshall 1991; Stock 1991) and Parastenocarididae in particular is one of the most ancient lineages, which colonized the Pangaea and dispersed through its freshwater habitats (Boxshall and Jaume, 2000). The affinities among the groups of these three Nearctic species and the remaining *Stammericaris*, which are confined to the Palearctic region, have a great biogeographical value because: i) all Parastenocarididae, and these taxa as well, are rare and exclusive of groundwater habitats; ii) there can not be any gene flow between the European and North American populations, and iii) the morphological differences between the taxa of the two biogeographical regions are most likely due to divergent evolution occurred after the opening of the Central Atlantic Ocean and the fragmentation of Laurasia. Affinities between Nearctic and Palearctic species have been shown for other copepods such as reported by Reid (1998) for two groundwater cyclopoids, *Acanthocyclops sensitivus* (Graeter and Chappuis, 1914) distributed in Europe and *A. parasensitivus* Reid, 1998, living in eastern North America, which are identical in the main morphological characters (appendage segmentation and setation), and can be distinguished only for certain proportions and finer ornamentation. Reid (2001) concluded that these two taxa have diverged only slightly since the continents separated.

A second species in Strayer (1988), *Parastenocaris* sp. 3, is relevant as the basis and exp-1 of the male P3 are enlarged and the exp-2 distal apophysis is short and as long as the thumb, the P4 endopod is very peculiar, represented by an elongated segment, enlarged in the middle, ornamented with a longitudinal row of denticles and with two small apical teeth; the endopod complex includes a thin and apically pointed and slightly curved process almost as long as the endopod. If this process were unquestionably inserted between the enp and the exp (the figure lacks the drawing of the exp, but by comparison with the drawings of the other two species it seems this is the case), *Parastenocaris* sp. 3 would be a *Proserpinicaris* (see Bruno *et al.* 2020), if confirmed by other important diagnostic characters, such as the shape and armature of P5 and caudal rami of both sexes, and of the P4 endopod and genital field of the female. If this were the case, the groundwater copepod fauna of North America would be enriched by a new taxon of great faunistic and biogeographic value.

The discovery of *Stammericaris* in North America considerably extends the distribution area of the genus, which so far was reported only from Central-Southern Europe (Fig. 5). As a result, the very extensive distribution range of this genus could imply a much wider diversity than what is currently known. This could be true both for the Palearctic region where, for example, there are at least four other species to study and describe (Cottarelli and Bruno, personal observation), as well as for the Nearctic region where, as discussed above, there might be at least one other, perhaps two species of *Stammericaris* and other species of other genera of Parastenocarididae (*Minutacaris*? *Proserpinicaris*?) that could have arrived into North America via the Bering Land Bridge from Siberia to Alaska (Reid 2001).



**FIGURE 5.** Distribution map of all known *Stammericaris* (including unpublished records), of *Parastenocaris* sp. 1, and *Parastenocaris* sp. 3.

As far as the ecology is concerned, in the Palearctic, *S. stammeri* is present in caves in Spain/ France, and *S. phreatica* is present in surface ground waters of Central Europe (Romania, Czech Republic, Republic of North Macedonia, Bulgaria) (Dussart and Defaye 1990, and citations therein; Apostolov 1997); the Anatolian *Stammericaris* sp. 3 was found in lacustrine psammion (Cottarelli and Bruno, unpublished). In Italy four species (*S. diversitatis*, *S. destillans*, *S. vincentimariae*, *Stammericaris* sp. 2) were collected exclusively in caves (epikarst, rimstone pools) (Cottarelli *et al.* 2012; Bruno *et al.* 2017, 2020, in prep.), whereas two (*S. orcina*, *S. trinacriae*) were collected in rimstone pools and lacustrine psammion, and rimstone pools and phreatic waters, respectively (Chappuis 1938; Cottarelli and Drigo 1972; Bruno *et al.* 2017). The remaining species (*S. acherusia*, *S. pasquini*, *S. amyclaea*, *S. lorenzae*, *Stammericaris* sp. 1) were collected in lacustrine psammion or in the shallow hyporheic (Noodt 1954; Cottarelli 1969, 1972; Pesce, Galassi and Cottarelli 1995, Cottarelli and Bruno, unpublished). Regarding the North American species discussed here, *Parastenocaris* sp. 1 was collected in the hyporheic sediments of a stream in New York State, *Stammericaris palmerae* **comb. nov.** and *Parastenocaris trichelata* from the hyporheic of Goose Creek, Virginia; these species were therefore found in an habitat already known for the genus, while *S. remotaeterrae* **sp. nov.** seems to occupy the particular niche represented by brackish groundwater or, in other words, lives in the ecotone between continental freshwater and marine waters. *Stammericaris remotaeterrae* **sp. nov.** was in fact found in samples of brackish interstitial water, collected with the Karaman-Chappuis method, from holes dug on sandy soil close to the shoreline and also near a stream and freshwater ponds which probably diluted the salinity of the interstitial seawater (Roberto Argano, pers. com.). Almost all Parastenocarididae live in continental groundwater and species found in brackish waters are very rare (e.g., *Parastenocaris vicesima* Klie, 1935, some species of *Cottarellicaris* Schminke, 2013, a genus phylogenetically close to *Stammericaris*, all collected in rivermouths, and *Proserpinicaris proserpina* (Chappuis, 1938) an Italian species frequent in groundwater but also collected in the brackish waters of the Lesina Lagoon, Apulia). Unfortunately, we do not have chemical-physical data on the collection station, or information on other harpacticoid fauna from the same area, but we think relevant to underline the particular habitat of the new *Stammericaris* and its (possible) wide ecological valence.

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