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REDESCRIPTION AND RELATIONSHIPS OF *EUCYCLOPS PERSISTENS* (COPEPODA: CYCLOPIDAE) ENDEMIC TO THE AZOV-BLACK SEA BASIN

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Abstract.— The cyclopoids of the Ponto-Caspian region has been discussed in numerous articles and seminal monographs of the late V. I. Monchenko, yet relationships of this peculiar fauna to other regions are still poorly understood. Two subspecies of *Eucyclops persistens* known from interstitial waters in the Black sea region are redescribed here, based on the type material. *Eucyclops persistens persistens* (estuary zone of Caucasian rivers) and *E. persistens tauricus* (wells in Crimea) differ from each other in the lateral surface ornamentation of the caudal rami in female (naked, vs. short serra present), and the relative length of the dorsal caudal seta in both female and male (seta longer in *E. persistens tauricus*). *Eucyclops persistens* s.l. share some characters, such as the reduced "serra"on the caudal rami, reduced lateral pilosity of pediger 5, lack of (or few) hairs on the distal margin of P4 intercoxal sclerite, and long aesthetasc on the ninth antennulary segment in female, with some European subterranean taxa in the *Eucyclops graeteri* complex. Sparse morphological information on the *graeteri*-complex hinders a rigorous phylogenetic analysis. Future revision of the *graeteri*-complex might shed light on a Western/Central Europe – Ponto-Caspian connection during the evolution of these subterranean *Eucyclops*.

Key words.— Eucyclopinae, taxonomy, subterranean, Ponto-Caspian, freshwater

INTRODUCTION

The Ponto-Caspian basin (Eastern Paratethys) has been an important centre of speciation of the euryhaline crustaceans, perhaps best exemplified by the diversity of the Onychopod cladocerans in the region (Dumont 1998, Rivier 1998). As to the Cyclopoida Monchenko (1998, 2003) listed 19 species endemic to the Ponto-Caspian region, including two *Eucyclops*, *E. orthostylis* Lindberg, 1952 and *E. persistens* Monchenko, 1978.

Seven other non-endemic *Eucyclops* species occur in the region. *Eucyclops serrulatus* (Fischer, 1851) has been reported from both mixohaline habitats of the Azov-Black Sea basin, the Caspian and Aral Seas, and fresh waterbodies (Pidgaiko 1984, Kovalchuk and Kovalchuk 1992, Monchenko 1974, 2003, Gaponova 2014). Monchenko (2003) considered *E. serrulatus* to be a euryhaline species. Two forms currently considered as synonyms of *E. serrulatus* s. str. (see Dussart and Defaye 2006) were also recorded from the Ponto-Caspian region: *Eucyclops serrulatus* var. *proximus* (Lilljeborg, 1901) from the Caucasus (Rylov 1936) and Danube River Basin (Pidgaiko 1957, Polischuk 1974, Polischuk and Garasevich 1986); and *E. serrulatus var. brachyurus* (Lilljeborg, 1901) from the Caucasus

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(Rylov 1936). Some historical records of *E. serrulatus* might however refer to other species, as it has been demonstrated by Hamrová *et al*. (2012) in a study on the genetic variation within *E. serrulatus* s. l., and our present finding of *E. roseus* Ishida, 1997 in the Arabat Spit (Arabatska Strilka), Ukraine (see Results).

Eucyclops denticulatus (Graeter, 1903), *E. macruroides* (Lilljeborg, 1901), *E. macrurus* (G.O. Sars, 1863) and *E. speratus* (Lilljeborg, 1901) occur in various types of freshwater biotopes in the Ponto-Caspian basin, and are considered as stenohaline freshwater species. They have been encountered in both low and high altitude habitats in the Azov-Black Sea and Caspian Sea basins, Eastern Carpathians, Transcarpathia (Zakarpattia), the Caucasus and Transcaucasia (Kasymov 1965, 1972, Pidgaiko 1984, Kovalchuk 2006, Gaponova 2014).

Anufriieva *et al*. (2014) and Anufriieva and Shadrin (2016) have recently found *E. roseus* in Crimea and Eastern Ukraine. Geographic range of this species is still poorly understood, *E. roseus* likely has wider distribution in Europe than it was previously thought (Gaponova and Hołyńska, in prep.).

Monchenko (2003) found *E. agiloides* (G.O. Sars, 1909) in a spring near Chatyr-Dag (South Crimea, Crimean Mts.) and in the waterbodies of the Lesser Caucasus and Talysh region (South Azerbaijan). The species originally described from African lakes (Victoria and Tanganyika) is in urgent need of revision (Anufriieva *et al*. 2014), the European records of *E. agiloides* require verification.

The morphological criteria used in *Eucyclops* taxonomy have significantly changed since Monchenko had published his great monographs (1974, 2003) on the Ponto-Caspian Cyclopoida. Taxonomic status of many common and alleged cosmopolitan *Eucyclops* species is still under discussion, some of them in fact represent species complexes (Alekseev and Defaye 2011, Mercado-Salas and Suárez-Morales 2014, Mercado-Salas *et al*. 2016).

We here redescribe a rare Ponto-Caspian endemic, *E. persistens,* represented by two subspecies in the region, and discuss its relationships to the European fauna.

Materials and methods

Qualitative and morphometric characters were examined both in the holotypes, and male and female paratypes of *Eucyclops persistens persistens* and *Eucyclops persistens tauricus*. The holotypes and some male paratypes of the two taxa were dissected by V. I. Monchenko; the mounting medium is unknown to us (likely canada balsam). Other paratype specimens were dissected and mounted in glycerine by the authors. Collection information on the specimens examined is provided in species descriptions. Drawings were made using a camera lucida attached to Olympus BX 50 compound microscope. Original pencil drawings of the diagnostic characters were edited in the program GIMP. Photos were taken by the aid of AxioCam HR camera attached to Zeiss Axio Imager M1 microscope in Schmalhausen Institute of Zoology, Kyiv. Telescoping somites were measured separately and summed for total body length (Koźmiński 1936). Width of a segment was measured across its widest part.

In illustration of the geographic distribution of the species we used map provided by Microsoft Encarta World Atlas 2001.

Collections:

IZAN – Schmalhausen Institute of Zoology, Vladyslav I. Monchenko Collection, Kyiv, Ukraine;
MIZ – Museum and Institute of Zoology, Warsaw, Poland.

Abbreviations used in the manuscript:

ae – aesthetasc,
Caudal seta II – anterolateral,
Caudal seta III – posterolateral,
Caudal seta IV – outer terminal,
Caudal seta V – inner terminal,
Caudal seta VI – terminal accessory,
Caudal seta VII – dorsal,
enp 1–3 – first to third endopodal segment,
exp 1–3 – first to third exopodal segment,
P1–P4 – first to fourth swimming legs,
sp – spine.

Results

Diagnosis of Eucyclops persistens sensu lato (unless mentioned otherwise all data pertain to adult female). Pediger 5 with short posterolateral hairs (Figs 1C; 9B). Caudal rami ca. 4–5 times as long as wide, "serra" absent or reduced to short longitudinal row of spinules (Fig. 10A) on lateral margin. Antennule 12-segmented, terminal segment with nearly smooth hyaline membrane, without distinct teeth (Fig. 2C). Ninth segment of antennule with long (>30 μm) aesthetasc inserted at obtuse angle to longitudinal axis of segment (Fig. 2B arrowed, cf. Fig. 2D,E). Antennal coxobasis without long hair-like spinules along distal margin on anterior surface (Fig. 3D,E), but hair-like spinules sometimes present at mediodistal angle (Fig. 3D). In male hair-like spinules present along distal margin on anterior surface of antennal coxobasis (Fig. 8B). Maxillulary palp naked (Fig. 4A). P4 intercoxal sclerite with sparse pilosity on posterior surface, hairs on distal margin not extending to whole width of segment (Figs 5D; 10C). Third exopodal and endopodal

segments of P4 with wide and flattened (spatulate) setae (Fig. 6A,B). None of setae of P4 enp3 reaching beyond tip of longer (medial) apical spine (Fig. 6B). First segment of male antennule with 8 setae including 2 brush setae, and single aesthetasc (ae_v) (Fig. 8A). Brush setae are also present on antennulary segments 2–5 (one on each segment), yet missing on segment 6 (two setae inserted on segment have typical seta shape).

Eucyclops persistens persistens Monchenko, 1978

Eucyclops persistens Monchenko, 1978: 50–58, Figs 1–3, Tables 1–3.

Type material. Holotype: Georgia, Adjara, Kintrishi River liman, river bank, interstitial, near Kobuleti city, 41.80N 41.77E, V. I. Monchenko 3 Oct. 1974, ♀ (IZAN). Paratypes: Russia, Kransnodarskiy Kray, Lazarevskoye, 43.92N 39.33E, Psezuapse river bank, interstitial, V. I. Monchenko 24 Oct. 1974, ♂ (IZAN), microscope slide preparatum was made by V. I. Monchenko; the same locality data as for holotype, 3♀♀ and 1♂, dissected by the authors (IZAN).

Other material examined. *Eucyclops macrurus* G.O. Sars, 1863: Poland, Warszawa, Jezioro Czerniakowskie, 52.19N 21.07E, lake shore, J. Brozi 8 Jul. 2012, 1♀ (MIZ: 13/2018/172). *Eucyclops roseus* Ishida, 1997: Ukraine, Arabatska Strilka [Arabat Spit], Strilkove village, 45.90N 34.88E, V. I. Monchenko, 1♀ (IZAN) originally labelled as *Eucyclops serrulatus*.

Differential diagnosis. *Eucyclops persistens* s. str. differs from *E. persistens tauricus* in the naked lateral surface of caudal rami, and relatively shorter length of caudal seta VII (VII/V index in female, and VII/caudal ramus length index in male – for morphometric data see Table 2 in Discussion).

Description. **Female** – unless mentioned otherwise all data refer to material examined by us. Body length 880–915 μm (holotype, 818 μm; data from Monchenko 1978) (Fig. 1A). Cephalothorax, length/width 1.0–1.2; prosome length/urosome length 1.3–1.5; width of cephalothorax/width of genital double-somite 2.4–2.7; genital double-somite, length/width 0.95–1.05. Pediger 5 bearing short posterolateral hairs (Fig. 1C). Anal somite with continuous row of spinules on posterior margin ventrally and laterally. Anal sinus with longitudinal row of hair-like spinules (Fig. 1B). Caudal rami (Figs 1B; 9A) 4.7–5.3 times as long as wide, without hairs on medial margin. On lateral margin spinules present at insertion of caudal setae II and III, yet longitudinal row of spinules ("serra") absent. Seta II 0.21–0.24 times as long as caudal rami, inserted at distance of 0.18–0.21 ramus length measured from posterior end. Relative length of seta VII, VI, V and IV in

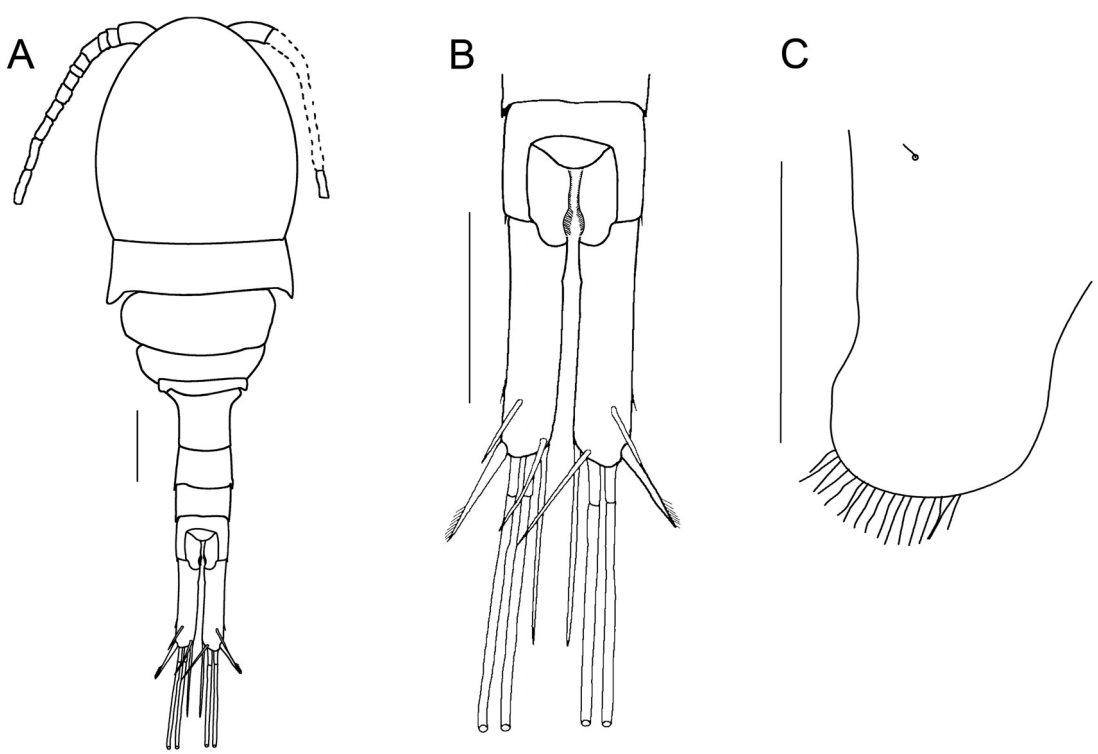

Figure 1. *Eucyclops persistens persistens* Monchenko, female paratypes: (A) habitus, dorsal [IZAN: ♀-2]; (B) anal somite and caudal rami, dorsal [IZAN: ♀-2]; (C) Pediger 5, lateral [IZAN: ♀-1]. Scale bars = 100 μm (A–B) and 50 μm (C).

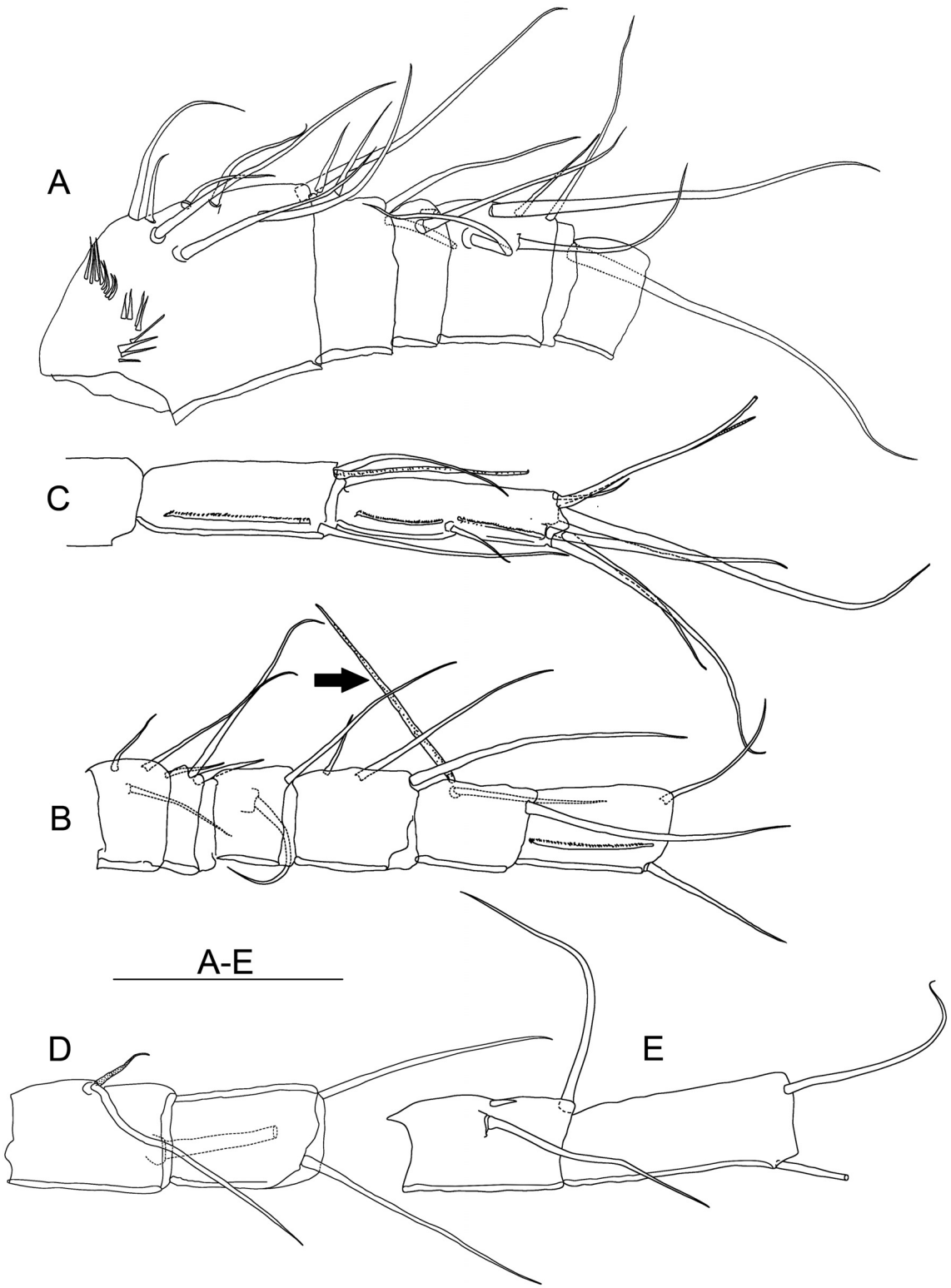

Figure 2. Armature of the antennule in *Eucyclops*. A–C. *Eucyclops persistens persistens* Monchenko, female paratype [IZAN:♀-3]: (A) antennulary segments 1–5, ventral (setae are not shown on segment 5); (B) antennulary segments 5–10, ventral, arrow shows aesthetasc; (C) antennulary segments 11–12, ventral. (D) *Eucyclops macrurus* (G.O. Sars), antennulary segments 9–10, dorsal [MIZ: 13/2018/172]. (E) *Eucyclops roseus* Ishida, antennulary segments 9–10, dorsal [IZAN; ♀-2]. Scale bar = 50 μm.

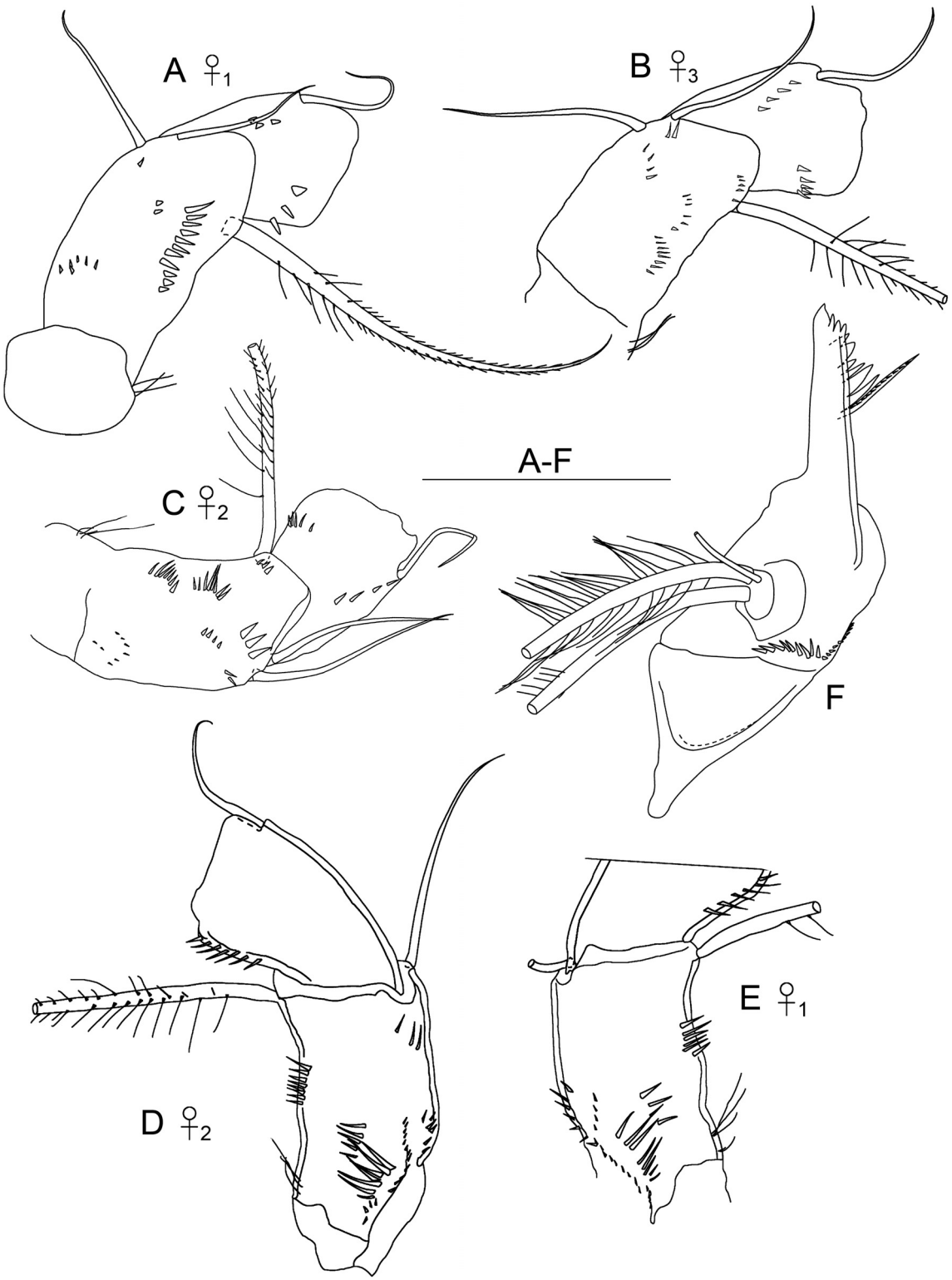

Figure 3. *Eucyclops persistens persistens* Monchenko, female paratypes. A–E. Intraspecific variation of the surface ornamentation of the antennal coxobasis: (A–C) posterior surface [IZAN]; (D–E) anterior surface [IZAN]. (F) Mandible, anterior [IZAN: ♀-3]. Scale bar = 50 μm.

comparison to length of caudal seta III: 1.1–1.3, 2.0–2.2, 8.8–9.5 and 5.5–6.0, respectively. Relative length of setae VII, VI, V, IV and III in comparison to length of caudal rami: 0.47–0.54, 0.86–1.0, 3.6–4.1, 2.3–2.6 and 0.38–0.45, respectively. Means of this same index for seta VII–III measured in larger sample (n=20) from the type locality: 0.50, 0.95, 4.32, 2.76 and 0.48 (data from Monchenko 1978). Seta V 1.0–1.1 times as long as urosome. Dorsal seta (VII) 12.4–13.8% of length of caudal seta V, and 18.1–22% of length of caudal seta IV.

Antennule (Figs 1A; 2A–C) 12-segmented (I–V, VI–VII, VIII, IX–XI, XII–XIII, XIV, XV–XVI, XVII–XX,

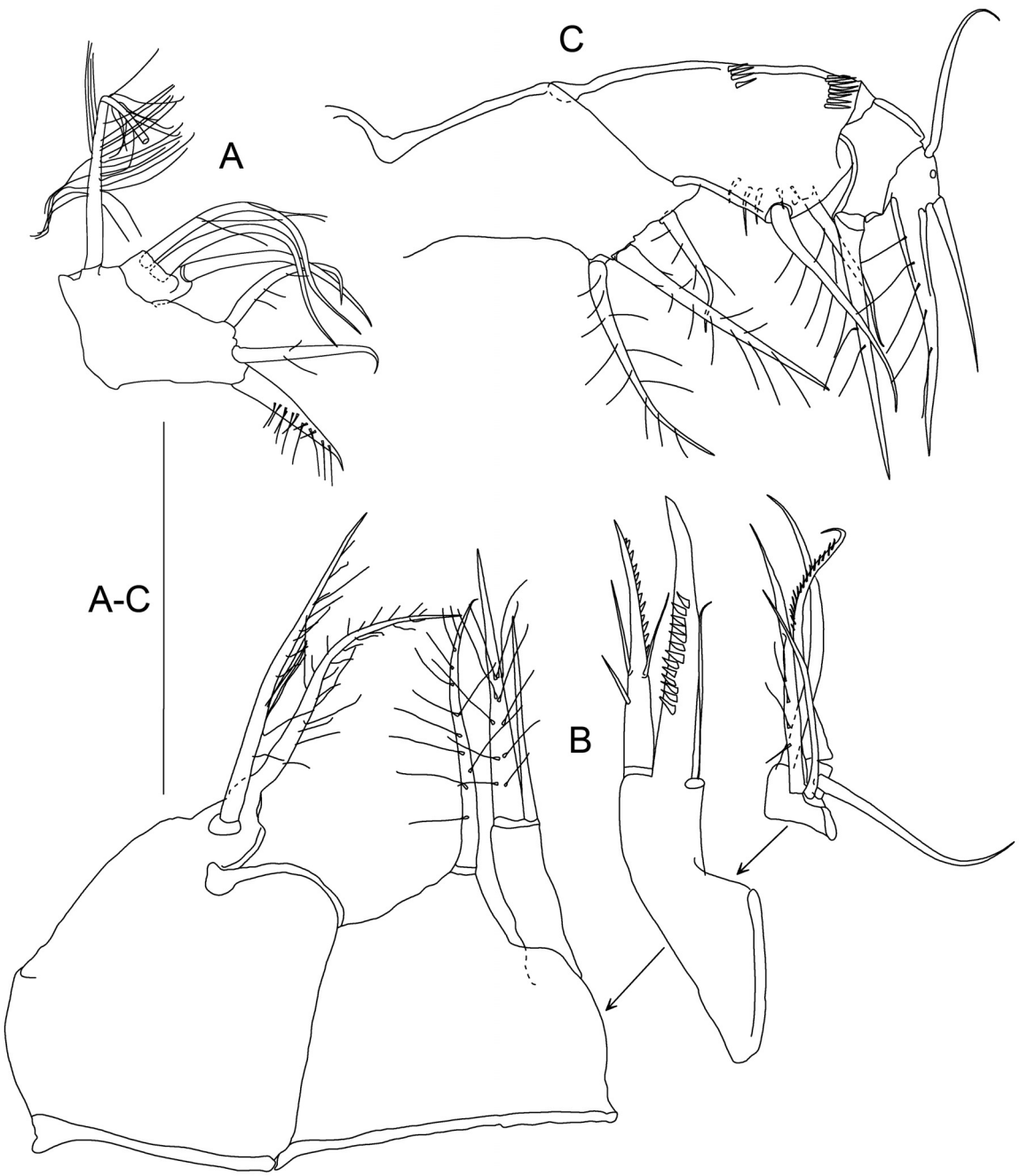

Figure 4. *Eucyclops persistens persistens* Monchenko, female paratype [IZAN: ♀-3]: (A) maxillulary palp; (B) maxilla, posterior; (C) maxilliped, posterior. Scale bar = 50 μm.

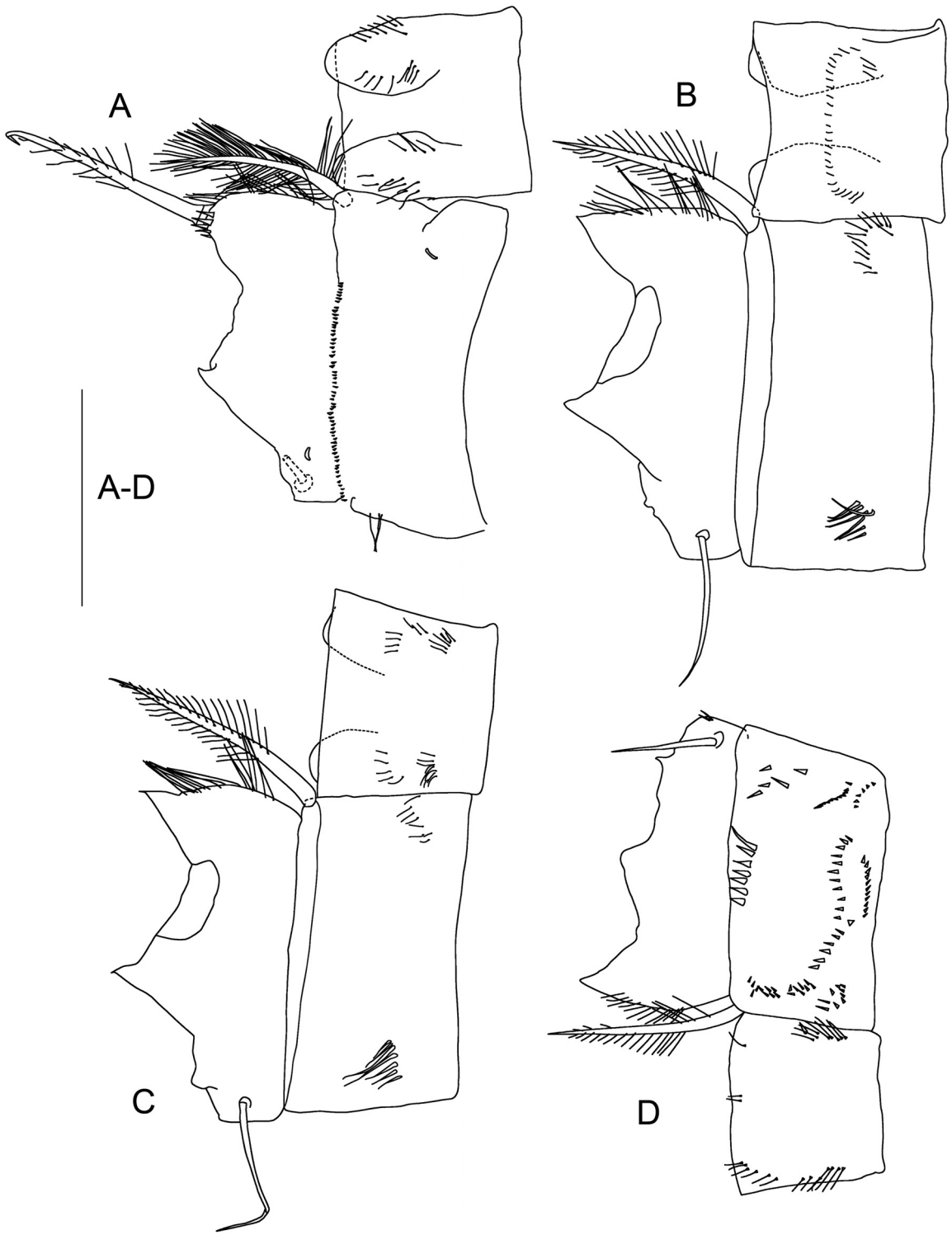

Figure 5. *Eucyclops persistens persistens* Monchenko, female paratype [IZAN: ♀-3]: (A) P1 protopodite, anterior; (B) P2 protopodite, posterior; (C) P3 protopodite, posterior; (D) P4 protopodite, posterior. Scale bar = 50 μm.

XXI–XXIII, XXIV, XXV, XXVI–XXVIII) reaching slightly beyond cephalothorax. Segments 10–12 (Fig. 2B,C) with finely serrate hyaline membrane. Seta formula: 8, 4, 2, 6, 4, 1+sp, 2, 3, 2+ae, 2, 2+ae, 7+ae. Spinules only present on ventral (anterior) surface of first segment. Aesthetasc (Fig. 2B, arrowed) on segment 9 conspicuously long (45–55 μm; ca. 5–6% of body length), inserted at obtuse angle to longitudinal axis of article. Segment 11 (Fig. 2C) with aesthetasc 42–45 μm long, 4.6–5.1% of body length.

Antenna 4-segmented, with 3, 1, 9, and 7 setae on coxobasis and endopodite 1–3, respectively. Exopodal seta reaching beyond enp3, long setules present on proximal part of seta (Fig. 3A). First endopodal segment (Fig. 3A–C) bearing oblique row of spinules near medial margin, and transverse row next to lateral margin on posterior surface. Posterior surface ornamentation of antennal coxobasis (Fig. 3A–C) comprising: long hair-like spinules on proximolateral margin; longitudinal double rows near lateral margin, spinules variable in length; spinules present or absent near exopodite seta; few large spinules present or absent at height of insertion of medial setae; oblique row proximally to insertion of medial setae; and arc of small spinules present or absent proximally near medial margin. Anterior surface of antennal coxobasis (Fig. 3D,E): hair-like spinules absent on distal margin; few long and thin spinules sometimes present at mediodistal angle; 6–8 spinules present in longitudinal row next to lateral margin in middle section of segment; in proximal half two oblique rows of long spinules and short spinules more laterally present.

Mandibulary palp (Fig. 3F) with two long and one short setae, transverse row of large spinules, and longitudinal row of shorter spinules present on anterior surface near palp. Maxillule with setation common in Cyclopidae, maxillulary palp (Fig. 4A) naked. Maxilla (Fig. 4B) comprising praecoxopodite and coxopodite fused on anterior surface, basipodite and two-segmented endopodite with 2, 3, 2, 2, and 3 setae, respectively. Field of tiny spinules sometimes present on anterior surface of coxopodite. Praecoxopodite sometimes bearing transverse row of spinules near proximal margin; spinules long in lateral half and short/tiny in medial half of segment. Maxilliped (Fig. 4C) composed of syncoxopodite, basipodite and two-segmented endopodite, with 3, 2, 1, and 3 setae, respectively. On second endopodal segment arthrodial membrane missing between long medial seta and segment. Basipodite bearing two transverse rows of spinules on posterior surface.

P1–P4 rami three-segmented, setation (Table 1) as typical of genus.

Aberrations in chaetotaxy, occurring only on one side of the legs, observed in paratype ♀-1 (P2 enp2 with one seta only: proximal seta missing) and paratype ♀-2 (P3 exp3 with three spines only: proximal spine failed to form; and P4 exp3 with four spines: one extra spine added proximally).

Intercoxal sclerites (Figs 5A–D; 6A) bearing hair-like or short spinules on both anterior and posterior surface in P1–P4. Distal margin of P4 intercoxal sclerite (Figs 5D; 6A) with few hairs, or naked. Medial seta (or spine) of P1 basipodite reaching middle to distal margin of enp3, and bearing long setules (Fig. 5A). Medial expansions of basipodites (Fig. 5A–D) with long hairs in P1–P3 and short hairs in P4. Coxopodite setae (Fig. 5A–D) with homonomous setulation in P1–P3 and heteronomous setulation in P4, setules long in P1 and short in P2–P3. P4 coxopodite seta (Figs 5D; 6A, arrowed) bearing few long setules proximally and spinule-like setules distally, with gap in the middle on lateral margin; medial margin of seta with short setules gradually decreasing in length. P4 coxopodite (Figs 5D and 6A) with complex pattern of spinules on posterior surface: 7–8 spinules on distal margin; spinules at laterodistal angle few (Fig. 5D) or absent (Fig. 6A); spinules arranged in one (Fig. 6A) or two (Fig. 5D) oblique rows at proximolateral angle; row of tiny spinules in middle, near proximal margin of segment; long row below proximal row; small spinules arranged in three groups near medial margin. Setae short and modified to spatulate (distal part of setae wide and flat) structures on exp3 and enp3 in P3 and P4 (Fig. 6A,B). Longest (terminal) spine of P4 exp3 0.6–0.7 times as long as segment. None of setae of P4 enp3 reaching tip of longer (medial) apical spine of segment. P4 enp3 1.9–2.1 times as long as wide; medial apical spine 1.2–1.5 times as long as lateral spine and ca. as long as segment. P5 (Fig. 9B) one-segmented, medial spine

Table 1. Armature of legs 1–4 in adult *Eucyclops persistens* s. str. Spines are denoted by Roman, setae by Arabic numerals. The armature on the lateral margin of any segment is given first, followed by the elements on the apical and medial margins.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-1	1-I	I-1; I-1; II-I, 2-3	0-1; 0-2; 1-I,1-3
Leg 2	0-1	1-0	I-1; I-1; III-I,1-4	0-1; 0-2; 1-I,1-3
Leg 3	0-1	1-0	I-1; I-1; III-I,1-4	0-1; 0-2; 1-I,1-3
Leg 4	0-1	1-0	I-1; I-1; II-I,1-4	0-1; 0-2; 1-II-2

2.0–2.3 times as long as segment, small spinules present at insertion of medial spine. Apical and lateral setae of P5 1.6–1.8 and 0.9–1.0 times as long as medial spine, respectively.

Male (only those characters are mentioned, which differ from the corresponding character states in female). K = Kobuleti, L = Lazarevskoye.

Body length 725 μm (676–775 μm in Lazarevskoye; data from Monchenko 1978). Cephalothorax (Fig. 7A), length/width 1.3 [K]; prosome length/urosome length 1.6 [K]. Pediger 5 with tiny posterolateral hairs/spinules [shown by Monchenko (1978) in fig. 3(5)], or naked on lateral surface (Fig. 9E). Caudal rami (Fig. 7B) 3.5 [K] times as long as wide (3.75–4.78 in Lazarevskoye population – data from Monchenko 1978). Seta II 0.23 [L], 0.30 [K] times as long as caudal rami, inserted at distance of 0.23 [L], 0.26 [K] ramus length measured from posterior end. Caudal seta III robust (Fig. 9C). Relative length of caudal setae in comparison to length of caudal seta III: seta VII – 1.1 [K], 1.3 [L]; seta VI – 1.9 [L], 2.3 [K]; seta V – 11.1 [L]; seta IV – 5.9 [K], 7.5 [L]. Relative length of caudal setae in comparison to length of caudal rami: seta VII – 0.43 [L], 0.57 [K]; seta VI – 0.63 [L], 1.1 [K]; seta V – 3.7 [L]; seta IV – 2.5 [L], 2.9 [K]; seta III – 0.33 [L], 0.5[K]. Seta VII – 12% [L] of length of caudal seta V, and 17% [L], 19% [K] of length of caudal seta IV.

Antennule 17-segmented: I–V, VI–VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII, XIX–XX, XXI–XXIII, XXIV–XXV, XXVI–XXVIII. Penultimate (XXIV–XXV) and terminal (XXVI–XXVIII) segments partly fused. Armature formula was verified on segments 1–6 (Fig. 8A) and 10–12: 8+1ae, 4, 2, 2+ae, 2, 2, and 2, 2, 2, respectively. Single aesthetasc (ae_V) present on segment 1 (Fig. 8A), inserted next to distal margin of article. Five proximal segments bearing 2, 1, 1, 1, and 1 brush seta ("sensory club"), respectively (Fig. 8A); tips of sensory clubs rounded. Setae of typical shape on segment 6.

Posterior surface ornamentation of antennal coxobasis similar to that in female, yet just few tiny spinules present at height of insertion of medial setae (verified in single male). Hair-like spinules (Fig. 8B) present next to distal margin on anterior surface. Surface ornamentation of maxillulary palp could not be verified; setation of mouthparts as in female. Transverse row of small spinules present on anterior surface of maxillar praecoxopodite, near proximal margin of segment.

P4 intercoxal sclerite devoid of hairs on distal margin, posterior surface ornamentation of coxopodite and setulation of coxopodite seta as in Fig. 8C. P4 enp3 1.95 [K], 2.1 [L] times as long as wide. Medial apical spine of segment 1.4 [L], 1.7 [K] times as long as lateral spine; none of setae of article reaching tip of longer (medial) spine. Medial apical spine 0.96 [L], 1.15 [K] times as long as segment. P5 as in Fig. 9E. P6 bearing three elements; length of medial spine, median and lateral setae 26 μm, 25 μm and 34 μm, respectively (measured in male from Kobuleti).

Eucyclops persistens tauricus Monchenko et Sopova, 1984

Eucyclops persistens tauricus Monchenko et Sopova, 1984: 10–14, Fig. 1, Tables 1–2.

Type material. Holotype: Ukraine, Crimea, Selo Zarechnoye (outskirts of Simferopol), 44.86N 34.27E, well, E. M. Sopova 7 Feb. 1984 (IZAN). Paratypes: Ukraine, Crimea, Simferopol, 44.95N 34.11E, well, E. M. Sopova 7 Feb. 1984, 1♂ (IZAN), microscope slide preparatum was made by V. I. Monchenko, and 2♀♀ and 1♂ labelled as "Eucyclops persistens f. dulcicola", dissected by the authors (IZAN).

Differential diagnosis. *Eucyclops persistens tauricus* differs from *E. persistens* s. str. in the presence of short "serra" on the lateral surface of caudal rami (Fig. 10A), and in relatively longer length of caudal setae VII (VII/V index in female, and seta VII/caudal ramus length index in male – for morphometric data see Table 2 in Discussion).

Because of folding and shrinkage of the cuticle of the preserved specimens, length of the somites and the surface ornamentation of some limbs could not be verified.

Description. **Female.** Pediger 5 with short posterolateral hairs. Anal sinus with 1–1 longitudinal row of hair-like spinules. Caudal rami 4.1–5.1 times as long as wide, naked on medial surface. Spinules present at insertion of caudal seta III, and short "serra" (Fig. 10A) comprising few (<10) spinules present anterior to insertion of seta II. Seta II 0.21–0.27 times as long as caudal rami, inserted at distance of 0.20–0.22 ramus length measured from posterior end. Relative length of seta VII, VI, V and IV in comparison to length of caudal seta III: 1.0–1.2, 2.1–2.2, 7.7–8.6 and 5.0–5.9, respectively. Relative length of setae VII, VI, V, IV and III in comparison to length of caudal rami: 0.44–0.66, 0.90–1.1, 3.7–3.9, 2.4–2.6 and 0.43–0.51, respectively. Seta V 1.0–1.1 times as long as urosome. Seta VII (dorsal) 12.7–16.8% of length of caudal seta V, and 19–26% of length of seta IV.

Antennule segmentation and setation formula same as in *E. persistens* s. str. Segment 9 with long aesthetasc (38 μm and 45 μm) inserted at obtuse angle to longitudinal axis of segment. Segment 11 with one aesthetasc 43 μm long (59 μm long on antennule on the other side), measured only in holotype.

Antenna segmentation and setation as in *E. persistens* s. str. Posterior surface ornamentation of antennal coxobasis shown in Fig. 10B, verified in single paratype (♀-2). Anterior surface ornamentation of

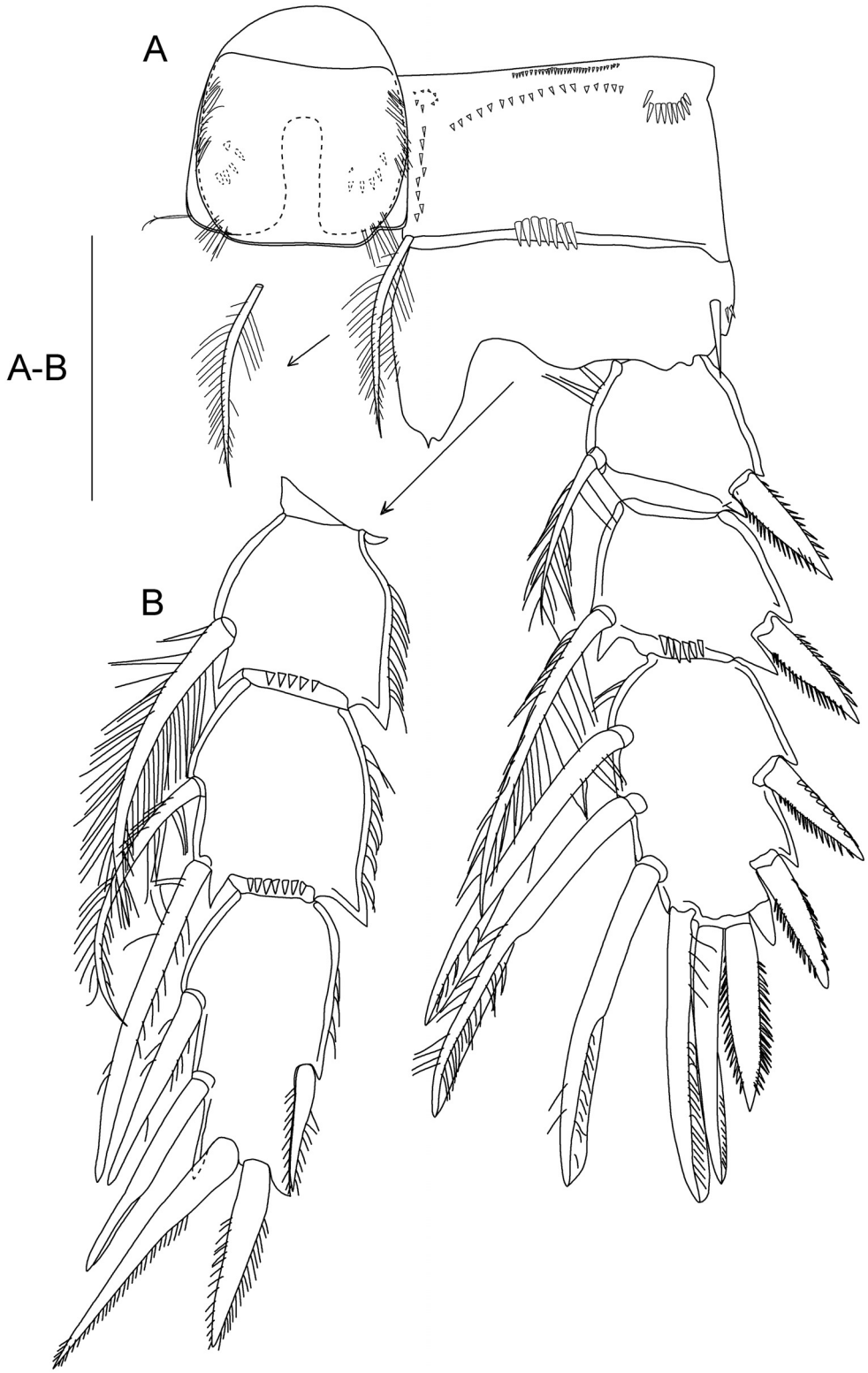

Figure 6. *Eucyclops persistens persistens* Monchenko, P4, female paratype [IZAN: ♀-1]: (A) protopodite and exopodite, posterior; (B) endopodite, posterior. Scale bar = 50 μm.

coxobasis: no hairs on distal margin, but few hairs present at mediodistal angle in holotype.

Segmentation, setation and surface ornamentation of mandible, maxillule, maxilla and maxilliped as *E. persistens* s. str. Anterior surface of maxilla could not be verified.

Chaetotaxy of swimming legs as in *E. persistens* s. str. (Table 1). Intercoxal sclerites with hair-like spinules on both anterior and posterior surfaces in P1–P4. P4 intercoxal sclerite (Fig. 10C) bearing few hairs on posterior side and distal margin. Posterior surface ornamentation of P4 coxopodite (Fig. 10C) similar to that in *E. persistens* s. str. Setulation of P4 coxopodite seta heteronomous with gap on lateral margin (Fig. 10C), or heteronomous (setules shorter and more sparse on lateral margin) yet without gap on lateral margin (holotype), or homonomous (paratype ♀-2). Setae short and modified to spatulate structures on exp3 and enp3 in P4, setae slightly modified on exp3 and enp3 in P3. None of setae of P4 enp3 reaching tip of medial apical spine of segment. P4 enp3 1.9–2.1 times as long as wide; medial apical spine 1.25–1.35 times as long as lateral spine and 1.0–1.1 times as long as segment. P5: medial spine 34 μm long, 1.8 times as long as segment; apical and lateral setae 1.5 and 0.74 times as long as medial spine, respectively (measured in holotype).

P6 composed of one seta 27 μm long, and two spines ca. 4 μm and 3.5 μm long (paratype ♀-2).

Male. Body length 880 μm. Cephalothorax, length/width 1.24; prosome length/urosome length 1.84 (single paratype). Pediger 5 with tiny posterolateral hairs or naked (ornamentation could not be verified with certainty). Anal sinus pilose. Caudal rami 3.1–4.2 times as long as wide. Seta II 0.25–0.27 times as long as caudal rami, inserted at distance of 0.21–0.24 ramus length measured from posterior end. Few robust spinules present at insertion of caudal seta II and III, yet "serra" absent anterior to insertion of seta II. Relative length of caudal setae VII, VI, V and IV in comparison to length of caudal seta III: 1.3–1.5, 2.2–2.7, 10.7 (single paratype) and 6.9 (single paratype), respectively. Relative length of caudal setae VII, VI, V, IV and III in

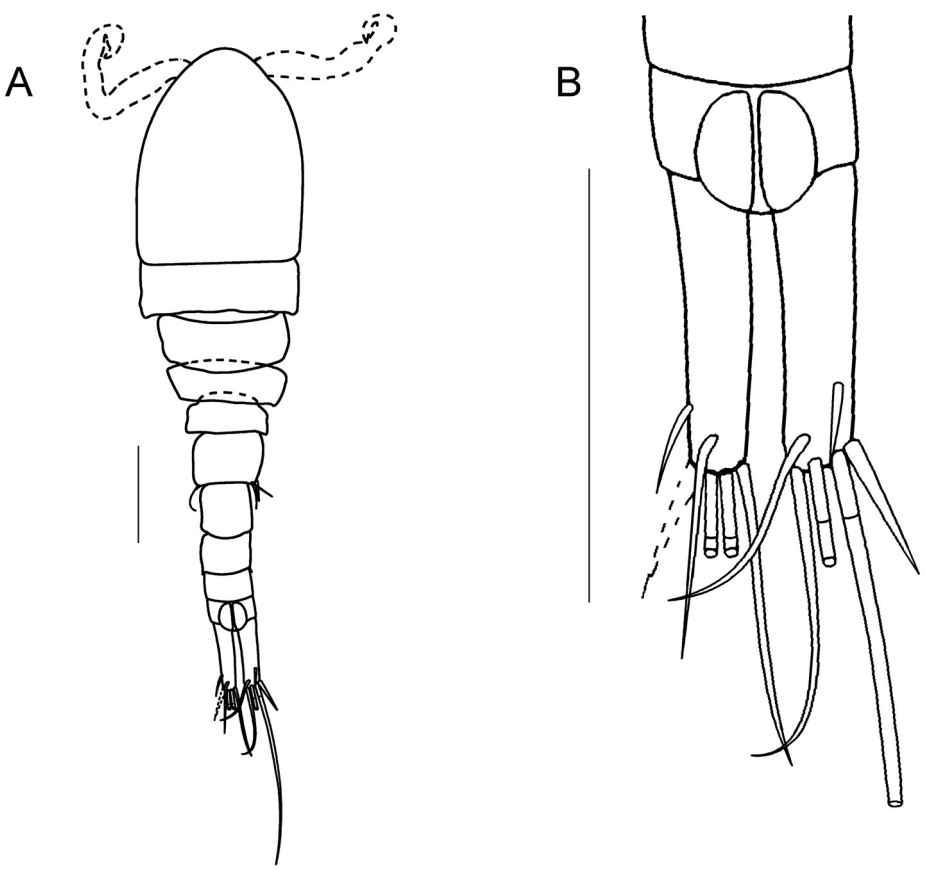

Figure 7. *Eucyclops persistens persistens* Monchenko, male paratype [IZAN: ♂-1, Kobuleti]: (A) habitus, dorsal; (B) anal somite and caudal rami, dorsal (broken seta III is indicated by dotted line). Scale bars = 100 μm.

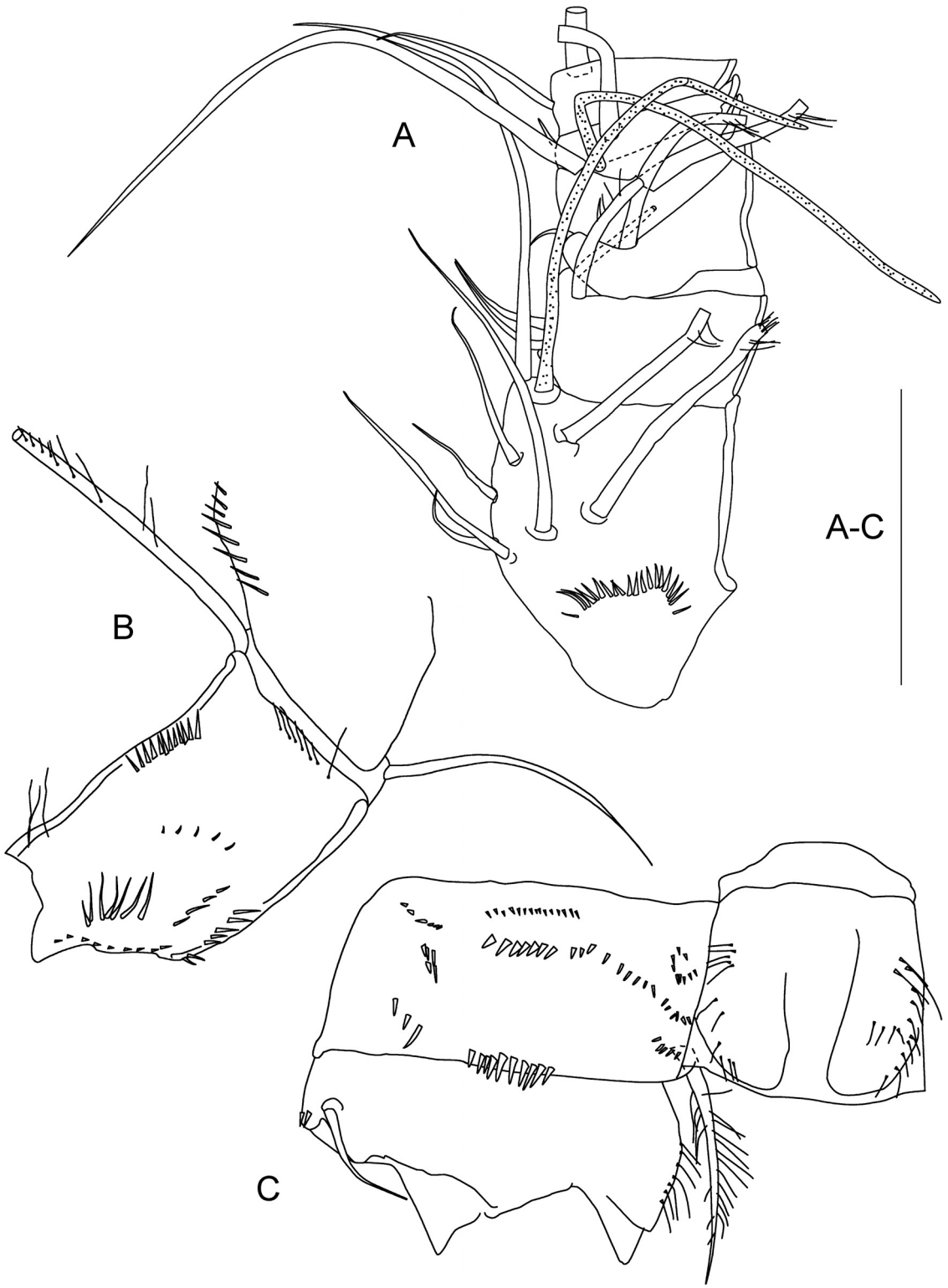

Figure 8. *Eucyclops persistens persistens* Monchenko, male paratype [IZAN: ♂-1, Kobuleti]: (A) antennulary segments 1–6, ventral; (B) antennal coxobasis, anterior; (C) P4 protopodite, posterior. Scale bar = 50 μm.

comparison to length of caudal rami: 0.60–0.72, 1.1–1.2, 4.9 (single paratype), 3.1 (single paratype) and 0.45–0.48, respectively. Seta VII (dorsal) 12.3% of length of seta V, and 19.1% of length of seta IV (single paratype).

Antennule segmentation as in nominotypical subspecies. Setae and aesthetascs were broken on many segments, the armature formula was inferred from insertion sites of the antennulary elements and verified on segments 1–10 in single paratype dissected by us: 8+1ae, 4, 2, 2+ae, 2, 2, 2, 2, 1+sp+ae, 2, respectively.

Antenna segmentation and setation as in female. Posterior surface ornamentation of antennal coxobasis similar to that in female (cf. Fig. 10B), but small spinules absent at insertion of exopodal seta, and spinules also absent at height of insertion of medial setae. Hair-like spinules present on anterior surface, next to distal margin (cf. Fig. 8B).

Segmentation and setation of mandible, maxillule, maxilla and maxilliped as in female. Maxillulary palp naked. Transverse row of long spinules present on anterior surface of praecoxopodite of maxilla, near proximal margin of segment.

P1–P4 segmentation and setation as in Table 1. Intercoxal sclerites bearing short spinules on posterior

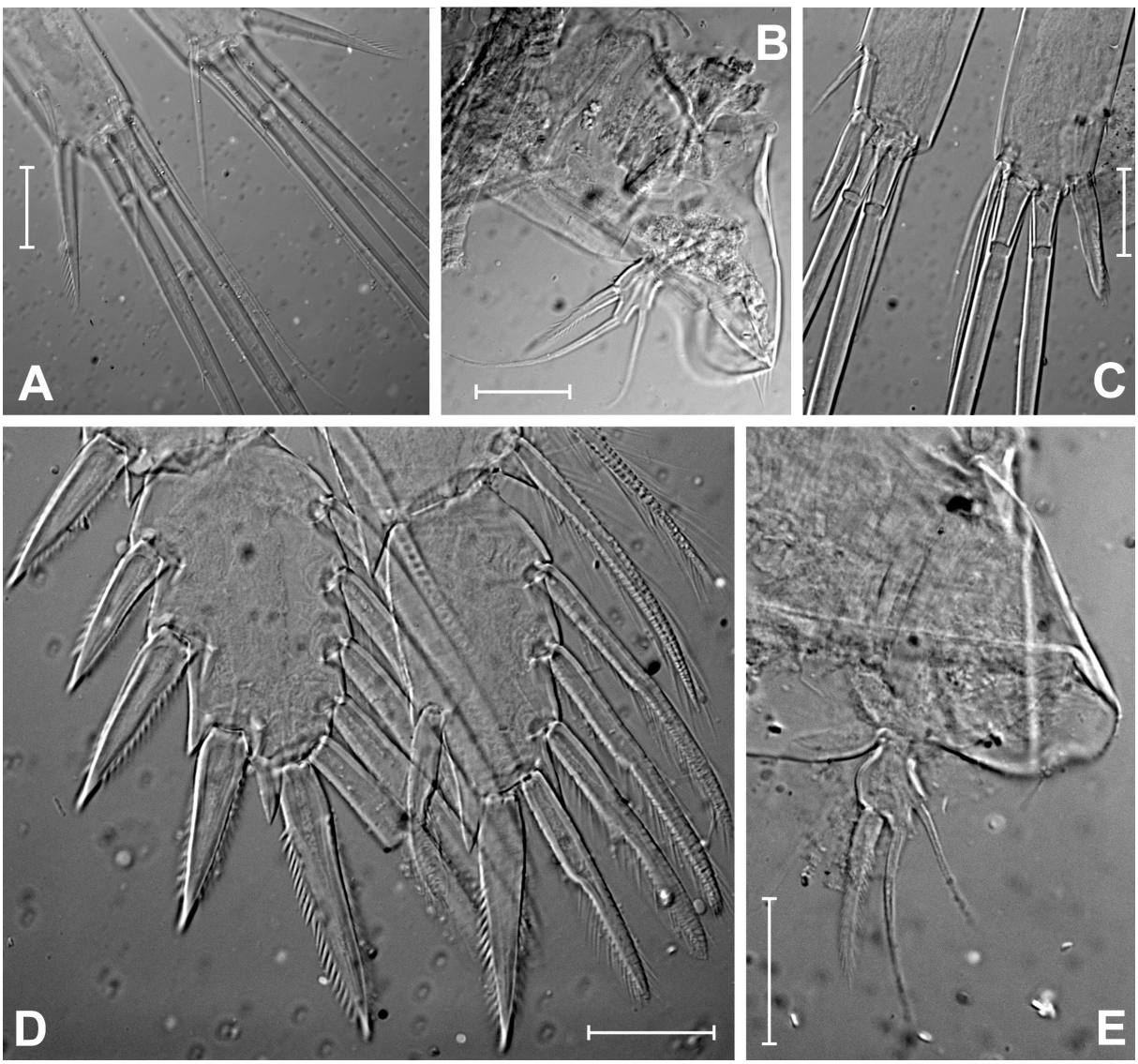

Figure 9. Light microscope photographs of *Eucyclops persistens persistens* Monchenko. A–B. Female [holotype, IZAN]: (A) posterior end of caudal rami with setae, dorsal; (B) pediger 5 and P5 – note short posterolateral hairs. C–E. Male [paratype, Lazarevskoye, IZAN]: (C) posterior end of caudal rami with setae, focused on ventral surface; (D) third exopodal and endopodal segments of P3 with spatulate setae; (E) pediger 5 and P5. Scale bar = 20 μm.

surface in P1–P3 and longer spinules in P4 (frontal surface could not be verified). Distal margin of P4 intercoxal sclerite naked. Setulation of P4 coxopodite seta more sparse on lateral margin yet without gap. Setae spatulate (cf. Fig. 9D) on exp3 and enp3 in P3 and P4. P4 enp3 2.0–2.3 times as long as wide, medial apical spine 1.3–1.5 times as long as lateral spine and 1.0–1.1 times as long as segment. None of setae of article reaching tip of medial apical spine. Length of P5 segment, medial spine, median and lateral setae: 12 μm,

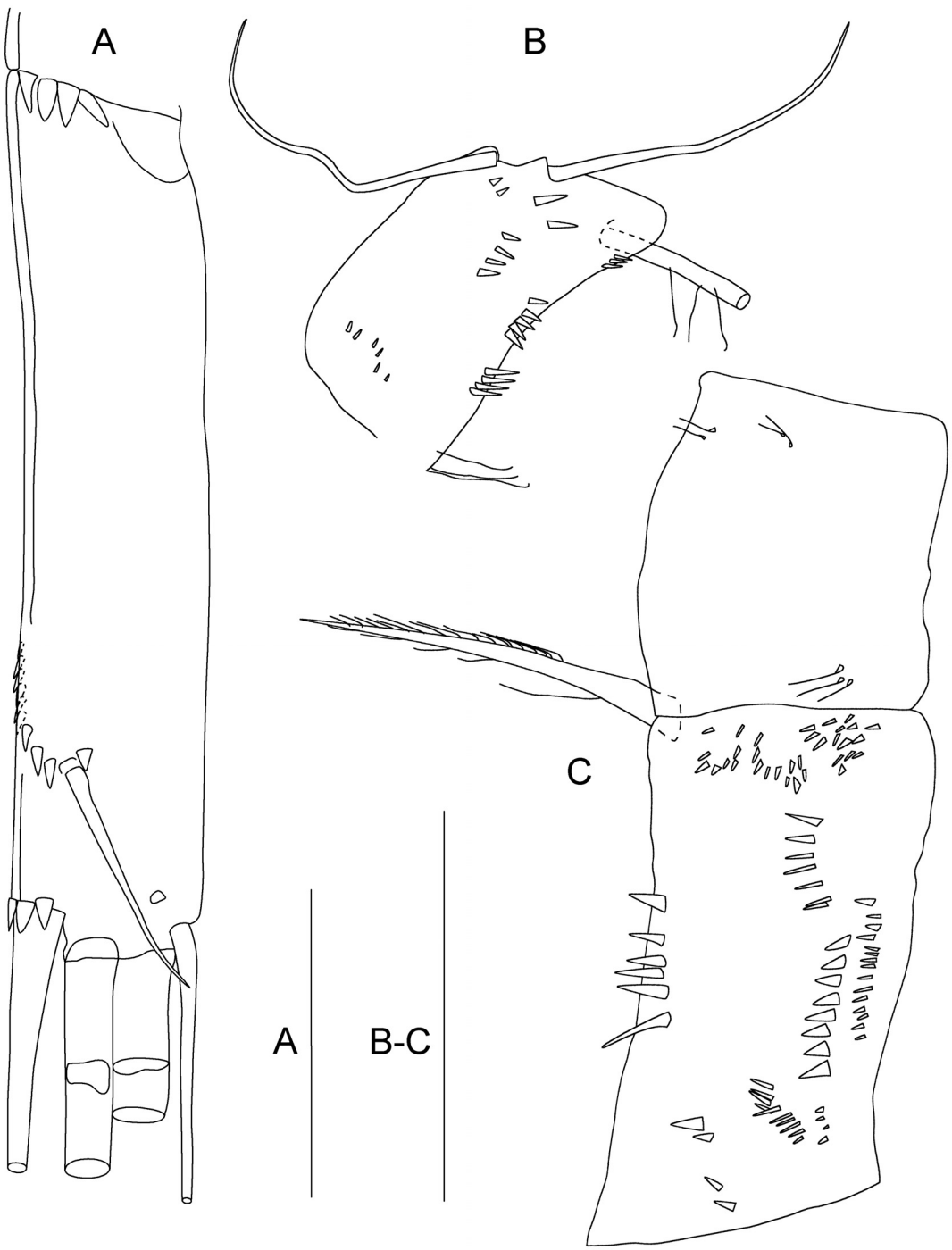

Figure 10. *Eucyclops persistens tauricus* Monchenko et Sopova, female paratypes: (A) caudal ramus, dorsal [IZAN: ♀-1]; (B) antennal coxobasis, posterior [IZAN: ♀-2]; (C) P4 coxopodite and intercoxal sclerite, posterior [IZAN: paratype ♀-1]. Scale bar = 50 μm.

22 μm, 40 μm and 24 μm, respectively (single paratype). P6 bearing three elements; length of medial spine, median and lateral setae, 23–26 μm, 23–24 μm and 26–35 μm, respectively.

Discussion

Taxonomic application of the subspecies concept have been criticized by several copepodologists (e.g., Einsle 1975, Nilssen 1979, Elgmork and Halvorsen 1998, Brancelj and Karanovic 2015, just to mention a few). The subspecies concept have remained particularly problematic in the subterranean taxa, in which (sub)species descriptions were often based on small material from single locality, and geographic isolation of the populations seems to be a rule rather than exception. Either "lumping" (favouring polytypic species with wide geographic range) or "splitting" (dividing polytypic taxa to species with less morphological variation and narrower range) can be justified if the taxonomic decision is supported by extensive set of data on the geographic variation of the diagnostic characters, and thorough knowledge of other morphological features and the geographic distribution of taxa (e.g., Stoch and Pospisil 2000a,b). Braby *et al*. (2012) provided a thought-provoking review of the subspecies concept, discussing the differences between 'evolutionary significant units' (ESUs), subspecies and species under the general lineage concept of species (de Queiroz 2007). The authors propose that "the definition of subspecies be restricted to extant animal groups that comprise evolving populations representing partially isolated lineages [a type of ESU] of a species that are allopatric, phenotypically distinct, and have at least one fixed [heritable] diagnosable character state, and that these character differences are (or are assumed to be) correlated with evolutionary independence according to population genetic structure". Also, Braby *et al*. (2012) advocate "the recognition of a single species (with two or more subspecies) as the null hypothesis for a given set of allopatric populations (lineages)", unless additional evidences, such as reciprocal monophyly or characters associated with reproductive isolation would support a species-level divergence of the allopatric populations. Here we follow this line of thought.

Eucyclops persistens s.l. is known only from the Black Sea region (Fig. 11). *Eucyclops persistens* s. str. was found in brackish interstitial waters (salinity between 0.05 and 0.14%) in the banks of small Caucasian rivers (Kintrishi in Georgia; Psezuapse in Krasnodarskiy Kray, Russia). *Eucyclops persistens tauricus* was described from freshwater wells in Crimea (Simferopol, Ukraine), ~ 400 and 700 km from the two Caucasian occurrences of the nominotypical subspecies (Monchenko 1978, Monchenko and Sopova 1984).

Eucyclops persistens tauricus differs from *E. persistens* s. str. in the lateral surface ornamentation of the caudal rami in female: a short "serra" is present in *E. persistens tauricus* (Fig. 9A), while the "serra" is absent in *E. persistens* s. str. The short-serra state appeared in all the three females of *E. persistens tauricus* and it was absent in all the four females of *E. persistens* s. str. examined by us. Monchenko and Sopova (1984) used the relative lengths of the caudal setae to separate *E. persistens tauricus* from the nominotypical subspecies. According to these authors *E. persistens tauricus* has relatively longer caudal setae VII (both in female and male), seta VI (male) and seta III (male). Monchenko and Sopova (1984) compared females from both Caucasian localities (Kobuleti and Lazarevskoye) to those from Crimea, while the morphometric traits in male were compared between single Caucasian (Lazarevskoye) and Crimean population. Our very few data fit the trends observed by Monchenko and Sopova (1984), except for the length proportions measured in the Kobuleti male of *E. persistens* s. str. (Table 2.). With the exception of seta VII/caudal rami index, in other indices the male from Kobuleti (Georgia) is definitely closer to the Crimean *E. persistens tauricus*, than to *E. persistens* s. str. from Lazarevskoye (Kransnodarskiy Kray, Russia). This might indicate a significant variation of the morphometric traits in question between the Caucasian populations, implying that those features at least might fail to distinguish the Caucasian populations from the Crimean ones. We need more data on the interpopulation variation of these characters to test whether *E. persistens* s. str. and *E. persistens tauricus* would really differ in these morphometric features.

Monchenko (1998, 2003) considered *Eucyclops persistens* to be a member of the Ponto-Caspian fauna-complex, and hypothesized the freshwater *E. persistens tauricus* to be the "direct ancestor" of *E. persistens* s. str. Also, Monchenko (2003) supposed a close relationship between *E. macrurus* (Palearctic, surface waters) and *E. persistens*, while *E. orthostylis* Lindberg, 1952 (Volga estuary), another Ponto-Caspian representative of the genus with smooth caudal rami, was thought to be more distantly related to *E. persistens*.

Comprehensive analysis of the evolutionary relationships within *Eucyclops* (~120 species) has not yet been attempted. Recent studies (Ishida 2002, Alekseev *et al*. 2006, Chang 2009, Alekseev 2010, Alekseev and Defaye 2011) have greatly improved our understanding of the morphology and geographic distribution of *Eucyclops* in the Palearctic region (~40 species including also the East Asian taxa), yet subterranean representatives of the genus have so far received less attention.

Eucyclops persistens share the reduced-serra state of the caudal rami with some European subterranean taxa. The caudal rami are laterally smooth in *E. graeteri* s. str. (Chappuis, 1927), *E. graeteri inarmatus* Kiefer, 1932, *E. graeteri damianae* Petkovski, 1971, *E. graeteri naphaeus* Petkovski, 1971, or bearing short "serra" consisting of few spinules in *E. graeteri intermedius* Damian, 1955 and *E. graeteri scythicus* Pleşa, 1989. *Eucyclops miurai* Ito, 1952 a Japanese subterranean species with smooth caudal rami, reported from Hokkaido, Honshu and the Ryukyu Islands (Ito 1952, 1954, 1962), is deemed to be also closely related to (or even a synonym of) *E. graeteri* (Dussart and Defaye 2006). Almost all members of the *graeteri*-complex have uncertain taxonomic position, therefore we provisionally used the names that are currently provided by the website "Fauna Europaea". Insufficient knowledge of the surface ornamentation of the limbs, and little information on the intraspecific variation of the morphological characters hamper discussion of the relationships of these taxa to *E. persistens*. All the more, that short "serra" (reduced to few spinules) or laterally smooth caudal rami are present in several tropical or subtropical *Eucyclops* species in the eastern hemisphere. "Serra" is absent in the African *E. laevimargo* (G.O. Sars, 1909), *E. angustus* (G.O. Sars, 1909), *E. dubius* (G.O. Sars, 1909), *E. caparti* Lindberg, 1951, *E. congolensis* Lindberg, 1951 and *E. bathanalicola* Boxshall et Strong 2006. With the exception of *E. bathanalicola* parasitic on a gastropod in Lake Tanganika, all the other African species are free-living and occur in surface waters. "Serra" is reduced to few spinules in *E. rarispinus* G.O. Sars, 1909 and *E. paucidenticulatus* Lindberg, 1951 from Lake Tanganika, *E. madagascariensis* (Kiefer, 1926) from Madagascar, *E. elburziensis* Lindberg, 1941 and *E. farsicus* Lindberg, 1941 from Iran, *E. defectus* Lindberg, 1937 from India, *E. thienemanni* Kiefer, 1930 from Java, *E. ruttneri* Kiefer 1933 from Sumatra Java and Australia, *E. neocaledoniensis* Dussart, 1984 from New Caledonia, *E. biwensis* Ishida, 1998 from Japan (Honshu). With the exception of *E. neocaledoniensis* known only from interstitial waters (psammon), none of these species is obligate subterranean. "Serra" is absent in putative close relatives of the genus, *Afrocyclops*, *Australoeucyclops*, *Ochridacyclops*, and *Paracyclops* (Karaytug 1999, Karanovic 2006). The outgroup comparisons and occurrence of smooth caudal rami in both some surface water and stygobiotic representatives of *Eucyclops* might indicate that complete lack of the "serra" in the *graeteri*-complex and *E. persistens* is an ancestral state rather than an apomorphic character loss in a subterranean clade. If such a character polarization would be correct, *E. persistens tauricus* can be defined by an apomorphy (i.e. the short-serra state), while *E. persistens persistens* retaining the plesiomorphic state of the caudal rami might be paraphyletic to *E. persistens tauricus*. The transformation in the relative length of the dorsal caudal seta, another character distinguishing these subspecies, might perhaps support monophyly of *E. persistens persistens*, but we lack information to infer the polarity of this character.

On the other hand, outgroup comparisons in the genera mentioned above indicate that reduced pilosity

Table 2. Differentiation between *Eucyclops persistens* s. str. and *Eucyclops persistens tauricus* in the relative lengths of the caudal setae. Means and standard deviation values of the relative lengths of the caudal setae are taken from Monchenko and Sopova 1984. Subscript numbers show the number of specimens measured; lack of subscript number means that data refers to single specimen. "III" to "VII" code caudal setae (for explanation see Materials and methods); body-l, total body length; caudr-l, length of caudal rami; K, Kobuleti (Caucasus, Georgia), L; Lazarevskoye (Caucasus, Russia); S, Simferopol (Crimea, Ukraine); SD, standard deviation. For female comparisons, from among the two Caucasian populations the Kobuleti population was chosen, as standard deviation values were available for the Kobuleti females only; the Kobuleti females showed slightly less difference in the morphometric features from the Crimean females than the Lazarevskoye population did (Monchenko and Sopova 1984).

In %	*E. persistens* s. str.			*E. persistens tauricus*		
	mean	SD	our study	mean	SD	our study
♀: VII/V	K: $11.6_{(20)}$	0.57	K: $12.4\text{-}13.8_{(3)}$	S: $13.6_{(21)}$	1.04	S: $12.7\text{-}16.8_{(2)}$
♂: VII/caudr-l	L: $51.9_{(8)}$	6.94	L: 43, K: 57	S: $71.6_{(19)}$	5.37	S: $60\text{-}72_{(2)}$
♂: VII/IV	L: $17.0_{(8)}$	2.33	L: 17, K: 19	S: $22.5_{(19)}$	2.00	S: 19.1
♂: VI/body-l	L: $7.64_{(8)}$	0.72	K: 11.0	S: $13.7_{(19)}$	3.16	S: 9.7
♂: VI/V	L: $16.3_{(8)}$	0.84	L: 17.1	S: $25.4_{(19)}$	2.16	S: 25.0
♂: VI/IV	L: $24.9_{(8)}$	1.20	L: 25.2, K: 39	S: $40.6_{(19)}$	2.89	S: 39
♂: VI/caudr-l	L: $75.6_{(8)}$	3.51	L: 63, K: 110	S: $128_{(19)}$	7.14	S: $110\text{-}120_{(2)}$
♂: III/caudr-l	L: $39.4_{(8)}$	4.52	L: 33, K: 50	S: $53.9_{(19)}$	5.22	S: $45\text{-}48_{(2)}$

on the dorsolateral surface of pediger 5 (hairs absent in *E. graeteri* s. str. and *E. graeteri inarmatus*; sometimes reduced to few short hairs in *E. graeteri scythicus*; and short in *E. persistens*) might be a phylogenetically informative (apomorphic) feature in some *Eucyclops* with reduced or complete lack of "serra". Pediger 5 is laterally pilose in *E. graeteri intermedius*, *E. graeteri damianae*, *E. graeteri naphaeus*, *E. orthostylis, E. macrurus* and *E. miurai*.

Reduced (or lack of) pilosity on the distal margin of P4 intercoxal sclerite (Figs 5D; 6A; 10C) has been observed in *E. graeteri inarmatus*, *E. graeteri intermedius*, *E. graeteri naphaeus* and *E. miurai* in the *graeteri*-complex (data from Kiefer 1932, Ito 1952, 1954, Pesce and Maggi 1979, and Petkovski 1971). Hairs are long but restricted to lateral part of the sclerite in *E. macrurus*; the character state is unknown in other members of the *graeteri*-complex and *E. orthostylis*. Lack (or few) hairs on the distal margin of P4 intercoxal sclerite is an uncommon feature in *Eucyclops*, therefore it might be worth to test diagnostic/phylogenetic significance of this character. The same holds for the long-aesthetasc state on the ninth antennulary segment in female (Fig. 2B), shared with *E. graeteri* (data from Lescher-Moutoué 1975); the character state is unknown in all the other members of the *graeteri*-complex.

The *graeteri*-complex in Europe occurs in Jura Mts. in France (*E. graeteri* s. str.), Switzerland (*E. graeteri* s. str. and *E. graeteri intermedius*), Danube valley in Austria (*E. graeteri* s. str.), mainland Italy and Sardinia (*E. graeteri* s. str., *E. graeteri intermedius* and *E. graeteri damianae*), Macedonia (*E. graeteri naphaeus*), Dalmatian coast in Croatia (*E. graeteri inarmatus*), western Bulgaria (*E. graete-ri intermedius*), Western Romanian Carpathian Mts. (*E. graeteri intermedius* and *E. graeteri damianae*), Dobruja (*E. graeteri scythicus*) in Romania, and Zakarpattia region in Ukraine (*E. graeteri* s. str.) (Graeter 1907, Chappuis 1927, Kiefer 1932, Damian 1955, Petkovski 1971, Pleşa 1971, 1989, Lescher-Moutoué 1975, Pesce 1978, Pesce and Maggi 1979, Pandourski 1992, 1994, 1999, Pospisil 1994, Stoch 2000, Mykitchak 2014, website "Cheklist of the Italian fauna").

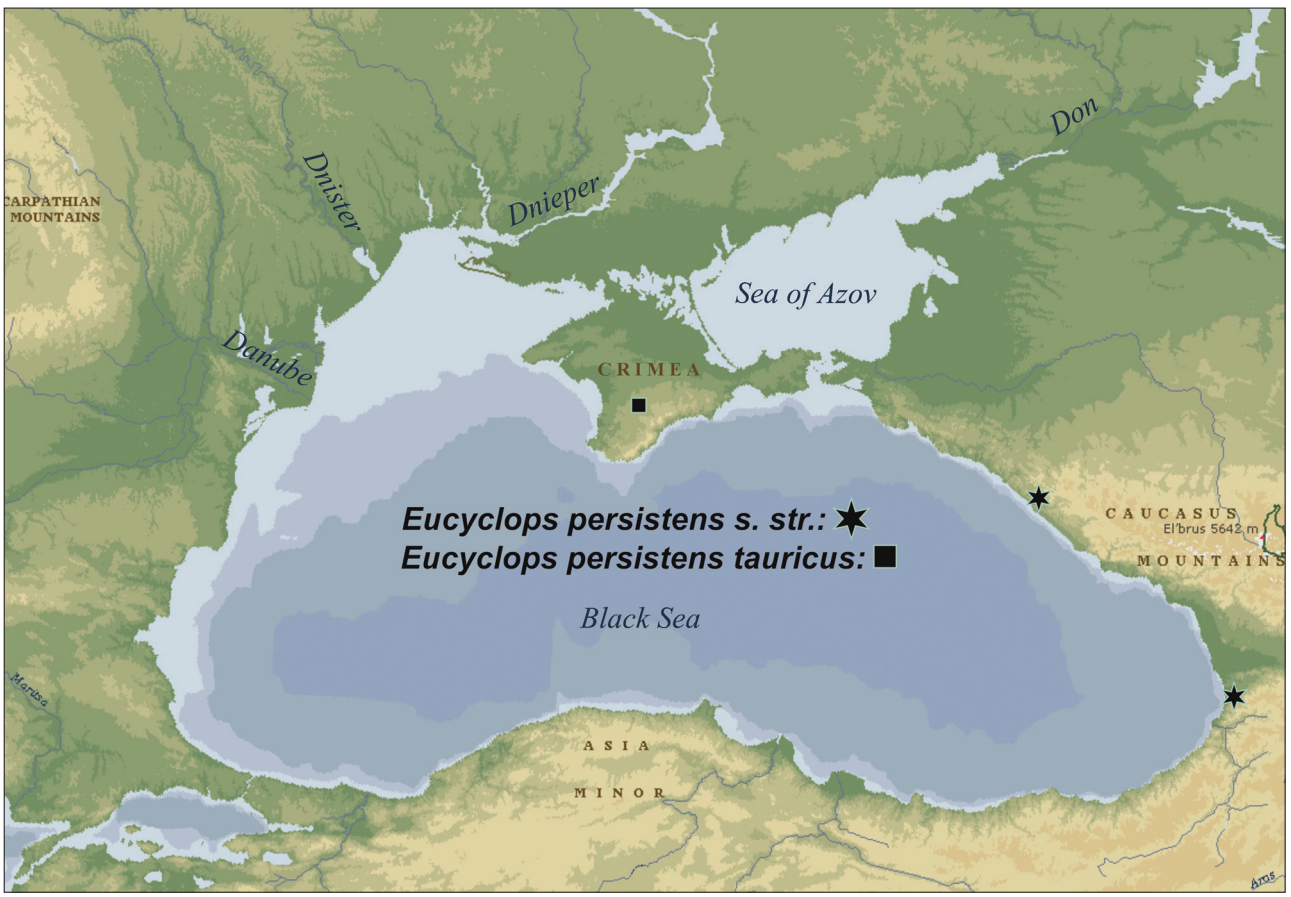

Figure 11. Geographic distribution of *Eucyclops persistens* s.l.

For species-diagnostic use, we here list the species distinguishing characters in the *graeteri*-complex. *Eucyclops graeteri* s. str. and *E. graeteri inarmatus* differ from *E. persistens* in the surface ornamentation of pediger 5 in female: posterolateral hairs are absent in *E. graeteri* s. str. and *E. graeteri inarmatus*, while short hairs are present in *E. persistens*. The brush setae on the male antennule have pointed tip in *E. graeteri* s. str. (data from Boxshall and Kihara 2011), while the homologous setae have wide apex (Fig. 8A) in *E. persistens*. Setae on the third endopodal segment of P4 are long, reaching beyond the tip of the longer (medial) apical spine of the segment in *E. graeteri intermedius, E. graeteri damianae* and *E. graeteri naphaeus*, while these setae are spatulate and short, not reaching the tip of the medial spine in *E. persistens*. Length and width proportion of the caudal rami in female distinguishes *E. persistens* (~4–5) from *E. orthostylis* (6.4–7.5), *E. macrurus* (8–10), and *E. graeteri scythicus* (2.3–3.0). The length proportion of caudal setae VI and III in female also separates *E. persistens* (1.8–2.2) from *E. orthostylis* (1.1–1.3) and *E. graeteri naphaeus* (1.3).

A future revision of the *graeteri*-complex could not only fix the taxonomic position of these taxa, but might also elucidate the evolutionary relationships of *E. persistens* in a wider European (Paratethys connections?) context.

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