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New arietellid copepods (Calanoida, Arietellidae) from anchialine caves in the Eastern Adriatic Sea

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Abstract

Two new species of calanoid copepods are described; *Metacalanus adriaticus* sp. nov. from an anchialine cave on Vis Island, and *Paramisophria tvrtkovici* sp. nov. from Orljak Cave, located in the lower part of River Krka estuary, near the town of Šibenik (Croatia). This is the first report of arietellid copepods found in any anchialine cave along the coast of the Adriatic Sea. In *M. adriaticus* sp. nov. the antennules are asymmetrical in both sexes (the female left antennule is 18-segmented, right 20-segmented; male left 16-segmented and right 20-segmented); the uniramous fifth legs of the female are 2-segmented; the terminal segment of the fifth leg in both sexes is the longest; and in the male the fifth leg exopod is 2-segmented. In *P. tvrtkovici* sp. nov. the antennules of both sexes are asymmetrical with the left antennule longer than the right, the female antennule is 21-segmented on both sides; the male left antennule is 19-segmented, the right 21-segmented; the armature of the terminal exopod segment of leg 1 is II, 2 ,2; the male fifth legs have a rudimentary endopod on the left leg, the third exopodal segment is smallest and bears three unequal processes on its outer margin, and the terminal spine is completely separated from the segment. On the right leg the third segment carries two short, unequal processes on its outer distal margin, as well as a long sigmoidal spine which is fused to the segment. It is inferred that, after the last glaciation, these new Arietellids moved out from their southern Adriatic refuge, colonizing first the anchialine habitats of the outer eastern Adriatic islands and then spreading along the coast.

Key words: Stygofauna, Copepoda, Arietellididae, anchialine caves, Adriatic Sea

Introduction

Members of the calanoid family Arietellidae Sars, 1902 are widely distributed in oceanic plankton and are known to occur from the epipelagic to the bathypelagic zones. Only two species have been recorded thus far from the plankton community of the Adriatic Sea. The relatively rare species *Arietellus pavoninus* Sars, 1905 was mentioned by Shmeleva (1964) as occurring in the southern Adriatic. The epipelagic *Arietellus setosus* Giesbrecht, 1882/3 is slightly more common: Gamulin (1979) noted its presence in the central Adriatic but its overall abundance was low, while Hure & Kršinić (1998) found it sporadically throughout the Central and South Adriatic, mostly in deeper waters (1100-200 m).

Arietellids are also found in the near-bottom hyperbenthic zone and in both anchialine and littoral caves (Ohtsuka *et al.* 1994), and the eastern shore of the Adriatic Sea is a zone of Dinaric karst characterized by porous rock and numerous related geomorphological as anchialine caves (according to the redefinition of Bishop *et al.* (2015)). A special feature of these flooded caves is the reduced amplitude of the tidal oscillations within them. Thanks to the sustained efforts (since 2001) of the Bio-Speleological Society in Zagreb, preliminary investigations of copepods have been undertaken at 30 anchialine caves along the Croatian coast and on nearby islands. From a biogeographical perspective, the fauna of the Dinaric coast and associated islands generally exhibits a paralittoral distribution (see Sket, 1994, 1996). These samples contained multiple new calanoid species, several of which have already been described (Kršinić, 2005a, b; 2012; 2015).

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The morphological characteristics of the family Arietellidae were summarised by Boxshall & Halsey (2004), who also provided a key to the genera, updated from that produced by Ohtsuka *et al.* (1994). This key does not contain the two new genera established in 2005 by Ohtsuka et al. (2005); *Metacalanalis* Ohtsuka, Nishida & Machida, 2005 and *Protoparamisophria* Ohtsuka, Nishida & Machida, 2005. However, *Metacalanalis* can be distinguished from all other arietellids by the combination of an indistinctly 10-segmented antennal exopod, the presence of 6 outer setae representing the maxillulary epipodite, the presence of a single outer spine on the third exopodal segment of leg 1, and by the presence of 4 setal elements on the unsegmented exopod of the female fifth leg (Ohtsuka *et al.* 2005). *Protoparamisophria* can be distinguished from all other arietellids by the combination of the possession of 2 outer spines on the third exopodal segment of leg 1, an indistinctly 3-segmented exopod on the female fifth leg armed with 1 outer spine on the first segment, 1 on the second and 2 distally on the third, and by the presence of 2 distal setae on the endopod of leg 5 (Ohtsuka et *al.* 2005).

Many novel copepods have been described from littoral and anchialine cave ecosystems in recent years, including new species of the Arietellidae, belonging to the genera *Metacalanus* Cleve, 1901 and *Paramisophria* T. Scott, 1897 (Fosshagen, 1968; Ohtsuka, 1984, 1985; Ohtsuka *et al.* 1991; Ohtsuka *et al.* 1993; Jaume *et al.* 2000; Ohtsuka *et al.* 1994; Lim & Min, 2014; Zagami *et al.* 2019). Here we describe two new copepod species of the family Arietellidae which have been collected in anchialine caves along the coast of the Eastern Adriatic Sea.

Materials and methods

Specimens were collected between October 2004 and March 2020 during sampling expeditions in anchialine caves found along the eastern Adriatic coast from Rovinj to the Island of Mljet. The type locality for the new *Metacalanus* species is Supurina Cave on Vis Island in the Central Adriatic Sea. Supurina Cave is a shallow vertical cave with a narrow opening situated about 27 m from the tide line. The water column is 17.5 m deep and is in total darkness. It is not known whether it is directly connected with the open sea. The flooded parts of the cave are ornamented with stalactites and stalagmites, and the bottom is covered with a fine silt and detritus. The salinity in the water column below 3 m was between 37.00 ‰ and 38.00 ‰ while the temperature was approximately 15°C. The salinity and water temperature were measured simultaneously during sampling. The type locality for the new *Paramisophria* species is Orljak Cave, located in the lower part of the River Krka estuary, near the town of Šibenik. Orljak Cave has large opening situated 50 m from the estuarine coast: it extends for 90 m and has a height of up to 23 m. The water column within the cave is 7 m deep, it is in darkness and is well connected with the estuary. The temperature in column below 3 m was approximately 13°C and the salinity was 25 ‰ during summer 2009 (Cukrov *et al.* 2010; Geček *et al.* 2012).

Divers from the Croatian Natural History Museum (Zagreb) and the Croatian Bio-Speleological Society (Zagreb) made collections by hand-held hauls using a 20-cm diameter Nansen net with a 125 µm mesh. They sampled from the surface (0 m) to the floor of the cave. All samples were preserved in a 2.5% formaldehyde-seawater solution neutralized with $CaCO_3$. Specimens were dissected on slides in lactophenol. Drawings were made with the aid of a *camera lucida* on an Olympus BX51 differential interference contrast microscope. Specimens were measured using an ocular micrometer. The descriptive terminology employed largely follows Huys & Boxshall (1991).

Taxonomy

Order Calanoida Sars, 1903

Family Arietellidae Sars, 1902

Genus *Metacalanus* Cleve, 1901

Metacalanus adriaticus sp. nov.

(Figs 1-6)

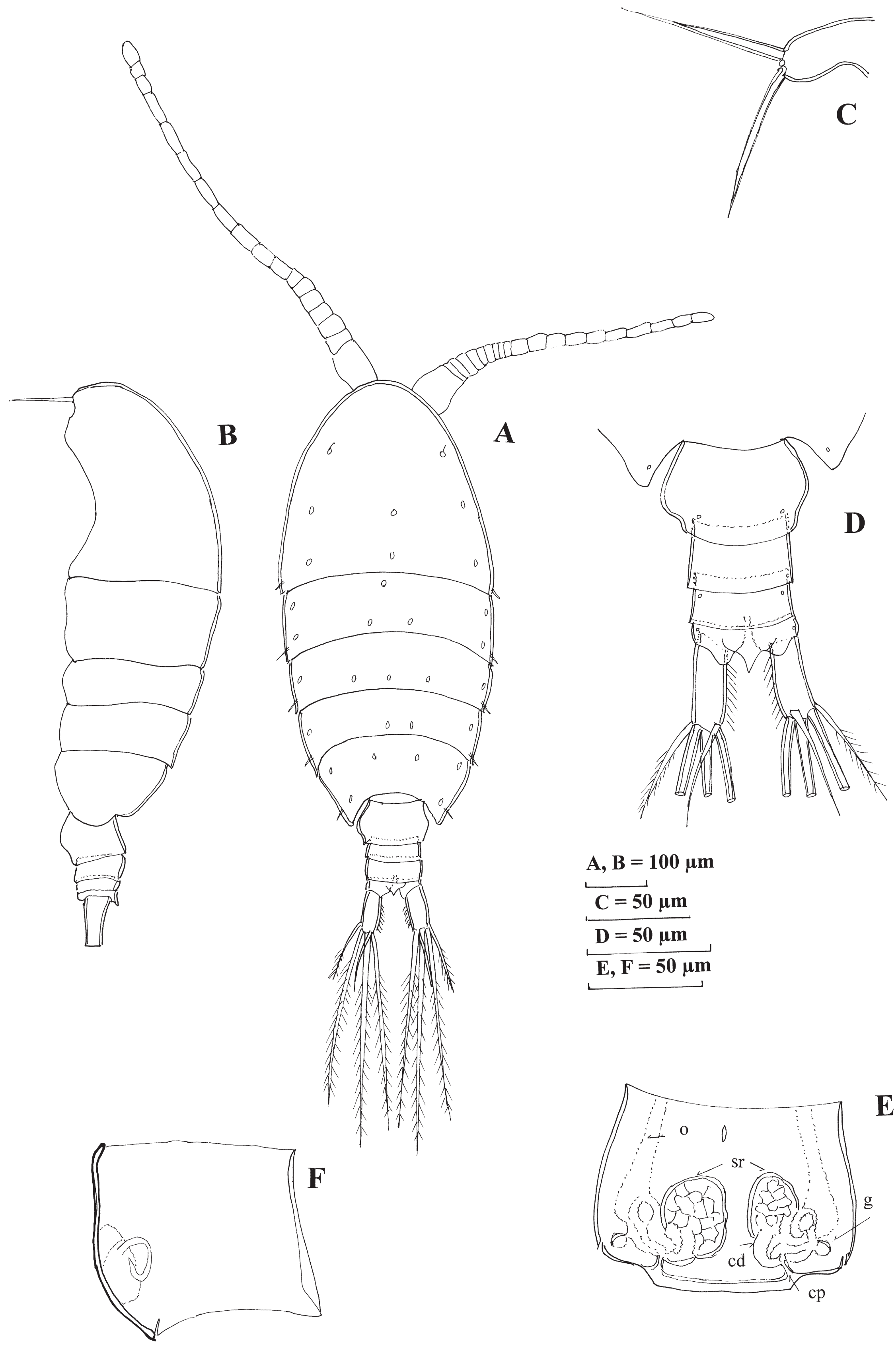

FIGURE 1. *Metacalanus adriaticus* sp. nov. adult female, paratype; (A) habitus, dorsal view showing positions of integumental pores and sensillae; (B) habitus, lateral; (C) rostrum; (D) urosome and caudal rami, dorsal view; (E) genital double-somite, ventral showing reproductive system, cd: copulatory duct, cp: copulatory pore; g: gonopore; o: oviduct; (F) genital double-somite, lateral.

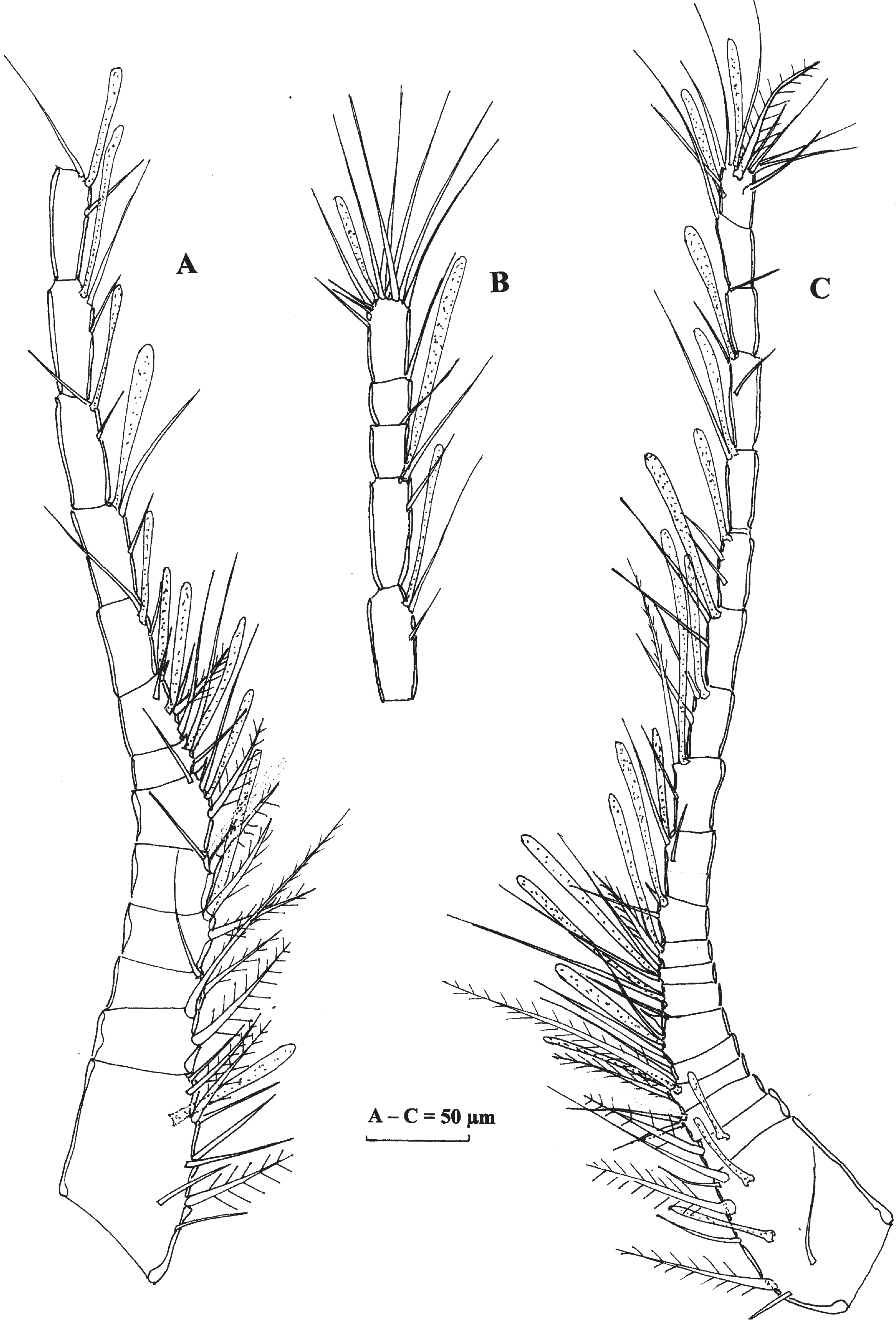

FIGURE 2. *Metacalanus adriaticus* sp. nov. adult female, paratype; (A,B), left antennule; (C) right antennule.

Material examined: *Holotype*: An adult female 880 µm in length from Supurina Cave, on Vis Island in the Central Adriatic Sea in Croatia (43º03'0.8"E;16º03'0.7"N), on 13 August 2007. The Holotype is deposited at the Croatian Natural History Museum, Zagreb, No. HPM-BSZ,1805; the paratype series comprises nine adult females and four males from different locations: 3♀, Supurina Cave, collected on 14 December 2017; 1♀, Supurina Cave collected in 2019; 1♀, Rogoznica, 11 January 2009; 2♀, ŽivaVoda, Hvar, 02 April 2005; 1♂, Supurina Cave, March 2019; and 1♂, Jama na punta Korente, Rovinj, 06 February 2005. These paratypes are all deposited at the Croatian Natural History Museum, Zagreb, No. HPM-BSZ,1806. Additional paratypes: 2♀ and 2♂ (Supurina Cave, 03 October 2005) were dissected on slides and are deposited in the first author's personal collection.

Etymology

This species is named after the Adriatic Sea.

Description

Female (Figures 1A, B) mean body total length (excluding caudal setae) 950 µm (± 50.2 µm, n=9), range 850 to 990 µm. Body calaniform in dorsal aspect. Nauplius eye absent. Prosome 5-segmented; cephalosome and first pedigerous somite separate. Rostrum well developed, rounded in dorsal aspect (Figure 1C). Prosome ornamented with integumental pores on dorsal surface and with sensillae dorsolaterally as indicated in Figure 1A. Proportional lengths of cephalosome and pedigerous somites; 50:13:11:11:15 = 100. Ratio of length of prosome to length of urosome, including caudal rami = 2.8:1. Prosome 2.1±0.08 (n=9, the paratypes) times longer than wide. Urosome 4-segmented (Figure 1 D): proportional lengths of urosomites and caudal rami 31:17:14:11:27 = 100. Genital double-somite (Figures 1F, E) about 1.3 times wider than long; genital area slightly asymmetrical, located anteroventrally, with paired seminal receptacles, gonopores and small copulatory pores. Anal somite small, with triangular operculum. Caudal rami symmetrical, about 2.4 times longer than wide; each ramus armed with 4 terminal setae corresponding to setae III-VI, and seta VII located on dorsal surface; setae I and II absent (Figure 1D).

Antennules (Figure 2) asymmetrical, left antennule longer than right and 18-segmented; right antennule 20-segmented, with segments 2 to 9 very short: segmentation and setation patterns for right antennule (Figure 2C) as follows: compound segment 1 (fused ancestral segments I-IV) 7 setae+2 ae; segment 2 (ancestral V) 1 seta+ae; segment 3 (ancestral VI) 2 setae; segment 4 (VII) 2 setae+ae; segment 5 (VIII) 1 seta; compound segment 6 (IX-X) 3 setae+process+ae; segment 7 (XI) 1 seta+ae; segment 8 (XII) 2 setae+ae; segment 9 (XIII) 1 seta+ae; segments 10 (XIV) 1 seta+1 spine+ae; segments 11 to 15 separate (ancestral XV to XIX) each with 2 setae +ae; segment 16 (XX) 1 seta+ae; segment 17 (XXI) 2 setae+ae; segments 18 and 19 (XXII and XXIII) each with 1 seta; compound apical segment 20 (ancestral XXIV-XXVIII) 10 setae+2 ae. Left antennule (Figures 2A,B) segmentation and setation patterns as follows: compound segment 1 (ancestral I-IV) 9 setae + 1 aesthetasc; segments 2 and 3 (V and VI) 2 setae each; segment 4 (VII) 2 setae+ae; segment 5 (VIII) 2 setae; compound segment 6 (IX-X) 2 setae+process+ae; segment 7 (XI) 2 setae+ae; compound segment 8 (ancestral XII-XIV) 4 setae+process+2 ae; segments 9 to 15 (ancestral XV to XXI) separate, each with 2 setae+ae; segments 16 and 17 (ancestral XXII and XXIII) 1 seta each; compound apical segment 18 (ancestral XXIV-XXVIII) 10 setae+ae.

Antenna (Figure 3A) biramous, with endopod longer than exopod. Coxa unarmed; basis with seta. Exopod 5-segmented with armature as follows: 1, 1, 1, 1, 3. Endopod 2-segmented, proximal endopodal segment twice as long as distal; distal segment armed with 2 unequal setae on lateral margin and 5 setae on apex.

Mandible (Figures 3B) gnathobase cutting edge armed with 4 heterogeneous teeth; ventralmost tooth separated from other 3 teeth by gap: dorsalmost tooth trifid at tip; dorsal margin ornamented with 4 minute spinules subdistally. Basis longer than wide, bearing inner seta representing vestige of endopod. Exopod 4-segmented, setal formula 1, 1, 1, 3.

Maxillule (Figure 3C) praecoxal arthrite ornamented with row of hair-like setules along inner margin and armed with 2 unequal spines distally; coxal endite bulbous, unarmed; coxal epipodite with 5 setae. Endopod absent; exopod swollen, armed with 3 long curved plumose setae apically.

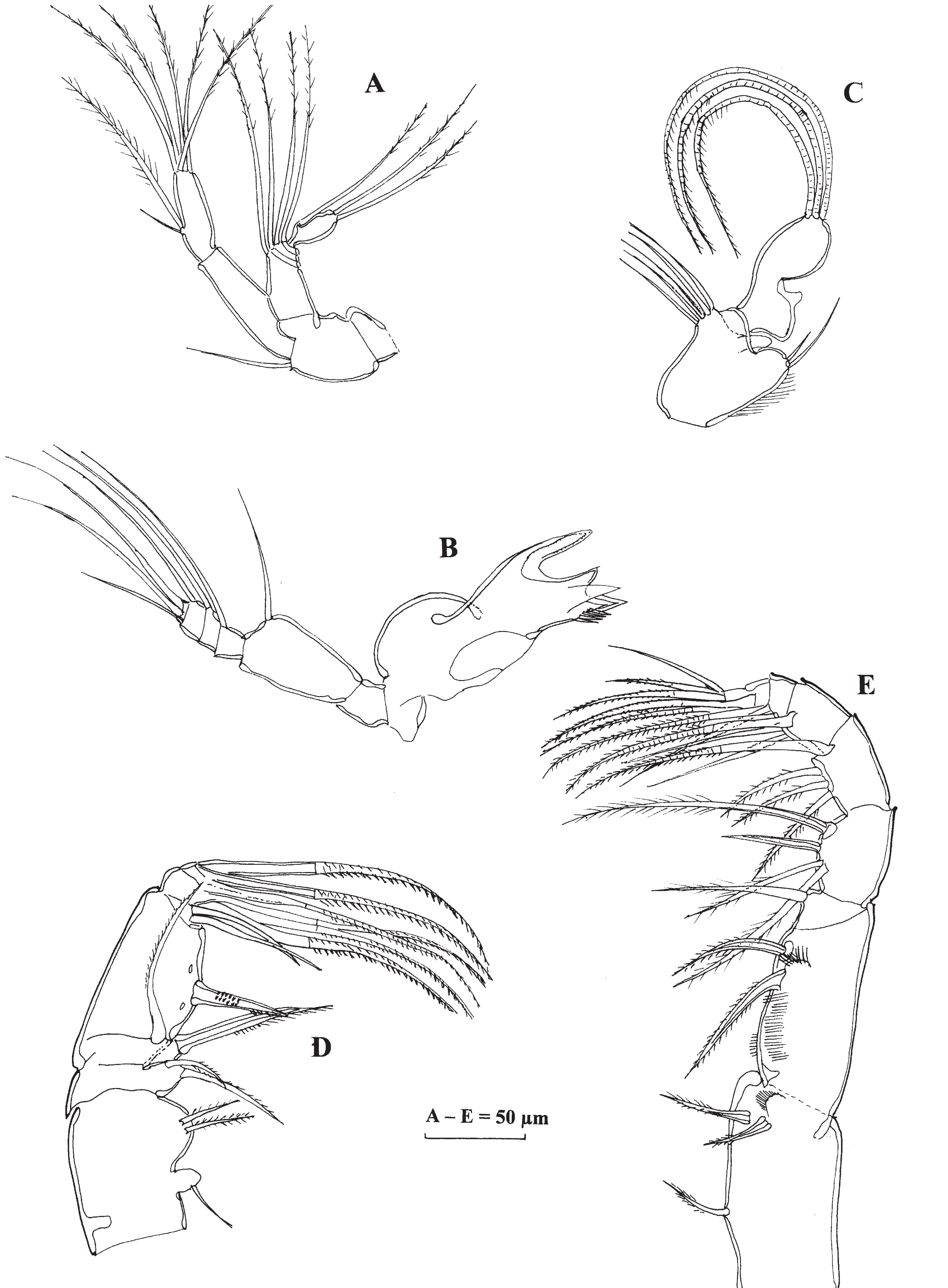

FIGURE 3. *Metacalanus adriaticus* sp. nov. adult female, paratype; (A) antenna; (B) mandible; (C) maxillule; (D) maxilla; (E) maxilliped.

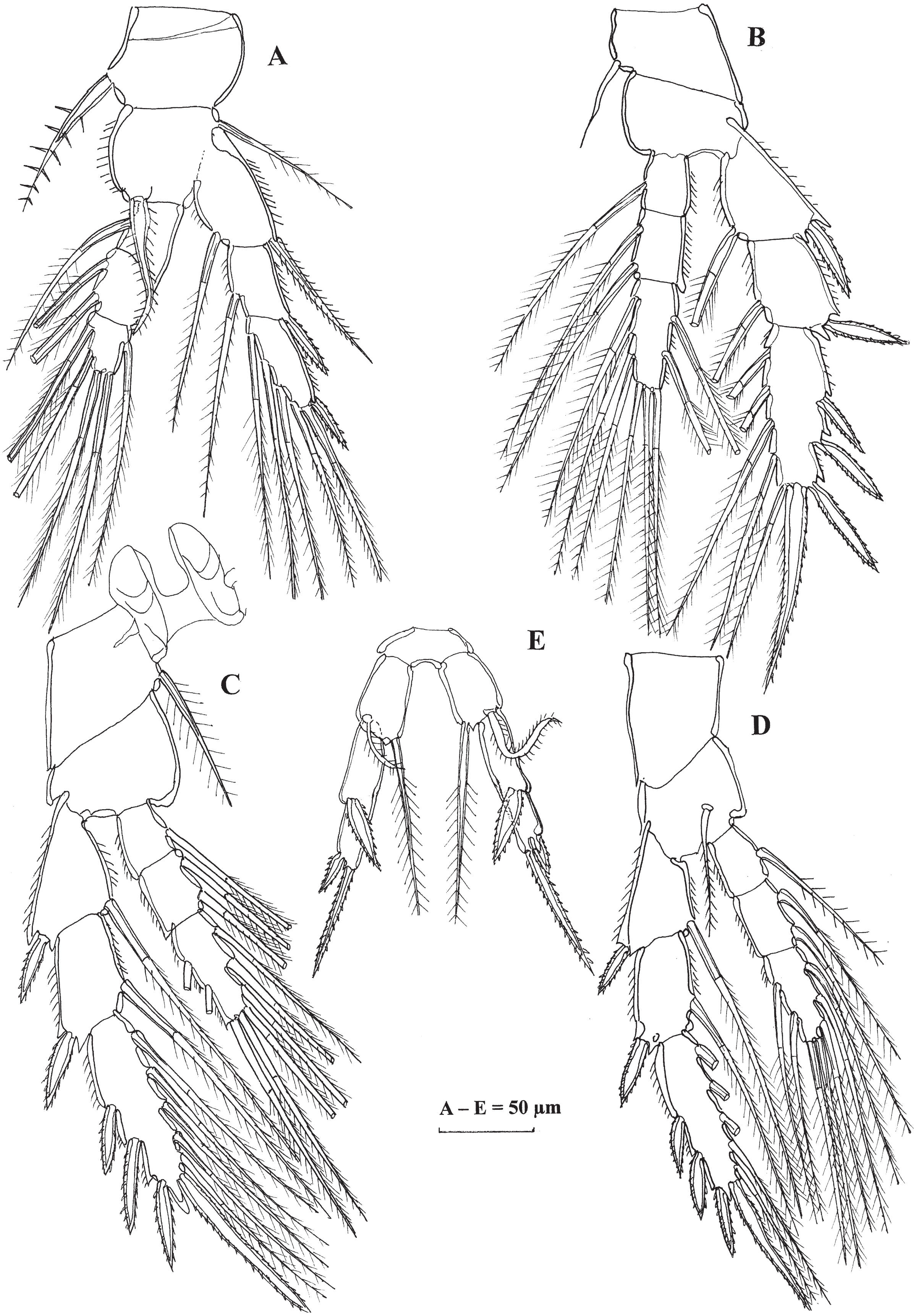

FIGURE 4. *Metacalanus adriaticus* sp. nov. adult female, paratype; (A) leg 1; (B) leg 2; (C) leg 3; (D) leg 4; (E) leg 5.

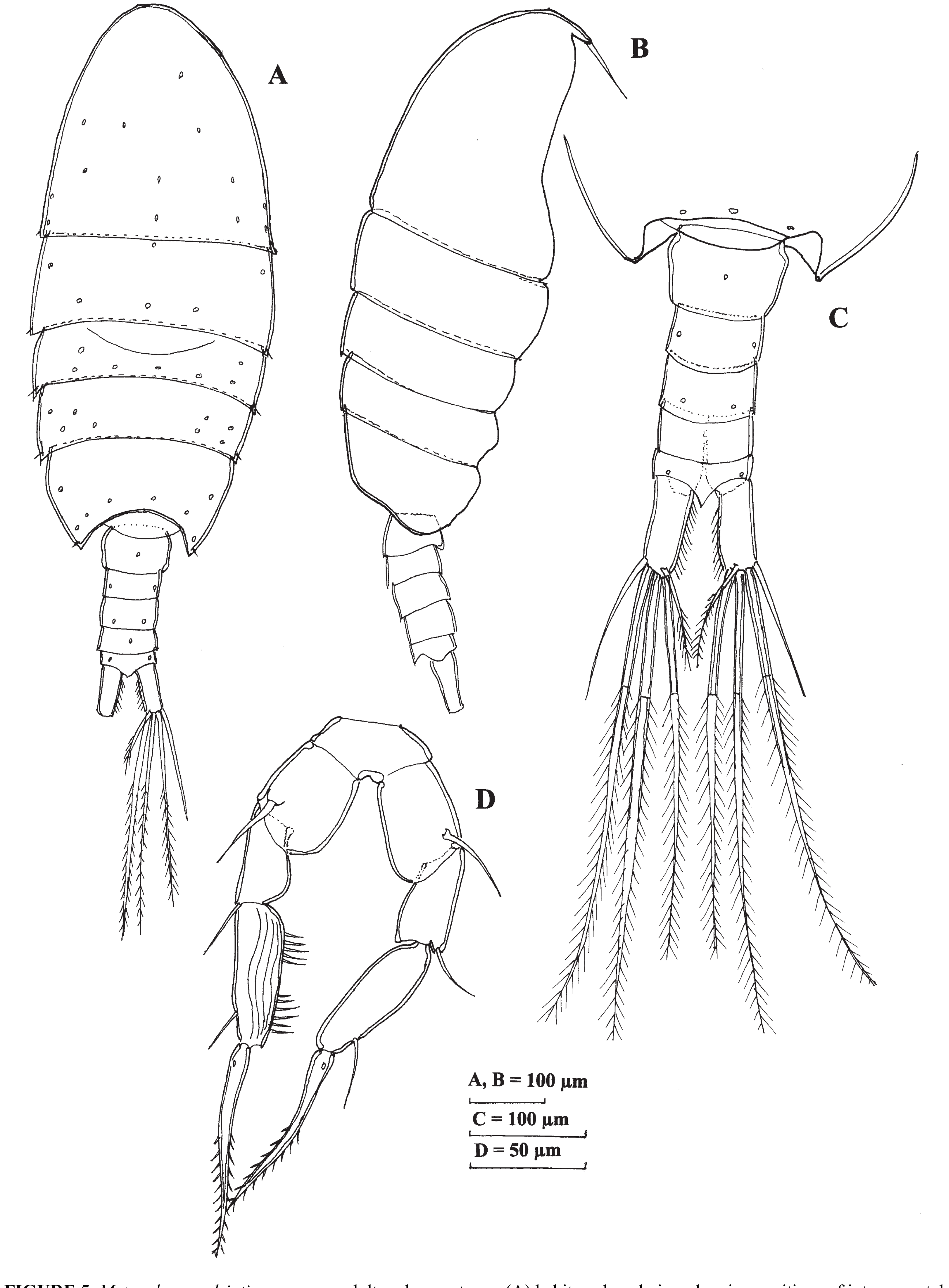

FIGURE 5. *Metacalanus adriaticus* sp. nov. adult male, paratype; (A) habitus, dorsal view showing positions of integumental pores and sensillae; (B) habitus, lateral view; (C); urosome and caudal rami, dorsal view; (D) leg 5, anterior view.

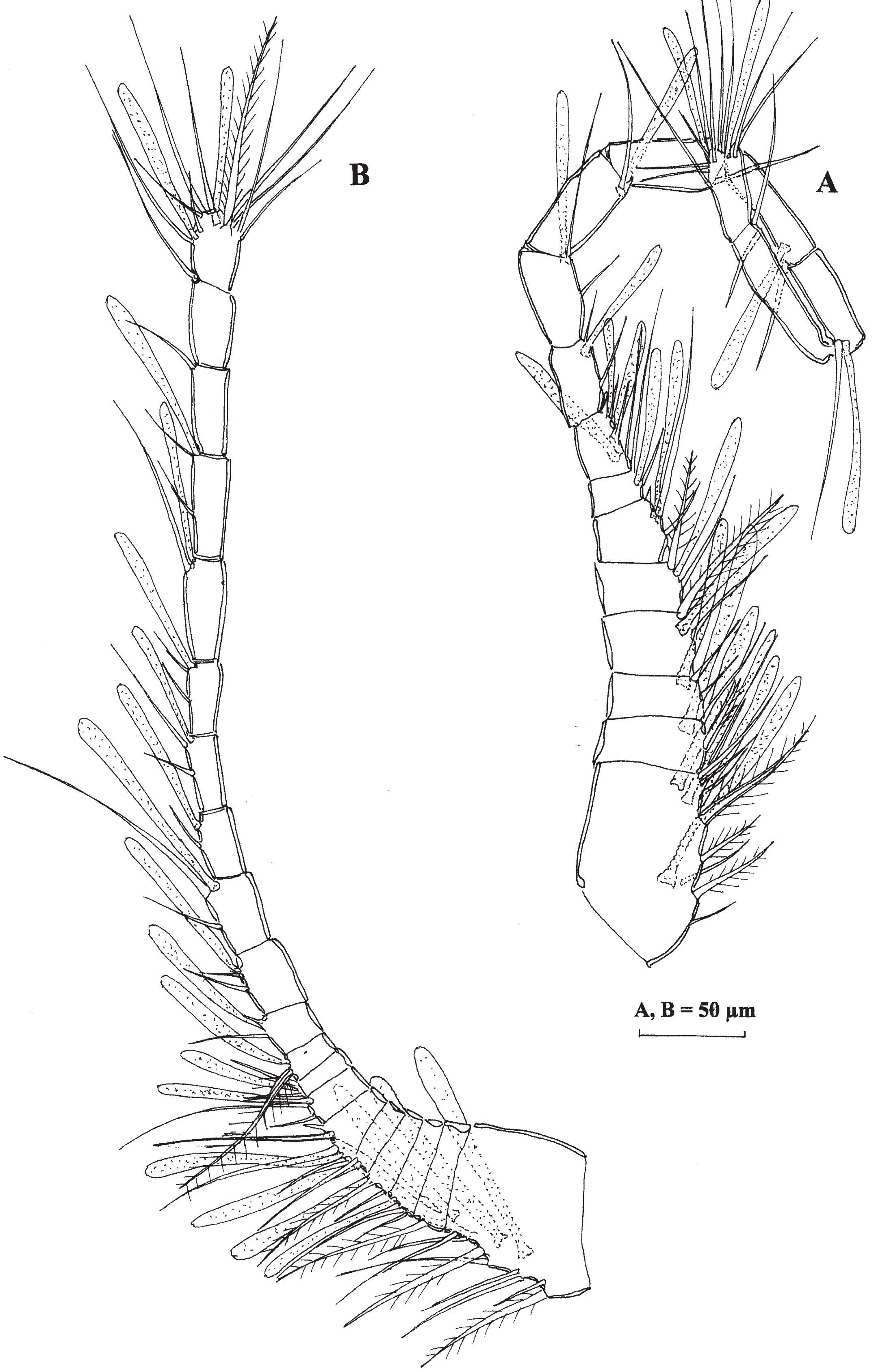

FIGURE 6. *Metacalanus adriaticus* sp. nov. adult male, paratype; (A) left antennule; (B) right antennule.

Maxilla (Figure 3D) praecoxa with slender naked seta and 1 minute, rudimentary element on first endite; second praecoxal endite with 2 short setae. Coxal endites each with 2 spinulose setae, proximal endite with 1 seta about twice as long as other, distal endite with stout seta on inner margin and long seta extending beyond distal margin of basis. Basis bearing stout spine ornamented with 2 short rows of minute spinules. Endopod 3-segmented; first segment with 2 short naked setae, second and third segments each with 3 long spines; spines ornamented bilaterally with rows of minute spinules in distal half.

Maxilliped (Figure 3E) with syncoxal endites incorporated into segment, represented by 1 seta about at mid-length and 2 setae plus small process fringed with small hairs distally. Basis armed with 2 setae on medial margin, and ornamented with fine spinules proximally on medial margin and tuft of minute spinules adjacent to insertion of distal seta. Endopod 6-segmented, with elongate sixth segment; armature formula 1, 4, 4, 3, 3, 4.

Legs 1- 4 (Figures 4 A-D) biramous with 3-segmented rami: armature formula as follows:

	coxa	basis	endopod	exopod
Leg 1	0-1	1-1	0-1; 0-2, 1, 2, 2	I-1; I-1; I, 1, 4
Legs 2 & 3	0-1	0-0	0-1; 0-2; 2, 2, 4	I-1; I-1; III, I, 5
Leg 4	0-0	1-0	0-1; 0-2; 2, 2, 3	I-1; I-1; III, I, 5

Basis of leg 1 ornamented with fine spinules along inner margin. Exopodal segments of legs 1– 4 ornamented with spinules along both inner and outer margins; endopodal segments on outer margins only.

Fifth legs (Figure 4E) uniramous, 2-segmented, almost symmetrical. Coxae fused with intercoxal sclerite; basis of right leg longer than on left, and bearing thicker plumose seta. Endopod represented by large plumose seta at inner distal corner of basis. Exopod 1-segmented, about 2 times longer than basis; armed with 3 spines, very stout bipinnate spine located about at mid-length, much smaller spine subterminally on outer margin, plus long apical spine.

Male (Figures 5A, B) mean total length 892 µm (± 69.9 µm, n=4), range 800 to 960 µm. Prosome 2.4 times longer than wide. Cephalosome and pedigerous somites similar to those of adult female; proportional lengths: 46:17:11:11:15 = 100. Rostral area as in female. Prosomites ornamented with integumental pores on dorsal surface and sensillae as indicated in Figure 5A. Prosome: urosome length ratio = 2.6: 1. Urosome 5-segmented (Fig. 5C); proportional lengths of urosomites and caudal rami: 20:15:14:12:10:29 = 100. Genital somite symmetrical, wider than long, not expanded ventrally. Caudal rami and anal operculum as in female.

Antennules (Figures 6A, B) asymmetrical, left antennule longer and 16-segmented, right antennule shorter and 20-segmented. Right antennule (Figure 6B) similar to that of female: compound segment 1 (fused ancestral segments I-IV) 8 setae+4ae; segment 2 (V) 1 seta; segment 3 (VI) 2 setae+ae; segment 4 (VII) 2 setae+ae; segment 5 (VIII) 1 seta+ae; compound segment 6 (fused ancestral IX-X) 3 setae+process+ae; segment 7 (XI) 2 setae+ae; segment 8 (XII) 2 setae+ae; segment 9 (XIII) 1 seta+ae; segment 10 (XIV) 1 seta+spine+ae; segment 11 (XV) 2 setae+ae; segment 12 (XVI) 2 setae+ae; segment 13 (XVII) 1 seta+ae; segment 14 (XVIII) 2 setae+ae; segment 15 (XIX) 2 setae+ae; segment 16 (XX) 1 seta+ae; segment 17 (XXI) 2 setae+ae; segments 18 and 19 (XXII and XXIII) each with 1 seta; compound apical segment 20 (ancestral XXIV-XXVIII) 10 setae+2 ae.

Left antennule geniculate between segments 14 (XX) and 15 (XXI): segmentation and setation pattern as follows: compound segment 1 (ancestral I-IV) 8 setae+4 ae; segments 2 to 5 (V to VIII) each with 2 setae+ae; compound segment 6 (IX-X) 2 setae+process+ae; segment 7 (X) 2 setae+ae; segment 7 (XI) 2 setae+ae; compound segment 8 (ancestral XII-XIV) 3 setae+process+3ae; segments 9 (XV) and 10 (XVI) each with 2 setae+ae; segment 11 (XVII) 1 seta+process+ae; segment 12 (XVIII) 1 seta; segments 13 and 14 (XIX and XX) each with 1 seta+ae; compound segment 15 (ancestral XXI-XXIII) 2 setae; and apical segment 16 (ancestral XXIV-XXVIII) 10 setae+2ae.)

Antenna, mouthparts and swimming legs 1-4 identical to those of female. Fifth legs (Figure 5D) asymmetrical, uniramous: coxae fused with intercoxal sclerite. Basis with naked seta; nearly equal on right and left leg. Endopod absent. Exopod long, 2-segmented, proximal segment with naked outer distal spine; distal segment longer than proximal armed with naked spine distally on outer margin plus large bipinnate spine apically; apical spine with integumental pore proximally; asymmetry expressed by concave surface of distal segment on right side and by presence of 2 patches of setules on inner margin of same segment.

Remarks

Ohtsuka *et al.* (1994) compared species of the genus *Metacalanus* from Okinawa with other arietellids and provided preliminary partial descriptions of two new species: *Metacalanus* species 1 (both sexes), and *Metacalanus* species 2 (female only). In addition to these unnamed species, four species were already known; *M. aurivillii* Cleve, 1901, *M. inaequicornis* (Sars, 1902), *M. acutioperculum* Ohtsuka, 1984, and *M. curvirostris* Ohtsuka, 1985. These known species have been reported in coastal waters, from the epipelagic as well as the shallow hyperbenthic zone. The new species, *M. adriaticus* sp. nov. was found exclusively in eastern Adriatic caves.

The female of the new species can be distinguished by its larger body size (850-990 µm) in comparison to *M. aurivilli* (530-650 µm) and *M. acutioperculum* (730 µm). *Metacalanus aurivilli* is found in the Indo-West Pacific and off eastern Australia (Greenwood, 1978), while *M. acutioperculum* was originally found in the Pacific, off the coast of Honshu, Japan (Ohtsuka, 1984) and has since been recorded from off the coast of Sicily, and in the Western Mediterranean (Campolmi *et al.* 1999). The remaining two named species have significantly larger females; *M. curvirostris* (1190 µm) which is found in Tanabe Bay, Japan, and *M. inaequicornis* (1100 µm) found off the Norwegian coast. The two unnamed species, *M*. species 1 and *M*. species 2, are similar body length to the new species.

The original description of *M. aurivillii* by Cleve (1901) lacked detail and contained numerous errors, so the comparisons here are based on the partial redescription of Greenwood (1978). There are major differences between *M. aurivillii* and the new species in the female fifth legs. In *M. aurivillii* the unsegmented exopod is broad (about 1.7 times longer than wide) and bears a sigmoid setal element distally on the outer margin plus two apical setae, a naked outer seta (about 1.4 times longer than the exopodal segment) and a long plumose inner seta (about 2.6 times longer than the segment). In contrast, in *M. adriaticus* sp. nov. the unsegmented exopod of the female fifth legs is slender (about 3.9 times longer than wide), and bears a stout bilaterally-spinulose spine on the outer margin plus 2 bilaterally-spinulose apical spines, the outer very short (only about 25% of the length of the inner apical spine) and the inner about as long as the segment. In addition, the basis of the female fifth leg carries the outer seta plus an inner seta representing the endopod in the new species, neither of these setae is present in *M. aurivillii. Metacalanus acutioperculum* has a female fifth leg with a broad unsegmented exopod which has very similar setation to that found in *M. aurivillii*. It also lacks the inner seta (representing the endopod) on the basis (Ohtsuka, 1984).

The new species is most readily distinguishable from *M. curvirostris* by the form of the female fifth legs, which are 3-segmented in *M. curvirostris* and bear a single apical spine (Ohtsuka, 1985) but only 2-segmented with 2 apical spines in *M. adriaticus* sp. nov. In addition, the rostrum is curved to the left in *M. curvirostris,* and the posterior angles of the prosome are rounded, as is anal operculum, whereas in the new species the rostrum is curved ventrally, and the posterior angles of the prosome and the operculum are triangular in shape. The praecoxal arthrite of the maxillule of the new species bears 2 unequal setae, whereas in *M. curvirostris* there is only a single minute seta, located on the apex. In addition, the male fifth legs are 5-segmented in *M. curvirostris* and bear a single long spine on the terminal segment, whereas in *M. adriaticus* sp. nov. they are 4-segmented and the terminal segment carries 2 spines.

Metacalanus inaequicornis has the most similar female fifth legs to the new species. They have a slender exopodal segment bearing a spine on the outer margin plus two unequal spines at the apex, the inner spine being about as long as the segment and markedly longer than the outer (Sars, 1902). In addition, setae representing the endopod are present on the basis in both species. However, the fifth legs differ in the lack of outer setae on the basis in *M*. *inaequicornis.* The anal operculum of *M*. *inaequicornis* is rounded and weakly developed whereas in the new species it is triangular with the apex extending well beyond the distal margin of the anal somite.

The new species has the same segmentation and setation pattern of leg 5 as the female of *Metacalanus* species 1 of Ohtsuka *et al.* (1994) but is readily distinguishable by the asymmetry of the genital double-somite of the female, in which the left gonopore and copulatory pore are completely absent. In addition, the male of *Metacalanus* sp. 1 has a 3-segmented exopod on the fifth leg including a small terminal segment, which contrasts with *M. adriaticus* sp. nov. which has a 2-segmented exopod.

Finally, the female fifth leg of the new species, with its unsegmented exopod, is very different than that found in *Metacalanus* species 2 of Ohtsuka *et al.* (1994), which has a 2-segmented exopod. These differences from the four nominal species and from the two as yet unnamed new species of Ohtsuka *et al.* (1994) are sufficient to justify the establishment of a new species to accommodate this material from caves along the Adriatic coast.

Genus *Paramisophria* T. Scott, 1897

***Paramisophria tvrtkovici* sp. nov.**
(Figs 7-12)

Material examined

Holotype: adult female, 1375µm in length, from Jama pod Orljakom cave, located in the estuary of the Krka River, in the central Adriatic Sea in Croatia (43º47'15.8964"E;15º50'16.962"N), collected on 19 October 2004: Holotype deposited in the Croatian Natural History Museum, Zagreb, No. HPM-BSZ,1807. The paratype series comprises eleven adult females and three males from the different locations. These are: 1 ♂, 1♀ Jama pod Orljakom cave, October 2004; 1♀ Supurina Cave, collected 10 March 2005; 1♀, Supurina Cave collected in 2019; 1 ♀ Živa Voda, Hvar, collected 02 April 2000; 1♀, Jama na punta Korente, Rovinj, collected 19 February 2005; 2♀, Vrtare cave, 07 October 2005; 1 ♀ Murter, 18 March 2005; 1 ♂, 1♀ Jama Zaglavica Cave, 10 April 2007 and deposited in the Croatian Natural History Museum, Zagreb, No. HPM-BSZ,1808. Additional paratypes, 2♀ and 1♂ (Supurina Cave, collected on 03 October 2005) were dissected on slides and deposited in first author's personal collection.

Etymology

This species is named in honor of Prof. Dr. Nikola Tvrtković, a prominent Croatian zoologist. His supportive investigations of anchialine caves along the eastern Adriatic coast have been extremely helpful.

Description

Female (Figures 7A, B) mean total length (excluding caudal setae) 1392.8 (±132.1 µm, n=7): range 1250-1625 µm. Body calaniform in dorsal aspect. Nauplius eye absent. Prosome 5-segmented; cephalosome and first pedigerous somite separate. Rostrum well developed with rounded tip in dorsal aspect, bearing paired rostral filaments (Figure 7C). Posterior corners of fifth pedigerous somite with dorsolateral processes. Prosome about 2.03 times as long as wide; proportional lengths of prosome segments: 51:15:11:6.5:16.5 = 100. Prosome: urosome (including caudal rami) length ratio = 2.8:1.. Urosome 4-segmented; proportional lengths of urosomites and caudal rami 28:20:12:8:32 = 100. Genital double-somite (Figures 7E, F) 1.3 times longer than wider; genital area asymmetrical, located anteroventrally, with single small copulatory pore, paired seminal receptacles and gonopores. Caudal rami symmetrical, ramus 1.7 longer than wide; each ramus armed with 7 setae, seta I developed, 4 terminal setae corresponding to setae III-VI (Figure 7 D).

Antennules (Figure 8A,B) 21-segmented, asymmetrical, differing in length, with left antennule longer. Proximal segments fringed with long setules along posterior margin. Segmentation and setation pattern of left antennule (Figure 8A) as follows: compound segment 1 (ancestral segments I – III) 7 setae+2ae; segments 2 to 5 (IV to VII) each with 2 setae+ae; segment 6 (VIII) 1 seta; segments 7 to 11 (IX to XIII) each with 2 setae+ae; segment 12 (XIV) seta+spine+ae; segments 13 to 19 (XV to XXI) each with 2 setae+ae; segment 20 (XXII) 1 seta; segment 21 (XXIII-XXVIII) 11 setae+2ae. Right antennule (Figure 8B) similar to left but with segments 2-10 very short; setation differences as follows: segment 1 (ancestral I-III) 6 setae+2ae; segment 6 (VIII) 2 setae+ae; segment 15 (XVII) 1 seta+ae.

Antenna (Figure 9A) biramous, with endopod longer than exopod. Coxa unarmed, basis with inner seta. Exopod 5-segmented; armature: 1, 1, 1, 1, 3. Endopod 2-segmented; proximal segment longer than distal, and bearing 1 short seta distally on inner margin; distal segment armed with 3 unequal setae on inner margin and 6 setae on apex.

Mandible (Figures 9B, C) gnathobase cutting edge with 4 teeth, ventralmost largest, and ornamented with two patches of spinules on dorsal surface. Basis longer than wide with row of short spinules distally on outer margin. Endopod as small bulbous swelling bearing 2 unequal setae on apex. Exopod 5-segmented, setal formula 1, 1, 1, 1, 2; setae on segments 1 and 2 located on flattened pedestal.

Maxillule (Figure 9D) praecoxal arthrite bearing 5+1 stout naked spines; coxal endite lobate, unarmed; coxal epipodite armed with 7 pinnate setae and 1 small naked seta; basis unarmed. Endopod with 2 unequal setae; exopod ovoid armed with 3 apical setae.

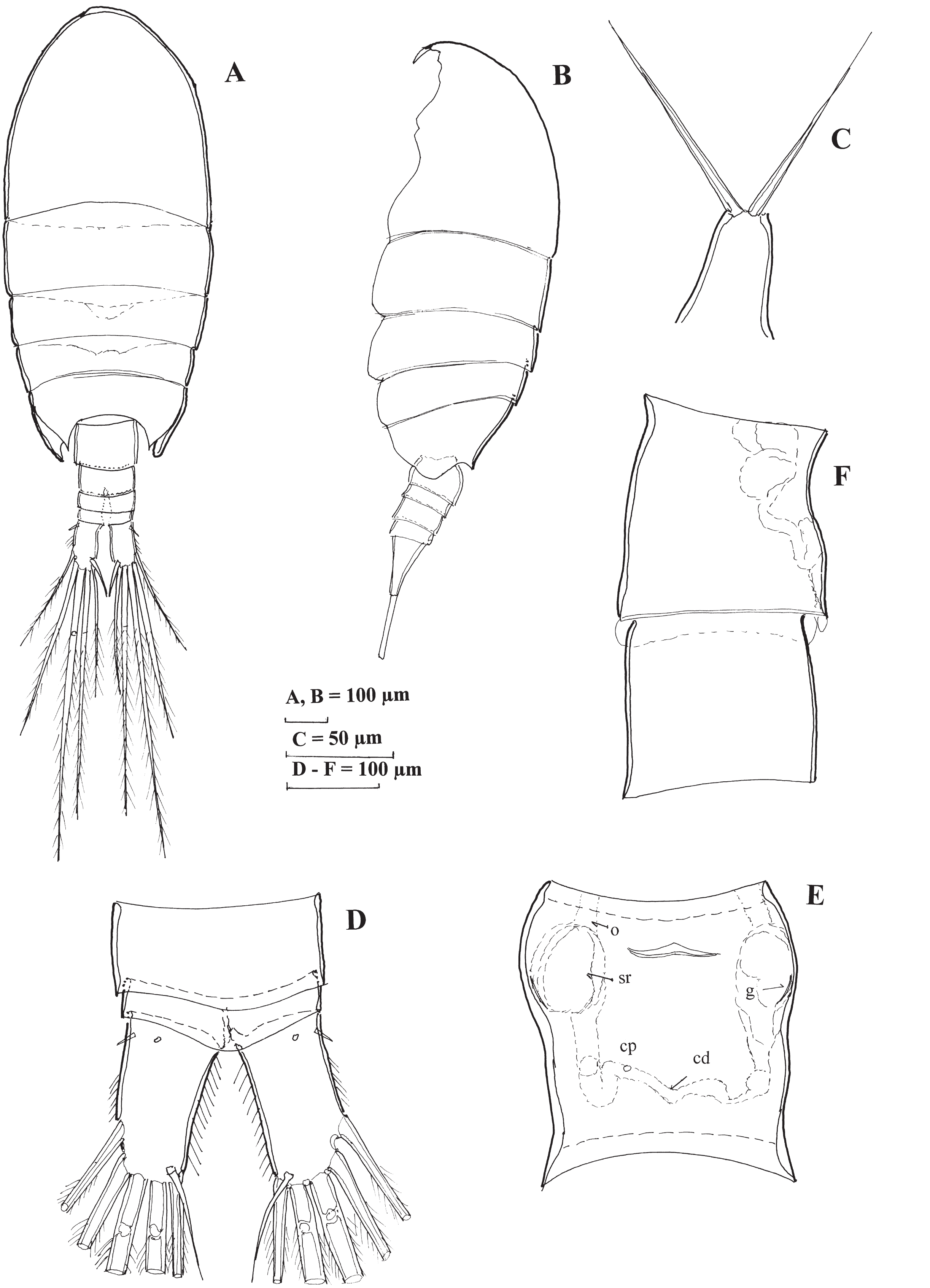

FIGURE 7. *Paramisophria tvrtkovici* sp. nov. adult female, paratype; (A) habitus, dorsal view; (B) habitus, lateral view; (C) rostrum; (D) posterior somites of urosome and caudal rami, ventral view; (E) genital double-somite, ventral view showing reproductive system, sr: seminal receptakle, cd: copulatory duct, cp: copulatory pore; g: gonopore; o: oviduct; (F) genital double-somite and first free abdominal somite, lateral.

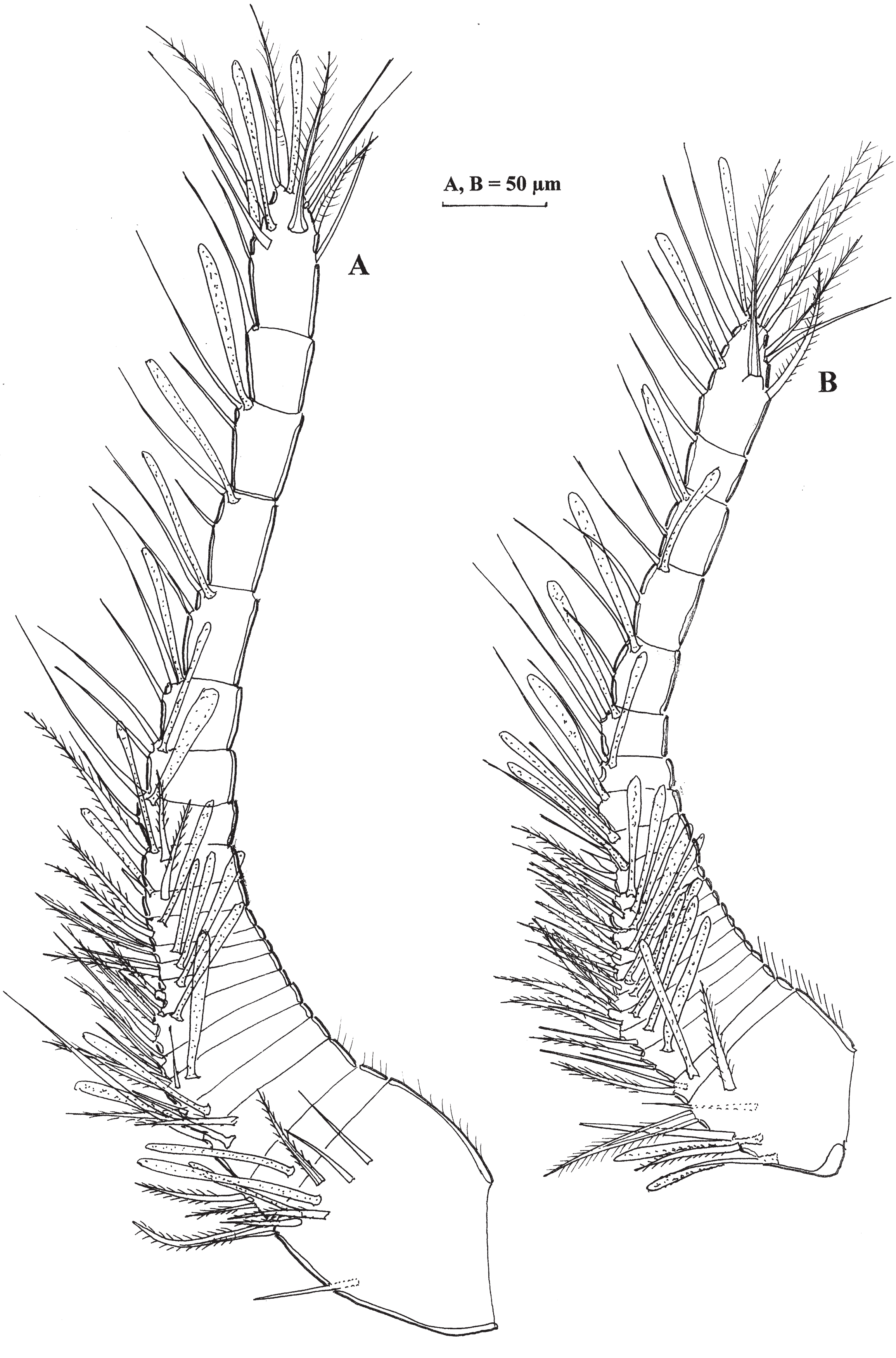

FIGURE 8. *Paramisophria tvrtkovici* sp. nov. adult female, paratype; (A) left antennule; (B) right antennule.

FIGURE 9. *Paramisophria tvrtkovici* sp. nov. adult female, paratype; (A) antenna; (B) mandibular palp; (C) mandibular gnathobase; (D) maxillule; (E) maxilla; (F) maxilliped.

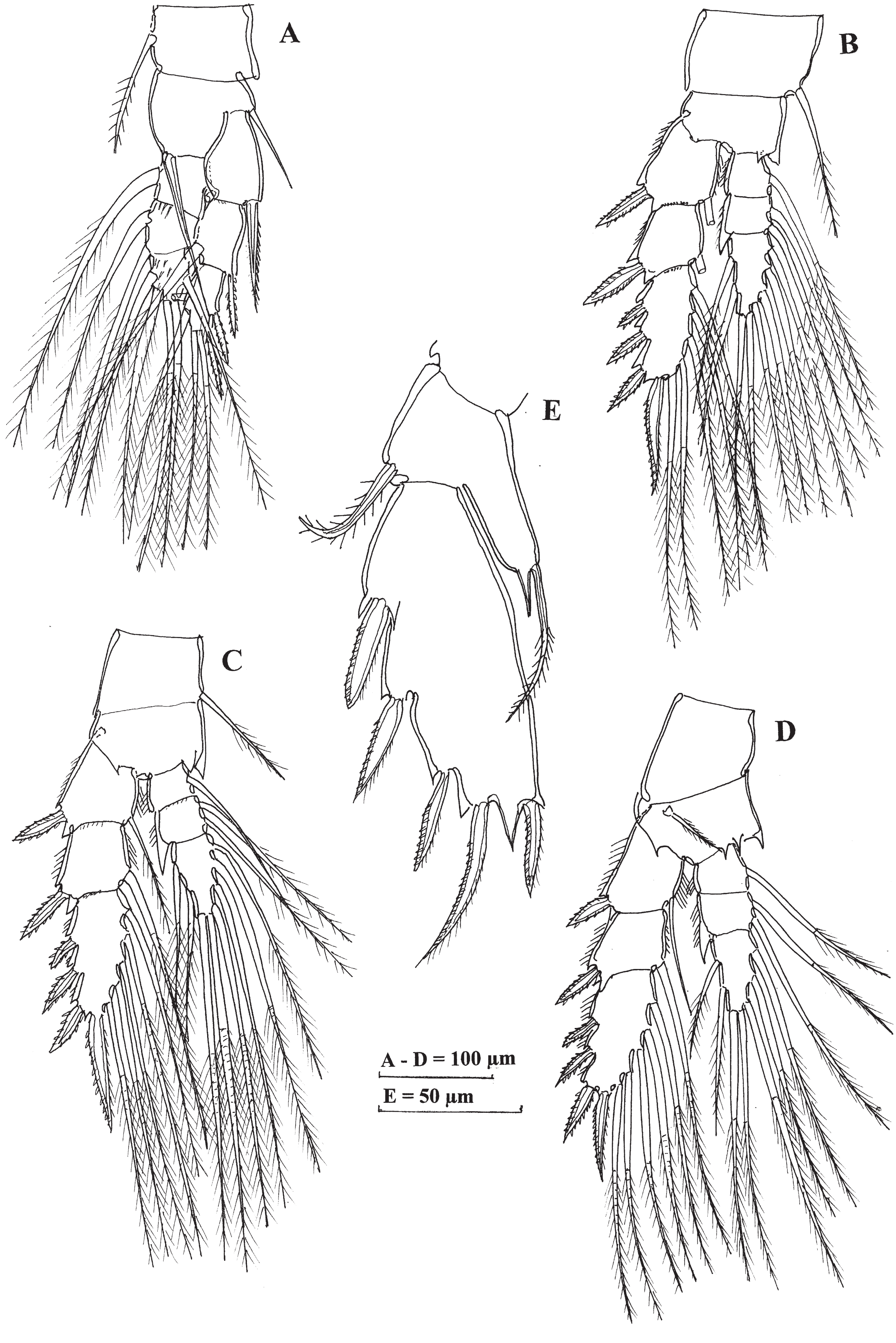

FIGURE 10. *Paramisophria tvrtkovici* sp. nov. adult female, paratype; (A) leg 1; (B) leg 2; (C) leg 3; (D) leg 4; (E) leg 5.

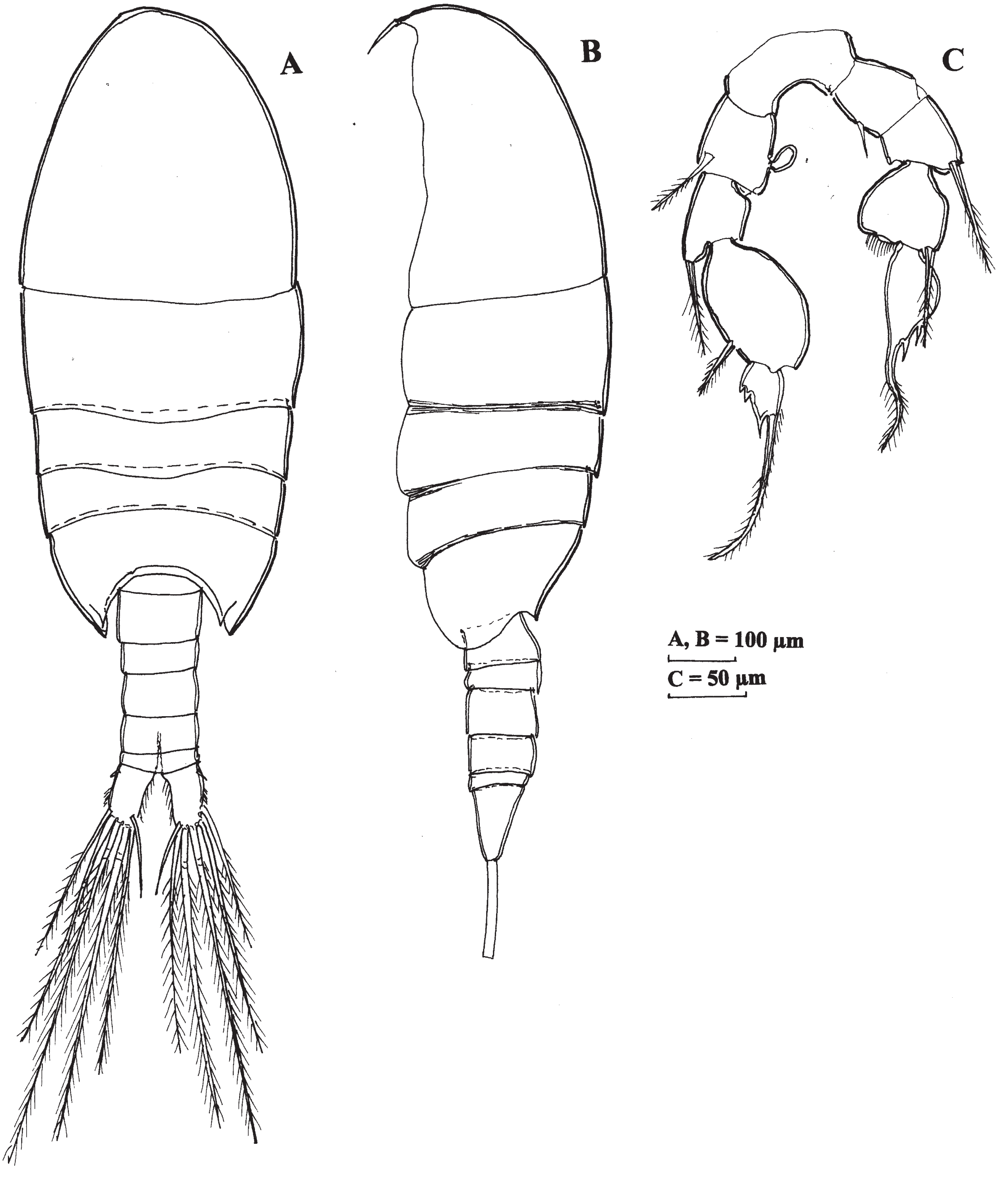

FIGURE 11. *Paramisophria tvrtkovici* sp. nov. adult male, paratype; (A) habitus, dorsal view; (B); habitus, lateral view; (C) leg 5, posterior view.

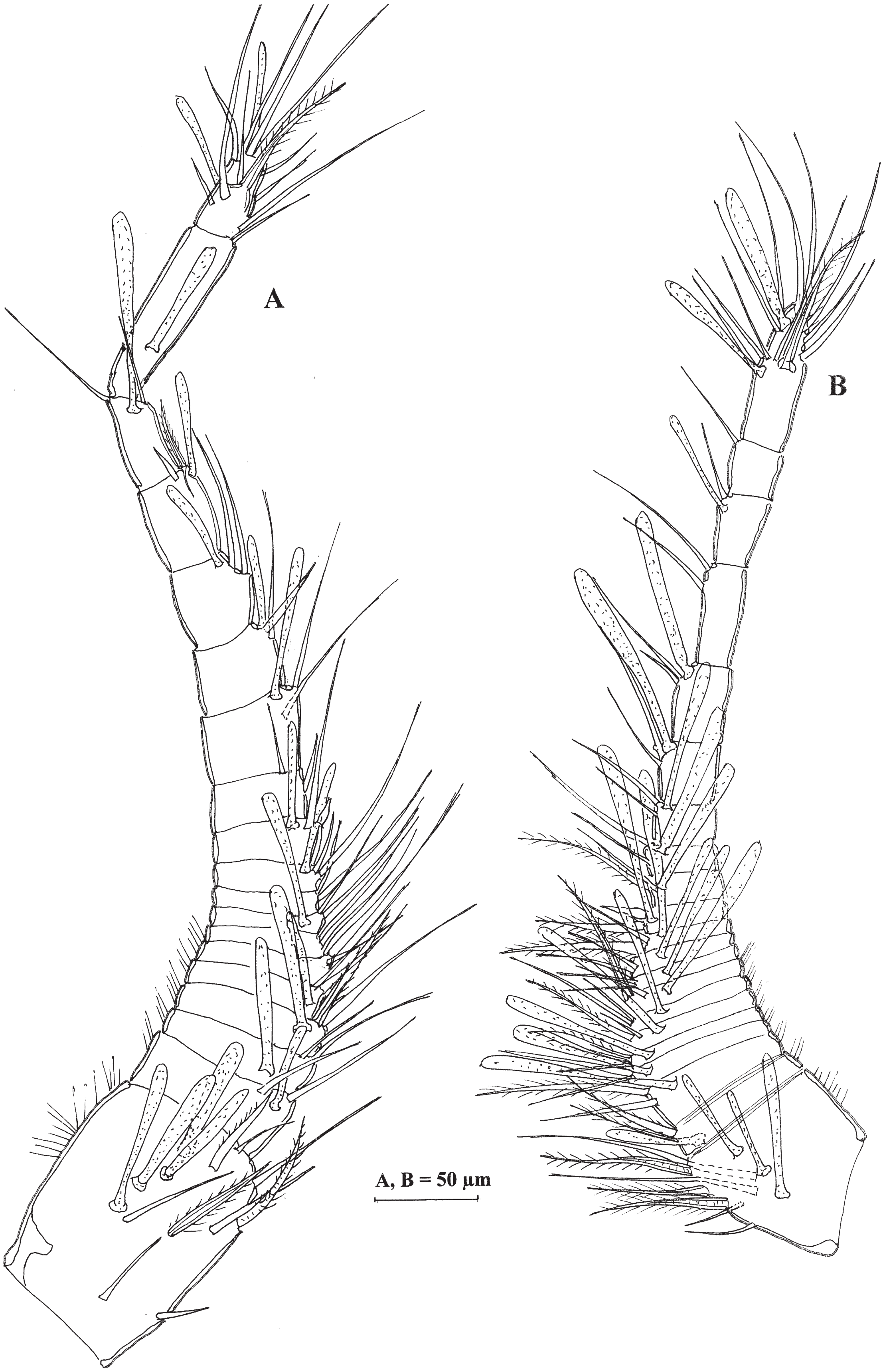

FIGURE 12. *Paramisophria tvrtkovici* sp. nov. adult male, paratype; (A) left antennule; (B) right antennule.

Maxilla (Figure 9E) proximal praecoxal endite with 1 seta, and distal endite with 2 setae; coxal endites each with 2 setae. Basis longest maxillary segment, armed with naked spine on inner margin. Endopod fused into single compound segment armed with 7 long pectinate setae and 1 small seta.

Maxilliped (Figure 9F) syncoxa with endites represented by 1 seta located proximally and 2 setae subdistally. Basis long, partially fused to first endopodal segment, armed with 2 setae on medial margin plus 1 seta on first endopodal segment; and ornamented with patch of surface spinules; free endopod 5-segmented, armature formula 4, 4, 3, 3, 4; 1 setae on free endopodal segment 3 and 2 setae on terminal segment stout and pectinate.

Legs 1- 4 (Figures 10 A-D) biramous with 3-segmented rami, armature formula as follows:

	coxa	basis	endopod	exopod
Leg 1	0-1	1-I	0-1;0-2, 1,2,2	I-1; I-1; II,2,2
Legs 2 & 3	0-1	0-0	0-1;0-2; 2,2,4	I-1; I-1; III,I,5
Leg 4	0-0	1-0	0-1;0-2; 2,2,3	I-1; I-1; III,I,5

Basis with 2 or 3 spinous processes on margin near origin of endopod, in legs 2-4. Exopodal segments of legs 2–4 ornamented with spinules along outer and inner margins; first and second endopodal segments with spinules along outer margin. Second endopodal segments of legs 2-4 produced into acute process at outer distal corner. Fifth legs (Figure 10E) symmetrical, uniramous; coxa unarmed, basis with seta at outer distal corner. Endopod fully fused with basis; armed with plumose seta and slender spinous process at apex. Exopod unsegmented, ellipsoidal in shape and about 2.7 times longer than wide; bearing 3 spines along outer margin, longest spine curved and located at outer distal corner, inner distal spine shortest; distal spines separated by stout spinous process with smooth margins.

Male (Figure 11A,B) mean total length 1325 µm (n=2), range 1250-1400 µm. Prosome 2.3 times longer than wide. Cephalosome and pedigerous somites similar to those of adult female; proportional lengths: 48:17:9:8:19=100. Rostral area as in female. Prosome: urosome ratio = 3.1: 1. Urosome 5-segmented. Proportional lengths of urosomites plus caudal rami: 22:11:19:13:7:28=100. Genital somite symmetrical, wider than long, not expanded ventrally. Caudal rami as in female.

Male right antennule 21-segmented (Figure 12B) similar to right female antennule, differing only as follows: segment 1 (ancestral I-III) 7 setae+3ae; segment 15 (XVII) 2 setae+ae; segment 18 (XX) 2 setae; and segment 19 (XXI) 1 seta+ae. Left antennule (Figure 12A) longer than right, 19-segmented, geniculate with geniculation between segments 17 and 18; segment 18 very long: segmentation and setation pattern as follows: compound segment 1 (ancestral segments I-IV) 9 setae+4 ae; segments 2 to 5 (V to VIII) each with 2 setae+ae; segments 6 and 7 (IX and X) each with 2 setae; segment 8 (XI) 2 setae+ae; segment 9 (XII) 2 setae; segment 10 (XIII) 2 setae+ae; segment 11 (XIV) seta+spine+ae; segment 12 (XV) 2 setae; segments 13 to 15 (XVI to XVIII) each with 2 setae+ae; segment 16 (XIX) seta+spine+ae; segment 17 (XX) 2 setae+ae; segment 18 (XXI-XXIII) 1 seta+ae; compound apical segment 19 (XXIV-XXVIII) 11 setae+2ae.

Antenna, mouthparts and swimming legs 1- 4 identical to those of female.

Fifth legs asymmetrical (Figure 11C). Coxae and intercoxal sclerite fused. Right leg with small seta (representing vestige of endopod) on inner margin of basis. Exopod 3-segmented; first segment with plumose seta distally on outer margin; second segment heart-shaped, bearing plumose seta on outer margin, and ornamented with tuft of small setules distally on inner margin; third segment with swollen, ovoid proximal part tapering distally towards base of long sigmoidal terminal spine (fused to segment); tapering part with 2 short unequal processes on outer margin. Left leg longer than right, basis with plumose seta, biramous; endopod small, ovoid, unarmed. Exopod 3-segmented; first segment with plumose seta distally on outer margin; second segment largest, ovoid in shape, bearing small seta distally on outer margin; third segment smallest, as long as wide and produced into 3 unequal spinous processes on outer margin, distalmost process longest; terminal spine long, and curved distally, and articulated at base.

Remarks

There is some uncertainty concerning the homology of the segments distal to the geniculation in the male left antennule of the new species. The neocopepodan geniculation lies between ancestral segments XX and XXI, so the two segments distal to the geniculation together comprise ancestral segments XXI to XXVIII (Boxshall & Huys, 1998). In other species of *Paramisophria* there can be three segments distal to the geniculation in males (e.g. *P.*

bathyalis Jaume, Cartes & Boxshall, 2000 and *P. reducta* Ohtsuka, Fosshagen & Iliffe, 1993), two segments (e.g. *P. intermedia* Jaume, Cartes & Boxshall, 2000 and *P. galapagensis* Ohtsuka, Fosshagen & Iliffe, 1993) or only a single segment (e.g. *P. mediterranea* Jaume, Cartes & Boxshall, 2000 and *P. aegypti* Zagami, Bonanzinga & Costanzo, 2019). In *P. tvrtkovici* sp. nov. there are two segments distal to the geniculation, the first bears only one seta and one aesthetasc while the second carries 12 setae plus 2 aesthetascs. From the proximal position of the aesthetasc, we infer that the long first segment is compound, derived from segments XXI to XXIII. This segment lacks the two fused, modified setal elements derived from segment XXI that are present in the other species, it also lacks the seta derived from segment XXII but retains the distal seta derived from segment XXIII. The distal segment is therefore derived from ancestral segment XXIV to XXVIII.

Paramisophria is the most species rich genus in the family Arietellidae. Only 14 species were known in 2004 (Boxshall & Halsey, 2004) but five more species were described during the next decade (see Lim & Min, 2014). With the discovery of *P. aegypti* from the Red Sea, 20 species are currently recognized as valid (Razouls *et al.* 2005-2020; Walter & Boxshall, 2021). The majority of species have been found in the waters around North-Eastern Asia, Australia and Madagascar, but *P. cluthae* T. Scott, 1897; *P. ammophila* Fosshagen, 1968; *P. spooneri* Krishnaswamy, 1959; *P. bathyalis*; *P. intermedia* and *P. mediterranea* were all either described from or have been found in the Western Mediterranean. The majority of *Paramisophria* species occur in the shallow water hyperbenthic zone, but some are bathyal and others inhabit anchialine caves (Jaume *et al.* 2000).

TABLE 1. Differences between species of *Paramisophria* found in the Mediterranean Sea and the new species (character set modified from Jaume *et al.* 2000).

Species/Characters	1	2	3	4	5	6	7	8	9	10	11	12
P. ammophila Fosshagen, 1968	1	?	?	0	1	2	1	1	1	?	1	?
P. cluthae T. Scott, 1897	1	?	?	0	0	2	1	1	1	?	1	1
P. bathyalis Jaume et al. 2000	1	1	1	0	1	0	0	0	1	0	1	?
P. intermedia Jaume et al. 2000	1	0	1	1	1	2	0	1	1	0	0	?
P. mediterranea Jaume et al. 2000	0	1	0	1	1	2	1	1	0	1	1	2
P. tvrtkovici sp. nov.	0	0	0	0	1	2	1	1	0	1	0	2

Key: Character 1, Last prosomite with (= 0) or without (= 1) ventrolateral process; character 2, Articulation between ancestral exopod segment of antenna partially expressed (= 0) or not expressed (= 1); character 3, Inner margin of outer spine on first exopodal segment of leg 1 pinnate (=0) or plumose (= 1); character 4, precoxal arthrite of maxillule with 5 + 1 setae (= 0) or 4 + 1 setae (= 1); character 5, coxal endite of maxillule retaining tiny remnant of seta (= 0) or unarmed (= 1); character 6, articulation between ancestral segments XXIII and XXIV on male left antennule fully expressed (= 0) or not expressed (= 1); character 7, articulation between ancestral segment XXV and XXVI on male left antennule fully expressed (= 0) or partially expressed (= 1); character 8, third exopodal segment of left leg 5 of male with 4 spines (= 0) or 3 spines (= 1); character 9, articulation between second and third exopodal segments of male right leg 5 fully expressed (= 0) or partially expressed (=1); character 10, second exopodal segment of male right leg 5 with remnant of inner seta (= 0) or lacking setal remnant (= 1); character 11, third exopodal segment of right leg 5 of male with 4 spines (= 0) or 3 spines (= 1); and character 12, female genital complex with single copulatory pore on left side (= 0) or on right side (= 1).

The character states of the species found in the Western Mediterranean are compared with those of the new species in Table 1. The new species differs in three characters from *P. ammophila* and *P. mediterranea*, in five characters from *P. cluthae*, in seven from *P. intermedia* (female unknown), and in nine from *P. bathyalis* (female unknown). It is the fifth legs of the male of the new species that provide the best characters to distingush this species from its congeners. The second segment of the left leg is the largest and the third segment is the smallest; the third segment is as wide as long, and is produced into three unequal process on its outer margin. The terminal spine is articulated at the base, and thus separate from the segment. The second segment of the right fifth leg is heart-shaped, the proximal part of the third segment is ovoid in shape, and carries two short unequal processes on the outer distal margin plus a long sigmoidal apical spine which is fused to the terminal segment. This distinctive form allows the new species to be identified unequivocally. Three of the species found in the Western Mediterranean, *P. mediterranea* and *P. intermedia* and *P. spooneri*, possess an elongate endopod on the left fifth leg of the male. This differs from the new species which only retains a rudimentary ovoid endopod on the left fifth leg of the male. The endopod is missing in *P. cluthae,* another of the Mediterranean species. The endopod of the left leg is reduced and variable in shape in *P. bathyalis* (Jaume *et al.* 2000) but this species differs from *P. tvrtkovici* sp. nov. in the lack of an inner seta representing the endopod on the basis of the right fifth leg. The two species also differ in the number of segments expressed distal to the geniculation in the male left antennule: three in *P. bathyalis* compared to only two in *P. tvrtkovici* sp. nov.

The antennal exopod of *P. cluthae* is 6-segmented whereas that of *P. tvrtkovici* sp. nov. is 5-segmented. The new species can also be distinguished from *P. ammophila* by the segmentation of the antennal exopod which consists of only four segments.

According to Ohtsuka *et al.* (1993) cave-dwelling species of *Paramisophria* such as *P. galapagensis* and *P. reducta* display a reduction in the setation of the swimming legs. The lack of processes on the last prosomal somite is also a primitive characteristic in calanoids. It seems likely therefore, that the evolution of these prosomal processes took place after invasion of the cave habitat. The new species, like most *Paramisophria* species, has pronounced processes on the last prosomal somite, but it also has reduced setation on the terminal exopodal segment of leg 1. Indeed, *P. tvrtkovici* sp. nov. can be distinguished by the unique setation pattern on leg 1: the terminal exopodal segment of leg 1 has the armature formula II, 2, 2, whereas in other species it is II, 1, 4.

Discussion

Cave-dwelling calanoid species previously discovered in the anchialine caves on the islands of Mljet, Korčula, Vis and Hvar, were located near the deepest part of the Adriatic Sea, the South Adriatic Pit, which has a maximum depth of 1250 m. These species are *Speleohvarella gamulini* Kršinić, 2005, *Badijella jalzici* Kršinić, 2005 and *Stephos grieveae* Kršinić, 2015 (Kršinić, 2005a,b; 2015). *Stephos boettgerschnackae* Kršinić, 2012 was described from material found in the Urinj cave near Rijeka, in the shallow Northern Adriatic. The list of taxa recorded from the anchialine caves of Croatia (Gottstein *et al.* 2012) included *Metacalanus* sp. and *Paramisophria mediterranea*, the latter species being misidentified due to the paucity of available specimens. These names can now be updated to *M. adriaticus* sp. nov. and from *P. tvrtkovici* sp. nov., respectively.

It might be assumed that *P. tvrtkovici* sp. nov. colonized anchialine caves along the Adriatic coast from an original deep-sea habitat, a colonization route that was briefly hypothesized for some misophrioid copepods by Boxshall (1989). In the case of anchialine speleophriids, the colonization of caves in the Mediterranean is difficult to explain, as noted by Jaume & Boxshall (1996a) and Boxshall & Jaume (2000). Recently described species, *Speleophria mestrovi* Kršinić, 2008 and *Speleophriopsis mljetensis* Kršinić, 2017, discovered in the Southern Adriatic, are of particular importance because they extend our knowledge of the biogeography of these Tethyan relicts, and provide further evidence against the possibility of a deep-sea origin for speleophriids.

Jaume *et al.* (2000) described three new species of *Paramisophria* from the Western Mediterranean and produced a phylogenetic analysis of all species known at that time. They rejected a possible deep-water origin for anchialine cave *Paramisophria* in the Mediterranean. They inferred that the ancestral habitat for *Paramisophria* was the shallow water hyperbenthic zone and that, from there, species were able to colonize both more inland anchialine habitats as well as extend into deeper water hyperbenthic habitats.

Both of the new species described in the present paper occur in numerous caves ranging from the southern to the northern Adriatic (Rovinj). As mentioned by Jaume & Boxshall (1996b), it is necessary to identify possible Quaternary glaciation habitat refuges in the area of the Southern Adriatic and in the deepest part of the Mediterranean, the Ionian Sea. According to Surić *et al.* (2005) anchialine habitats in the Middle Adriatic were created by changes in sea-level about 10,000 years ago. It seems likely that, after the colonization of anchialine habitats in the southern Adriatic, a gradual northward spread of the species could have occurred, especially in caves that are strongly influenced by the eastern Adriatic incoming current.

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