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# Disentangling of an *Ameira parvula* (Claus, 1866) species complex with the description of a new species and remarks on the genus *Ameira* Boeck, 1865 (Copepoda: Harpacticoida: Ameiridae)

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**Abstract.** The family Ameiridae is the third most diverse family within Harpacticoida, with 47 genera and up to 300 species. The genus *Ameira*, with 21 species and four subspecies, presents taxonomic challenges due to poorly defined diagnostic features. *Ameira parvula*, initially was described by Claus (1866) as *Canthocamptus parvulus*, and has been subject to taxonomic revisions. Variations in P1 endopod-1 length, A2 exopod segments, and the number of P4 exopod-3 setae have been observed by researchers worldwide. Questions regarding *A. parvula*'s cosmopolitan nature have led to doubts about its distribution. Given the diverse specimens examined in this study from various regions, including the Mediterranean, Aegean Sea, and Black Sea coasts of Türkiye, and material from Russia, England, and Egypt, it becomes evident that *A. parvula* represents a species complex. The study aims to define the boundaries of species belonging to an *A. parvula*'s species complex based on morphological disparities. This study entails the reexamination of *A. parvula* specimens from various collections, followed by a comprehensive redescription. This redescription is then juxtaposed with the existing literature on *A. parvula*, allowing for a thorough reassessment of the previously documented records. This reassessment results in describing two new *Ameira* species and the reevaluation of *A. parvula nana* Willey, 1935 as *Ameira nana*. Furthermore, a comprehensive literature review on the general traits within the genus revealed that *A. atlantica mediterranea* Noodt, 1958 and *A. atlantica atlantica* Kunz, 1974 should be relegated to species rank as *A. mediterranea* Kunz, 1974 and *A. atlantica* Noodt, 1958, respectively. Additionally, *A. lusitanica* Galhano, 1970 should be considered as *incertae sedis* within Harpacticoida.

**Keywords**: meiofauna, systematics, *A. venthami* sp. nov., *A. wellsi* sp. nov., *A. nana*.

## Introduction

The family Ameiridae Boeck, 1865 stands as the third most diverse family within Harpacticoida, encompassing 47 genera and up to 300 species, trailing behind Miraciidae Dana, 1846 and Canthocamptidae Sars, 1906 (Corgosinho et al. 2020). The genus *Ameira* Boeck, 1865 is represented by 21 species and 4 subspecies (Wells 2007, Gee 2009, Karanovic & Cho 2012). The original description of the genus *Ameira* has been notably lacking in terms of clear generic boundaries, an unfortunate characteristic shared with many genera within the family Ameiridae. Boeck (1865) initially established the genus *Ameira* with *A. longipes* Boeck, 1865 as its type species, with the specific traits that included: i) antennule consisting of eight segments, ii) short and one-segmented mandibular palp, iii) three-segmented exopods and endopods in P2–P4, iv) antennular second segment being the longest and the third segment the shortest, v) P1 enp-1 longer than the exopod. Following Boeck (1865), Sars (1911) provided a redescribed account of *Ameira*, highlighting key features such as: i) small and truncate rostrum, ii) a smooth anal operculum, iii) short caudal rami devoid of spinules, iv) the female antennule with eight segments, v) one-segmented antenna exopod, vi) maxillary basis and syncoxa fused into a one-

segmented structure, vii) P1 enp-1 longer than exopod, viii) absence of sexual dimorphism in the swimming-leg endopods in males. Subsequent to this, Lang (1948) undertook a re-descriptive effort, introducing additional traits such as: i) mandible without an exopod, ii) maxilla with two endites, iii) P2–P4 exp-1 lacking an inner seta, iv) antenna possessing a basis. The taxonomy of this genus, along with many other harpacticoid genera, remains problematic due to inadequately defined diagnostic features. As a result of imprecise initial descriptions, many species within the genus *Ameira* require revision.

One of these problematic species is *Ameira parvula*, which Claus (1866) described initially from Nice, France, as *Canthocamptus parvulus* Claus, 1866. However, Claus (1866) provided only a very concise description and illustrations limited to the antennule, antenna, cephalothorax, mandible, maxilliped, and P1. Giesbrecht (1881) described *Nitocra tau* Giesbrecht, 1881, which was later redefined by Sars (1911), leading to the reassignment of *Nitocra tau* to the *Ameira*. Brian (1921) synonymized *Canthocamptus parvulus* with *Amphiascus parvulus*, and subsequently, Brian (1926) transferred *Canthocamptus parvulus* to *Ameira*, designating it as *Ameira parvula* (Claus, 1866) and further synonymized *Nitocra tau*, *Canthocamptus parvulus* and *Ameira tau* as *Ameira parvula*.

Willey (1929, 1935) described two forms of *Ameira parvula*, namely *A. parvula tenuiseta* and *A. parvula nana*. According to the description of Willey (1929, 1935), *A. parvula nana* was differentiated from other *A. parvula* forms by the presence of a small fourth seta on the P5 exopod. Lang (1948) compiled an exhaustive list of synonyms and provided insights into the distribution of *A. parvula*. After Lang (1948), several researchers reported *A. parvula* worldwide (Wells & Rao 1987, Chang 2007, and see also Bodin 1997). However, these records frequently lack detailed descriptions or comparisons.

Researchers have observed variations in *A. parvula* in certain characters, such as the length of the P1 enp-1, which is reported as slightly longer or shorter than the exopod (with Wells (2007) reporting the length of P1 endopod-1 as between 71–85% of the exopod's length), the number of exopodal segments of the antenna being either one or two, and the number of setae on P4 exp-3 being seven or eight (Mielke 1974, 1975, Moore 1976). Moore (1976) was the first who discussed the number of segments in the antenna exopod and speculated that the distal segment might have been overlooked due to its minute articulation. Chang (2007) redocumented Korean populations, albeit without detailing mouthparts. Karanovic and Cho (2012) described two new species closely related to *A. parvula* based on micro-characters, acknowledging that *A. parvula* actually forms a species complex.

Upon reviewing the literature, questions arose regarding the opinion that *Ameira parvula* is a cosmopolitan species exhibiting an extensive variation, leading to doubts about the accuracy of its widespread distribution pattern. In light of the substantial variation documented in the literature and the observed morphological divergence among *A. parvula* specimens that were examined in detail as part of this study from regions such as the Mediterranean, Aegean Sea, Black Sea coasts of Türkiye, as well as material from Russia, England, and Egypt, it became evident that *A. parvula* represents a species complex.

Thus, this study aims to redefine the species boundaries of *A. parvula*, a species believed to encompass a complex of variations based on morphological disparities. In pursuit of this objective, a meticulous morphological character comparison was undertaken among specimens collected from Turkish shores, the Black Sea (Russia), the Cara Sea (Russia), and loaned museum material from the Natural History Museum of London originating from Egypt and Brighton (England). This study involves the redescription of *Ameira parvula* and subsequent

comparison with previously recorded *A. parvula* literature, thereby reassessing the existing records. The outcome of this assessment includes the description of two new *Ameira* species and the reevaluation and reinstatement of *Ameira parvula nana* as *Ameira nana*.

Furthermore, a comprehensive literature review on the general traits within the genus (Please see discussion section) revealed that *A. atlantica mediterranea* should be reinstated as *A. mediterranea* Kunz, 1974. Additionally, *A. lusitanica* Galhano, 1970 should be considered a species *incertae sedis* within Harpacticoida.

## Material and methods

Material from the Turkish coasts was loaned from the zoology collections of Balıkesir University and Mersin University. These specimens were labeled as *Ameira parvula*, which had been collected during various projects from the medio-littoral zones of the Black Sea (project number: TBAG-1962 100T120), the Mediterranean Sea (project number: TBAG-106T590), Aegean Sea (project number: TBAG-111T576), and the Saros Bay (project number: TBAG-212T105). Additional materials labeled *A. parvula* were loaned from the Natural History Museum of London. Materials collected from the Black Sea coast of Russia and the Cara Sea were provided kindly by Dr Lesya Garlitska from her personal collection. All localities` information are presented in Table 1.

The type specimens are deposited in the Natural History Museum United Kingdom (NHMUK) and the Turkish Copepod Research Collection (TCRC). The collected samples were prepared for examination following the methods described by Sönmez (2019). Dissection and mounting of specimens on slides were carried out using a lactophenol medium. Drawings were created using an Olympus BX-51 Differential Interference Contrast microscope equipped with a camera lucida. Figures were generated using Adobe Photoshop CC software in conjunction with a Wacom Intuos Pro Graphical tablet.

Table 1. Localities of *A. parvula* and *A. venthami* sp. nov.

| St. No | Date | Localities | Coordinates |
|---|---|---|---|
| St. A1 | 24/11/2007 | Mağaracık (South)/ Hatay | 36° 08.315′ N; 35° 54.598′ E |
| St. A2 | 24/11/2007 | Arsuz- Mağaracık /Hatay | 36° 14.008′ N; 35° 50.220′ E |
| St. A3 | 24/07/2007 | Payas Beach/Hatay | 36° 45.604′ N; 36° 11.834′ E |
| St. A4 | 13/05/2008 | Yumurtalık/ Adana | 36° 45.180′ N; 35° 47.515′ E |
| St. A5 | 09/04/2007 | Viranşehir Beach /Mersin | 36° 44.357′ N; 34° 32.478′ E |
| St. A6 | 26/11/2007 | Kızkalesi/Mersin | 36° 27.473′ N; 34° 08.647′ E |
| St. A7 | 13/04/2007 | Göynük Beach/ Antalya | 36° 39.667′ N; 30° 33.670′ E |
| St. A8 | 02/10/2007 | Kaş /Antalya | 36° 12.395′ N; 29° 36.087′ E |
| St. A9 | 29/07/2007 | Anamuryum / Mersin | 36° 01.959′ N; 32°48.749′ E |
| St. A10 | 27/07/2007 | Nato Port/Mersin | 36° 17.094′ N; 33°49.928′ E |
| St. A11 | 31/07/2007 | Mavikent Beach / Antalya | 36° 17.269′ N; 30°20.491′ E |
| St. A12 | 28/07/2007 | Eskur-2 Beach / Mersin | 36° 09.315′ N; 33°26.548′ E |
| St. A13 | 24/07/2007 | Gölovası Beach / Adana | 36° 51.329′ N; 35°54.389′ E |
| St. A14 | 09/04/2007 | Kazanlı Beach / Mersin | 36° 48.617′ N; 34°45.442′ E |
| St. E15 | 17/05/2012 | Letonya / Fethiye | 36° 38.264′ N; 29° 05.390′ E |
| St. E16 | 17/05/2012 | Büyükboncuklu Bay/ Fethiye | 36° 37.390′ N; 29° 04.380′ E |
| St. E17 | 18/05/2012 | İztuzu Beach Inner Lagoon/Fethiye | 36° 46.379′ N; 28° 37.584′ E |
| St. E18 | 02/10/2012 | İncekum/Marmaris/Muğla | 36° 59.006′ N; 28° 12.207′ E |

***Table 1 – continued next page***

*Table 1 - continuation*

| St. No | Date | Localities | Coordinates |
|---|---|---|---|
| St. E19 | 21/05/2012<br>11/06/2013 | Akbük/Marmaris/Muğla | 37° 23.526′ N; 27° 25.542′ E |
| St. E20 | 23/05/2012 | İçmeler /Urla | 38° 18.383′ N; 26° 41.080′ E |
| St. E21 | 16/06/2013 | Badembükü,Karaburun/İzmir | 36° 37.280′ N; 26° 21.466′ E |
| St. E22 | 24/05/2012<br>16/06/2013 | Yeniliman /Karaburun | 38° 40.153′ N; 26° 26.078′ E |
| St. E23 | 24/05/2012 | Pırlanta Beach /Çeşme | 38° 17.065′ N; 26° 15.053′ E |
| St. E24 | 21/05/2012 | Ortakent/Yahşi Beach/Bodrum | 37° 01.148′ N; 27° 20.560′ E |
| St. E25 | 26/10/2012<br>13/06/2013 | Altınkum 3rd Bay, Didim/Aydın | 37° 20.358′ N; 27° 15.453′ E |
| St. E26 | 11/06/2013 | Hayıtlı (Next Bay)/Muğla | 37° 01.595′ N; 28° 10.306′ E |
| St. E27 | 24/06/2013 | Mersinderesi Dilek Peninsula NP./Kuşadası | 37° 40.525′ N; 27° 05.207′ E |
| St. E28 | 17/06/2013 | Hayıtlı/Muğla | 38° 59.239′ N; 26° 47.568′ E |
| St. E29 | 08/06/2013 | Kuleli Bay / Fethiye | 36° 38.341′ N; 29° 04.339′ E |
| St. E30 | 16/06/2013 | Küçükbahçe/Karaburun | 38° 33.268′ N; 26° 22.138′ E |
| St. S31 | 29/09/2013<br>23/02/2014 | Seddülbahir Beach (Ertuğrul Koyu)/ Çanakkale | 40° 04.268′ N; 26°18.462′ E |
| St. S32 | 25/05/2013 | Suvla Bay (Anafartalar beach)/Çanakkale | 40° 31.423′ N; 26°24.087′ E |
| St. S33 | 29/09/2013 | Kabatepe Beach/ Çanakkale | 40° 21.166′ N; 26°27.507′ E |
| St. S34 | 26/05/2013<br>27/09/2013 | Danışment Beach/Keşan/Edirne | 40° 59.914′ N; 26°41.403′ E |
| St. S35 | 27/05/2013 | Sultaniçe Beach/Enez/Edirne | 40° 59.211′ N; 26°14.025′ E |
| St. S36 | 27/05/2013 | 1. Tuzla Beach (Vakıf Motel)/Edirne | 40° 59.773′ N; 26°24.320′ E |
| **St. No** | Date | Localities | Coordinates |
| St. S37 | 26/05/2013<br>29/09/2013<br>22/02/2014 | Yeniköy Beach/ Çanakkale | 40° 49.364′ N; 26°58.605′ E |
| St. S38 | 25/05/2014 | Anzak Bay 500 M. North/Çanakkale | 40° 24.949′ N; 26°28.117′ E |
| St. S39 | 28/09/2013 | Güneş Sitesi Beach (After Yeniköy)/Çanakkale | 40° 50.872′ N; 26°63.656′ E |
| St. S40 | 28/09/2013 | Koyun Limanı/Çanakkale | 40° 38.705′ N; 26°38.411′ E |
| St. S41 | 28/09/2013 | Enderkent Holiday Cite/Gelibolu/Çanakkale | 40° 58.335′ N; 26°83.727′ E |
| St. S42 | 29/09/2013 | Karaağaçlı Bay/Çanakkale | 40° 43.955′ N; 26°45.517′ E |
| St. S43 | 29/09/2013<br>23/02/2014 | Kanlısırt Beach/Çanakkale | 40° 23.109′ N; 26°27.644′ E |
| St. S44 | 22/02/2014 | İtalyan Bay (Mecidiye Altı)/Edirne | 40° 59.603′ N; 26°51.068′ E |
| St. S45 | 23/02/2014 | Kömürlimanı Bay/Çanakkale | 40° 45.619′ N; 26°51.112′ E |
| St. S46 | 23/02/2014 | Kum Limanı Holiday Cite Mercan Street Beach/ | 40° 16.248′ N; 26°24.680′ E |
| St. S47 | 22/02/2014 | Sazlıdere (East)/Edirne | 40° 64.288′ N; 26°72.029′ E |
| St. K48 | 17/09/2001 | Şile Liman/ İstanbul | 41° 10.795′ N; 29° 36.713′ E |
| St. K49 | 15/07/2002 | Göbü Beach/ Zonguldak | 42° 32.116′ N; 31° 57.032′ E |
| St. K50 | 14/09/2002 | Kurucaşile Beach/Bartın | 41° 50.683′ N; 32° 43.511′ E |
| St. K51 | 08/07/2001 | Çatalzeytin/Kastamonu | 41° 57.21.8′ N; 34° 12.200′ E |
| St. K52 | 10/09/2002 | Keşap Camping/Giresun | 40° 56.705′ N; 38° 35.288′ E |
| St. K53 | 09/09/2002 | Araklı Beach/Giresun | 40° 55.483′ N; 40° 04.653′ E |
| St. R1 | 09/2011<br>11/2011 | Cara Sea/Russia | 78° 0.15′ N; 87° 37.05′ E |
| St. E1 | 01/10/1994 | Brighton/England | 50° 47.620′ N; 00 ° 00.000′ E |
| St. E2 | 04/07/1993 | Brighton/England | 50° 44.800 N; 00 ° 08.800′ E |
| St. Eg1 | 1924 | Lake Manzeleh/Egypt | – |

For scanning electron microscopy (SEM) preparation, the guidelines outlined in the work of Kaymak and Karaytuğ (2014) were followed. SEM examination was conducted using a field emission scanning electron microscope located at the Mersin University Advanced Technology Education Research and Application Center (MEITAM). Collection numbers are given in the material examined section. Terminology in the text adheres to Huys et al. (1996). Scale bars in figures are denoted in micrometers (μm). Abbreviations used in the text include A1 for antennule, A2 for antenna, ae for aesthetasc, exp for exopod, enp for endopod, and exp- or enp-1, 2, 3 for the proximal, middle, and distal segments of the ramus. Swimming legs are referred to as P1–P6.

**Results**

Order Harpacticoida Sars, 1903
Family Ameiridae Boeck, 1865
Genus *Ameira* Boeck, 1865

Redescription of
*Ameira parvula* (Claus, 1866)
(Figures 1–5)

Material examined.

1♀ (dissected on 4 slides), 1 ♂ (dissected on 3 slides), 41♀♀, 31♂♂ (preserved in alcohol), found on *Heterosiphonia plumosa* at a depth of 6.7 meters (Ventham 2011), collected from Southeast Hove, Southeast rocks, Brighton, England 50° 47.620′ N; 00° 00.000′ E. 01/10/1994. Leg. David Ventham (material originally registered as NHMUK reg. no. 2015-1061-1070). Mediterranean Sea: St. A1 (2♀♀, 1♂) (reg. no. TCRC-2007/11), St. A3 (1♀) (reg. no. TCRC-2007/3), St. A5 (1♀) (reg. no. TCRC-2007/1), St. A8 (1♀) (reg. no. TCRC-2007/9), St. A9 (2♀♀) (reg. no. TCRC-2007/6, TCRC-2007/7), St. A10 (1♀) (reg. no. TCRC-2007/4), St. A11 (1♀) (reg. no. TCRC-2007/8), St. A12 (1♀) (reg. no. TCRC-2007/5), St. A13 (2♀♀) (reg. no. TCRC-2007/13, TCRC-2007/14), St. A14(1♀) (reg. no. TCRC-2007/2); Aegean Sea: St. E19 (1♀) (reg. no. TCRC-2013/8), St. E20 (2♀♀) (reg. no. TCRC-2012/7), St. E22 (1♀) (reg. no. TCRC-2012/8), St. E23 (2♀♀) (reg. no. TCRC-2012/9), St. E27 (1♀) (reg. no. TCRC-2013/11); Saros Bay: St. S31 (1♀) (reg. no. TCRC-2013/17), St. S32 (1♂) (reg. no. TCRC-2013/1), St. S34 (2♀♀) (reg. no. TCRC-2013/2; TCRC-2013/12), St. S42(1♀) (reg. no. TCRC-2013/18), St. S43 (3♀♀) (reg. no. TCRC-2013/19; TCRC-2013/20; TCRC-2014/5), St. S45 (1♀) (reg.no. TCRC-2014/6), St. S46 (1♂) (reg. no. TCRC-2014/7), St. S47 (1♀) (reg. no. TCRC-2014/1) Black Sea: St. K48 (1♀, 1♂) (reg. no. TCRC-2001/2; TCRC-2001/3), St. K49 (1♀) (reg. no. TCRC-2002/1), St. K50(1♀) (reg. no. TCRC-2002/5), St.51 (1♂) (reg. no. TCRC-2001/1), St. K52 (1♀,1♂) (reg. no. TCRC-2002/3; TCRC-2002/4), St. K53 (1♀) (reg. no. TCRC-2002/2); Russia: St. R1 (>20 ♀♀).

Redescription of female (drawings based on a female from Hove, Brighton, England).

Body cylindrical, pores, and sensilla ornamentation as figured (Figure 1 a, b). Total body length measured from tip of the rostrum to posterior margin of caudal rami 467μm. Whole body integument pitted as in *Ameira venthami* sp. nov. (Figure 10d, f). All somites with straight/smooth hyaline frill. Cephalothorax about 1.2 times as long as wide. Second and third pedigerous somites ornamented with one pore antero-medially. Genital double-somite about as long as wide, with spinules dorsally and ventrally as figured (Figure 1a, b). Second and third abdominal somites bear spinule rows posteriorly on ventral and medio-ventral surface respectively. Anal somite (Figure 1a, b) bears a convex, flat operculum that with one sensilla on each side; lined with spinule rows on ventral surface that extending from the middle of the somite to both sides along the midline and along the posterior edges. Caudal rami squarish, with a pore at the dorsal surface, bears strong spinules as figured (Figure 1a–c); with 7 setae. Seta I small and naked, located distal outer corner on dorsal; seta II located near distal on the lateral, about

three times as long as seta I and naked; seta III slightly longer than seta II and located in the outer distal corner on ventral; seta IV bipinnate; seta V broken; seta VI as long as seta II, and located inner distal corner; seta VII naked, tri-articulated, and located near inner margin dorsally.

Antennule (Figure 1d) 8-segmented, 2nd being the longest and 7th the shortest, aesthetasc on fourth segment with accompanied with one long and slender seta. Setal formula: 1-[1 plumose], 2-[9], 3-[8], 4-[2 + (1+ ae)], 5-[2], 6-[3], 7-[4], 8-[5+ acrothek].

Rostrum (Figure 2h) small with two dorsal sensilla.

Antenna (Figure 2a) composed of coxa, basis, two-segmented exopod and one-segmented endopod, although basis and proximal endopodal segment incompletely fused on posterior surface (Figure 2a). Coxa small, bare. Basis with long spinules and three spinules laterally as figured (Figure 2a). Endopod with surface frill subdistally and with spinules as figured; lateral armature consisting of two spines; apical armature consisting of five geniculate setae, with longest one fused basally to smaller seta. Exopod (Figures 2a, 10c) two segmented, the proximal segment elongated, ornamented with a row of minute spinules and one strong spinule, bearing one smooth distal seta apically, distal segment small and with one bipinnate robust seta and one geniculate seta apically.

Mandible (Figure 2d, e), gnathobase elongated and with strong teeth ventrally; with one unipinnate seta dorsally. Mandibular palp with basis and one-segmented endopod; basis with one apically pectinate inner seta and one strong plumose outer seta; endopod with three naked distal setae, and a plumose inner seta.

Maxillule (Figure 2b,c) with large praecoxa bearing a row of spinules; Praecoxal arthrite rectangular, with two naked anterior surface setae, one naked lateral spine, distal armature consisting of two pectinate and two unipinnate distal spines (Figure 2c); coxal endite shorter than praecoxa, and with one bipinnate and one naked seta; basis shorter than coxal endite, with fine setules on the anterior surface, with two apical and two subapical naked setae; endopod proximally represented by minute segment with one plumose seta; exopod absent.

Maxilla (Figure 2f) syncoxa with a row of strong long spinules on the distal corner of the outer margin; proximal endite squarish, with one robust bipinnate seta and one plumose seta; distal endite with one strong unipinnate seta and two naked setae. Allobasis drawn out into claw accompanied by one naked seta at its base. Endopod represented by minute segment with two naked setae.

Maxilliped (Figure 2g) subchelate. Syncoxa with spinules as figured, bearing one bipinnate distal seta; basis with a row of spinules on each side; endopod modified into a strong, naked claw accompanied at its base by small naked seta.

P1–P4 (Figure 3a–e) with three segmented rami. P2–P4 intercoxal sclerites with spinules on anterior surface. Praecoxa triangular, with a row of spinules on outer margin (P1–P4). Coxa rectangular; outer margin ornamented with a row of long spinules distally (P1), or minute spinules (P2–P4). Basis with a plumose (P1, P2) or naked (P3, P4) outer basal seta, spinular ornamentation as figured.

P1 (Figure 3a, b), basis with one plumose outer seta, one pore on the anterior surface near the outer margin; one bipinnate strong inner spine, ornamented with a row of strong spinules near the origin of inner and outer basal seta and endopod. Exp-1,2 with a strong bipinnate outer spine; ornamented with strong spinules at outer margin, and a row of setules on inner margin. Exp-3 with two bipinnate outer spines, a long unipinnate spine at outer distal corner, and two geniculate setae, inner one relatively longer and plumose. Enp-1 ornamented with a row of transverse spinules on outer distal corner and long spinules along inner margin, armed with one plumose seta subdistally, relative length of P1 end-1/exp 1,32; enp-2 small and squarish-like

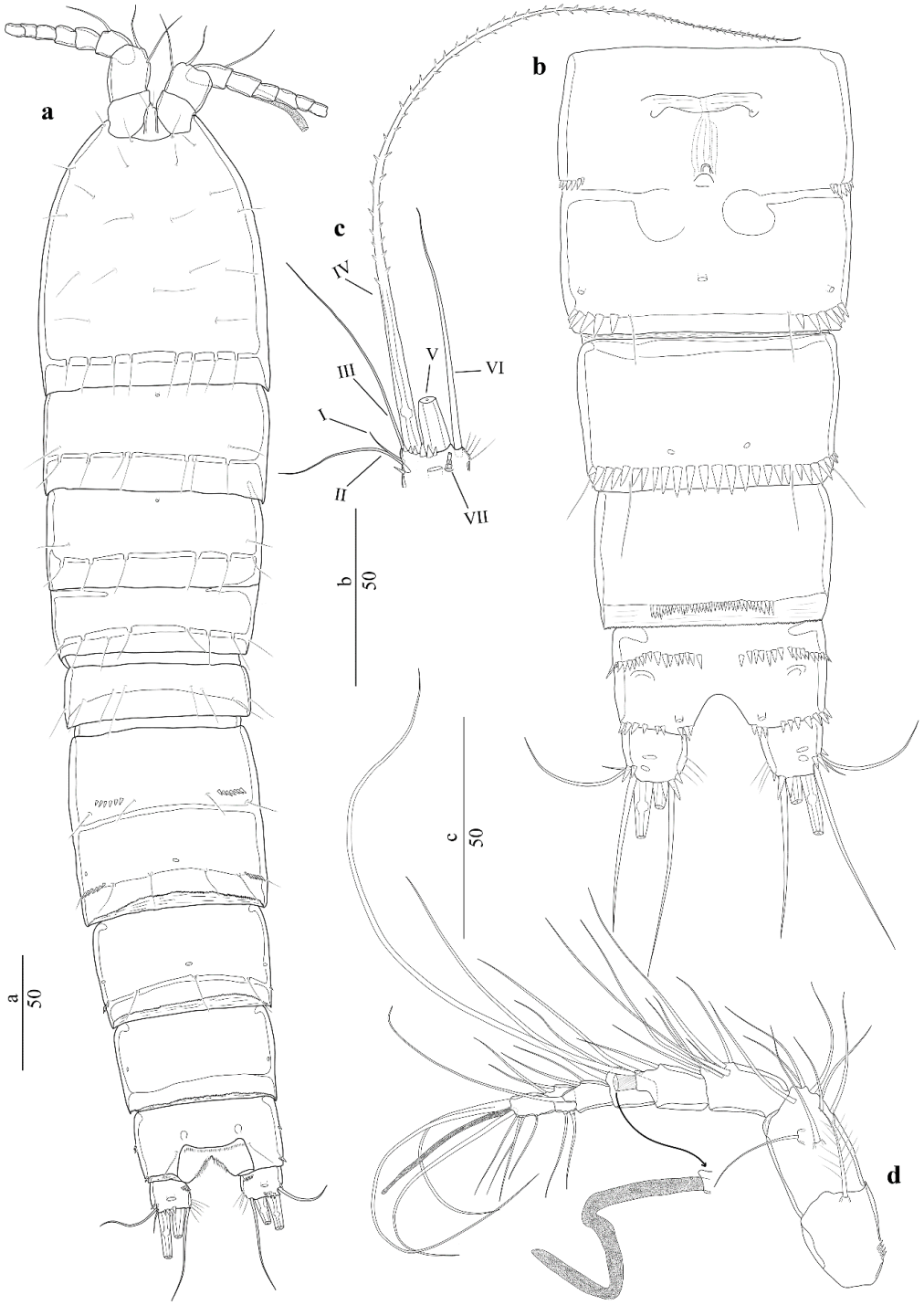


Figure 1. *Ameira parvula* ♀ a) habitus, dorsal; b) abdomen, ventral; c) caudal rami, dorsal; d) A1

segment, bearing a row of robust spinules on the outer margin and one plumose inner seta distally; enp-3 with a row of spinules on the outer margin, one unipinnate outer spine, one geniculate seta distally and one short plumose seta at the inner distal corner.

P2–P4, (Figure 3c–f), exp 1,2 with frills on inner distal margin, with spinules and a bipinnate spine on outer margin, ornamented with spinules at inner margin (except P3 exp 1); exp-2 with a plumose seta. P2, P3 exp-3 with two plumose inner seta, one plumose and one semiplumose seta distally, three bipinnate outer spines; P4 exp-3 (Figure 3f) with one unipinnate,

one plumose, and one small naked inner seta, one plumose and one semiplumose distal seta, three bipinnate outer spines. Enp segments with spinules on the outer margin with a long, plumose inner seta (P2–P4); P2 enp-3 with a plumose inner seta, two plumose distal setae, one bipinnate subapical spine; P3, P4 enp-3 with two plumose inner setae, two plumose distal setae, one bipinnate subapical spine. Pores on the anterior surface near the outer distal margin of the endopodal and exopodal segments.

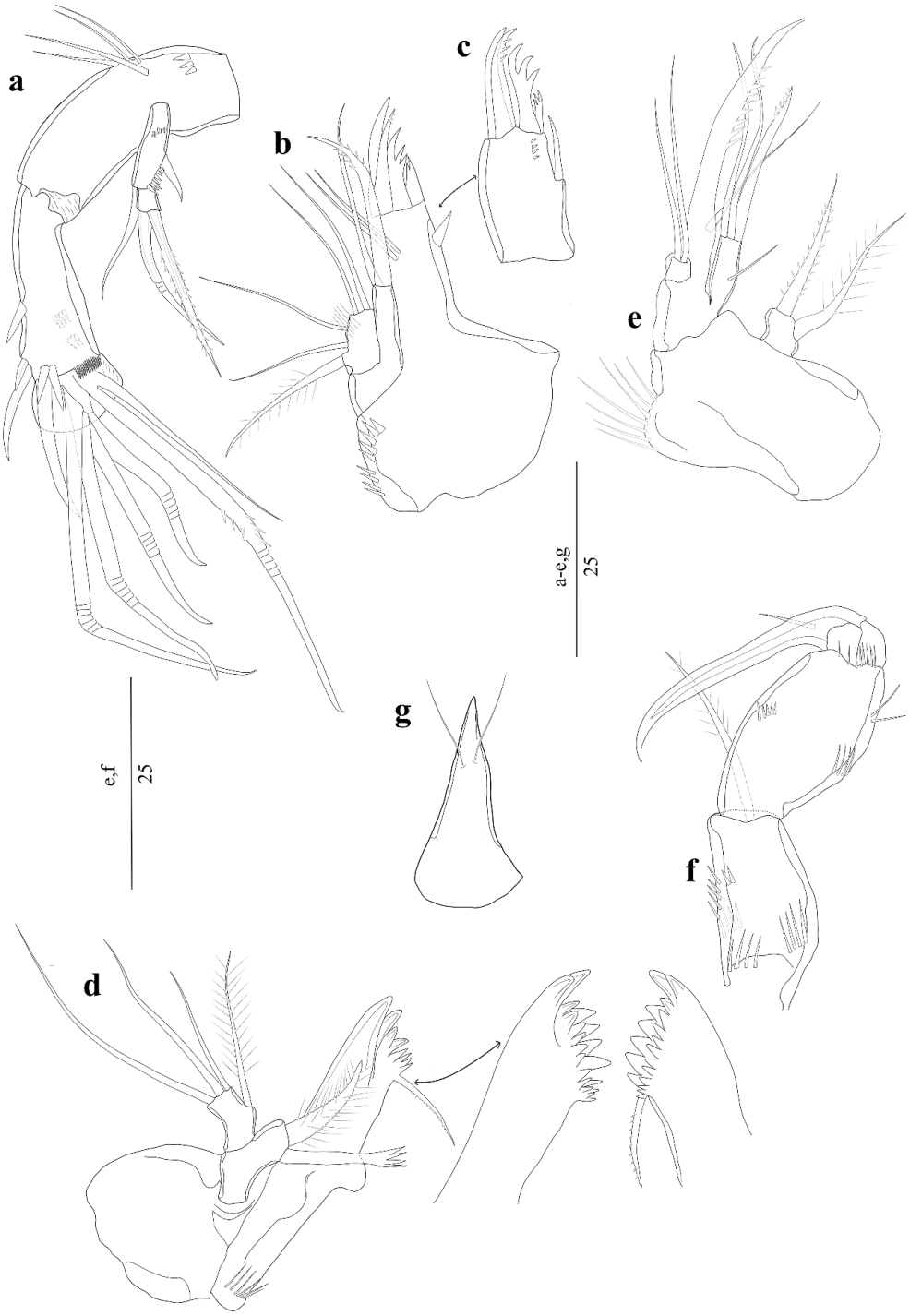


Figure 2. *Ameira parvula* ♀ a) A2; b) maxillule anterior; c) maxillule praecoxal arthrite; d) mandible; e) mandible gnathobase; f) maxilla; g) maxilliped; h) rostrum.

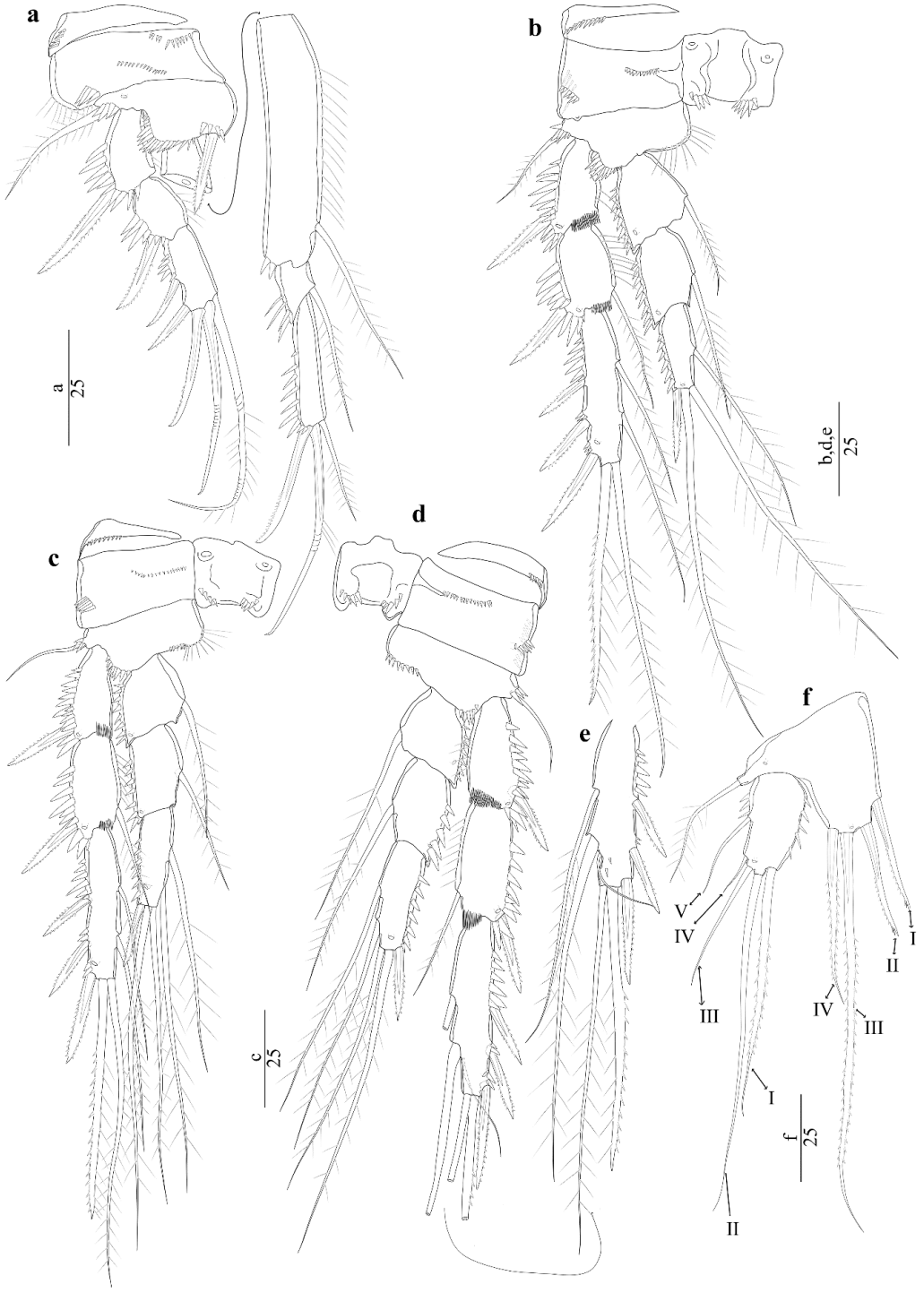


Figure 3. *Ameira parvula* ♀ anterior a) P1; b) P1 endopod; c) P2; d) P3; e) P4; f) P4 exp-3; g) P5

P5 (Figure 3g), baseoendopod and exopod distinct; baseoendopod with a plumose outer basal seta, and with a pore near the outer margin on anterior surface. Endopodal lobe with four setae; innermost setae (seta I and II) unipinnate, apically bifurcated, almost equal in size, seta III the longest and bipinnate, seta IV longer than seta I and II, bipinnate. Anterior surface of endopod and exopod with a pore distally. Exopod with a row of spinules along the inner

margin and proximal half of outer margin, armed with five setae; innermost seta (seta I) bipinnate, seta II naked and the longest, seta III about 1/3 shorter than seta I and naked, seta IV minute and naked, seta V originates from 1/2 of the outer margin, naked.

Setal formula of the swimming legs:

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.0.023 | 1.1.111 |
| P2 | 0.1.223 | 1.1.121 |
| P3 | 0.1.223 | 1.1.221 |
| P4 | 0.1.323 | 1.1.221 |

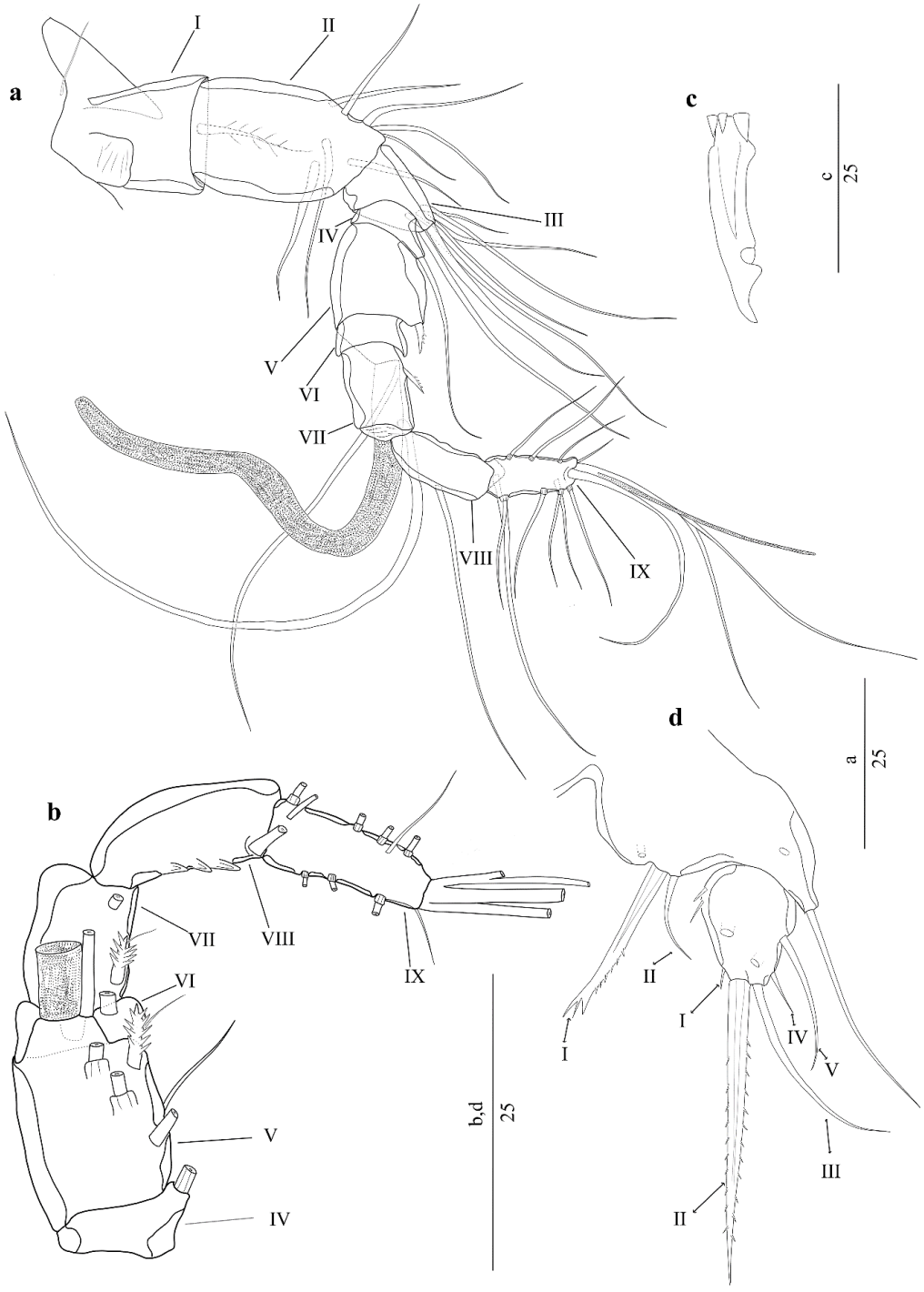


Figure 4. *Ameira parvula* ♂ a) A1; b) A1 (4th to 9th segments); c) P1 basal inner spine; d) P5.

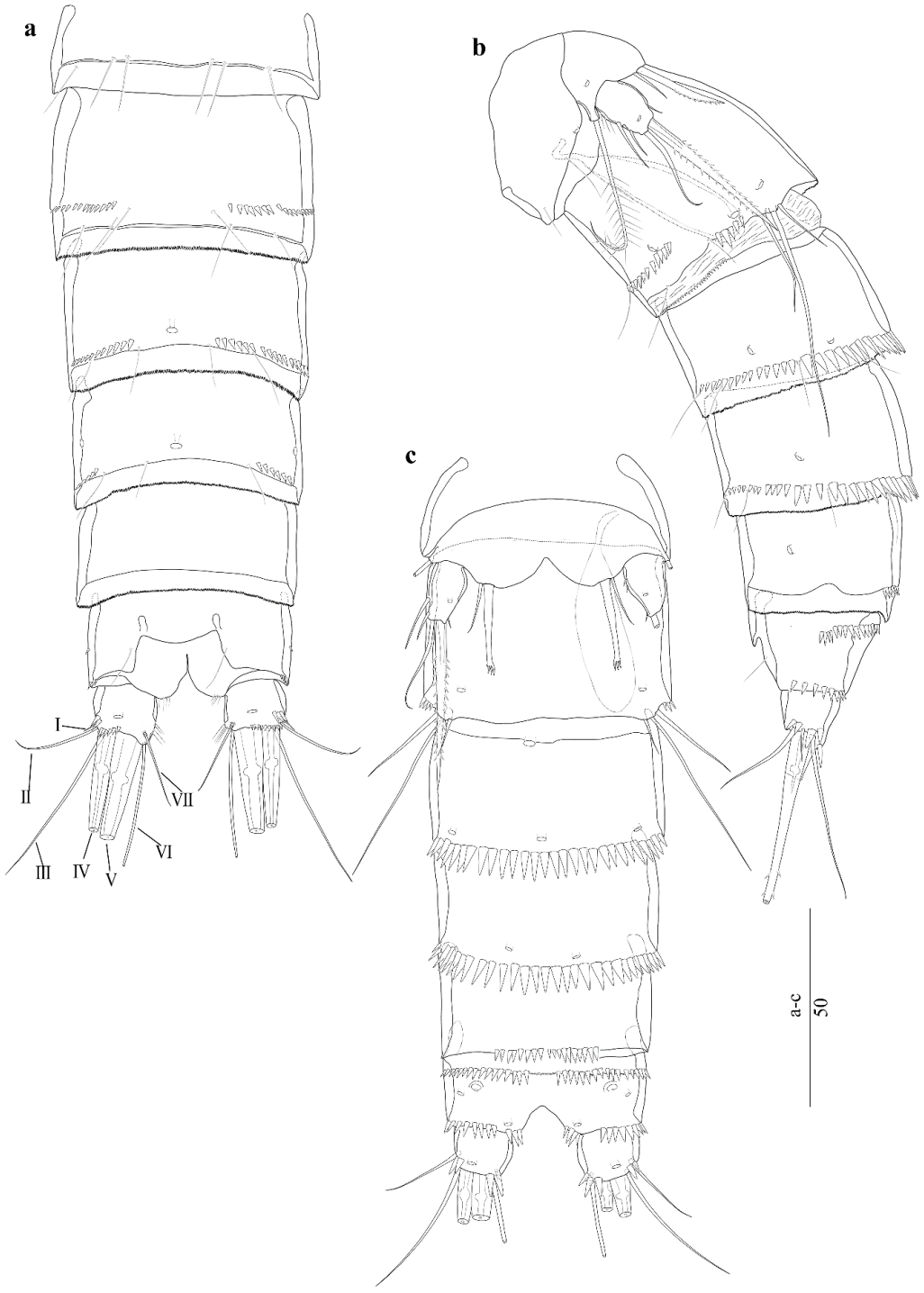


Figure 5. *Ameira parvula* ♂ a) urosome, dorsal; b) urosome, lateral; c) urosome, ventral.

Redescription of male (drawings based on a male from Hove, Brighton, England).

Sexual dimorphism in the antennule, the inner spine of P1 basis, P5 and P6, and genital segmentation.

Antennule (Figures 4a, b; 10b) haplocer and 9-segmented, setal formula as 1-[1, plumose], 2-[8], 3-[7], 4-[1], 5-[4 +1, modified (multipinnate spine)+ (1+ae)], 6-[1], 7-[1+1, modified (multipinnate spine)], 8 [1], 9-[9 +acrothek]; geniculation between 7th and 8th segment.

P1 basis armed with hook-like inner spine

(Figure 4c). Dorsal, lateral, and ventral ornamentation of urosomites as shown in Figure 5 a–c. P5, both baseoendopods unified at the inner margin, each with two setae (Figures 4d, 5c), inner seta thick and distally furcate; outer seta very short and naked. Exopod innermost seta short, seta II strong, bipinnate and spiniform, seta III naked, seta IV small, seta V naked and longer than seta IV. P6 (Figure 5c) represented by three naked setae.

*Ameira venthami* sp. nov.
(Figure 6–9)
https:/zoobank.org/zoobank.org/9EBC80E1-CAD1-402A-88A8-8C9313D92600

Type material.
Holotype 1♀ (reg. no. TCRC-2012/1), Allotype 1♂ (reg. no. TCRC-2012/2) Aegean Sea St. E15 (Interstitial) Letonya Beach (Fethiye, Türkiye). 36° 38' 26.4 "N; 29° 05' 39.0" E. Date: 17/05/2012. Leg: Drs Serdar Sönmez, Serdar Sak, Alp Alper.

Paratypes
St. E15 (>20 ♀♀, >10 ♂♂) (reg. no. TCRC-2012/3).

Other materials
Mediterranean Sea; St. A4 (1♀) (reg. no. TCRC-2008/1), St. A6 (1♀) (reg. no. TCRC-2007/12); Aegean Sea: St. E16 (3♀♀) (reg. no. TCRC-2012/4), St. E17 (2♀♀) (reg. no. TCRC-2012/5), St. E18(1♀) (reg. no. TCRC-2012/13), St. E19 (2♀) (reg. no. TCRC-2012/13), St. E20 (1♀) (reg. no. TCRC-2013/24), St. E22 (1♀) (reg. no. TCRC-2013/9), St. E23(1♀) (reg. no. TCRC-2012/10), St. E24(1♀) (reg. no. TCRC-2012/11), St. E25(2♀) (reg. no. TCRC-2012/14), St. E26 (1♀) (reg. no. TCRC-2014/9), St. E28 (1♀) (reg. no. TCRC-2013/10), St. E29 (1♀) (reg. no. TCRC-2013/6, TCRC-2013/7), St.E30 (1♀) (reg. no. TCRC-2013/25); Saros Bay: St. S33 (1♀) (reg. no. TCRC-2013/21), St. S35 (1♂) (reg. no. TCRC-2013/4), St. S36 (2♀♀) (reg. no. TCRC-2013/5), St. S37(1♀, 2♂♂) (reg. no. TCRC-2014/2), St. S38 (1♀) (reg. no. TCRC-2014/8), St. S39 (1♀) (reg. no. TCRC-2013/13), St. S40 (2♀♀) (reg. no. TCRC-2013/22; TCRC-2013/23), St. S41 (1♀) (reg. no. TCRC-2013/15), St. S44 (2♀♀) (reg. no. TCRC-2014/3; TCRC-2014/4).

Etymology
The specific name is given in honor of David Ventham with his contribution to copepod taxonomy.

Description (Female).
Body (Figure 6a) generally similar to *A. parvula*. Pore ornamentation as figured (Figure 6a, b). Total body length measured from tip of the rostrum to posterior margin of caudal rami 450 μm. Hyaline frill of somites smooth between cephalothorax and fourth pedigerous; other urosomites with narrow frill. Cephalothorax about 1.6 times as long as wide. Genital double somite (Figures 6a; 7a) fused dorsally and ventrally; with six sensilla on anterior of somite and four sensilla on posterior of somite dorsally. Ventral of the genital double somite with a row of spinules on both posterio-lateral regions and a medial pore. Close to the posterior margin the second and third abdominal segments are surrounded dorsoventrally by a row of spinules. (Figure 7a). Anal operculum (Figures 6a; 10e) with a serrated margin; anal somite with spinules from median to lateral, and posterior end of somite with spinules. Caudal rami (Figure 7a, e) with setules on inner side and with pores dorsally and ventrally. Seta I small and naked, located distal outer corner on dorsal; seta II located near distal on lateral, about four times as long as seta I and naked; seta III shorter than seta II, and located outer distal corner on ventral; seta IV, V bipinnate and located distally; seta VI slightly longer than seta II, and located inner distal corner; seta VII naked, tri-articulated, and located near inner margin on dorsal.

Antennule 8-segmented (Figure 6c) setal formula as in *A. parvula*. Antenna (Figure 7b, c) generally similar to that of *A. parvula*, except for: allobasis unornamented; endopod with spinules as figured (Figure 7b, c); lateral spines pinnate. Exopod (Figures 7b, 10a) one-segmented; with a

row of spinules on outer margin; proximal spinule well-developed.

Maxilliped (Figure 7d) similar to that of *A. parvula*, except for: basis with a row of spinules on outer and distal margin; syncoxa with a short strong plumose seta. Endopod represented by a strong claw, as long as, basis with one accessory seta.

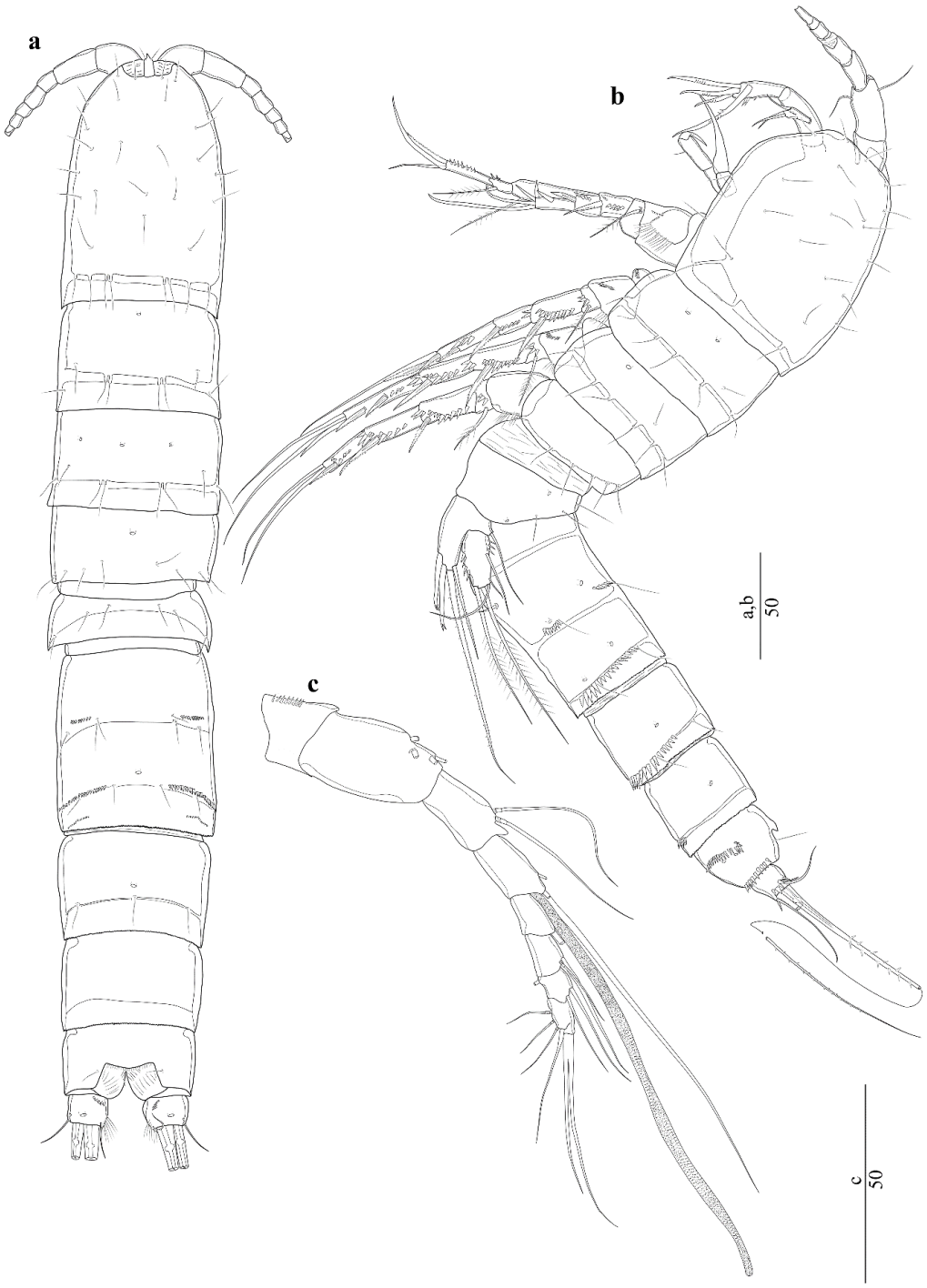


Figure 6. *Ameira venthami* sp. nov. holotype ♀ a) habitus dorsal; b) habitus lateral; c) A1.

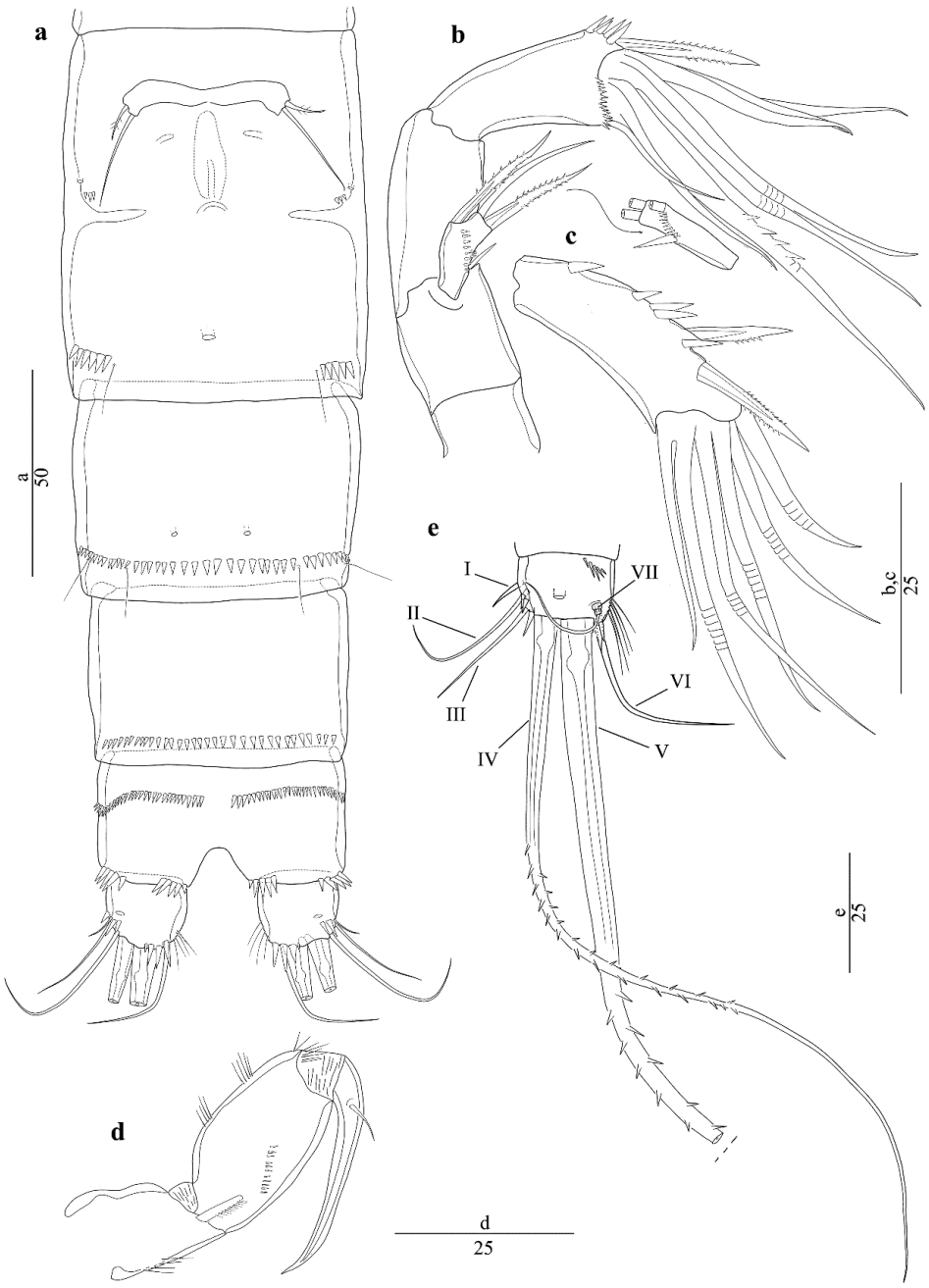


Figure 7. *Ameira venthami* sp. nov. holotype ♀ a) urosome, ventral; b) A2; c) A2 enp-2 innerside; d) maxilliped; e) caudal rami, dorsal.

P1–P4 (Figure 8a–d) with three-segmented rami. Coxa trapezoid, with a row of spinules on anterior surface (P1–P4); covered with fine setules on outer margin (P1) or naked (P2–P4); anterior surface near outer margin with a row of spinules (P2–P4). Basis pentagonal; with a pinnate inner spine (P1), with plumose (P1, P2) or naked (P3, P4) outer basal seta, spinulose ornamentation as figured. Exp-1 without inner seta (P1–P4); spinulose ornamentation as figured (Figure 8a–d).

P1 (Figure 8a), exp-1 with pore distally, exp-

1,2 with pinnate outer spine; exp-3 with three outer marginal spines, two apical setae, of which outer is geniculate, naked, and the inner naked. Enp-1 as long as whole exopod, relative length P1 end-1/ exp 0,94; outer margin bare; with three spinules distally; covered with transverse fine setules on inner margin; one plumose inner seta located near distal. Enp-2 shortest segment, with a row of spinules on outer margin; with a short, plumose inner seta. Enp-3 3–4 times longer than enp-2, with three setae; a naked outer seta, a geniculate distal seta and one naked inner seta.

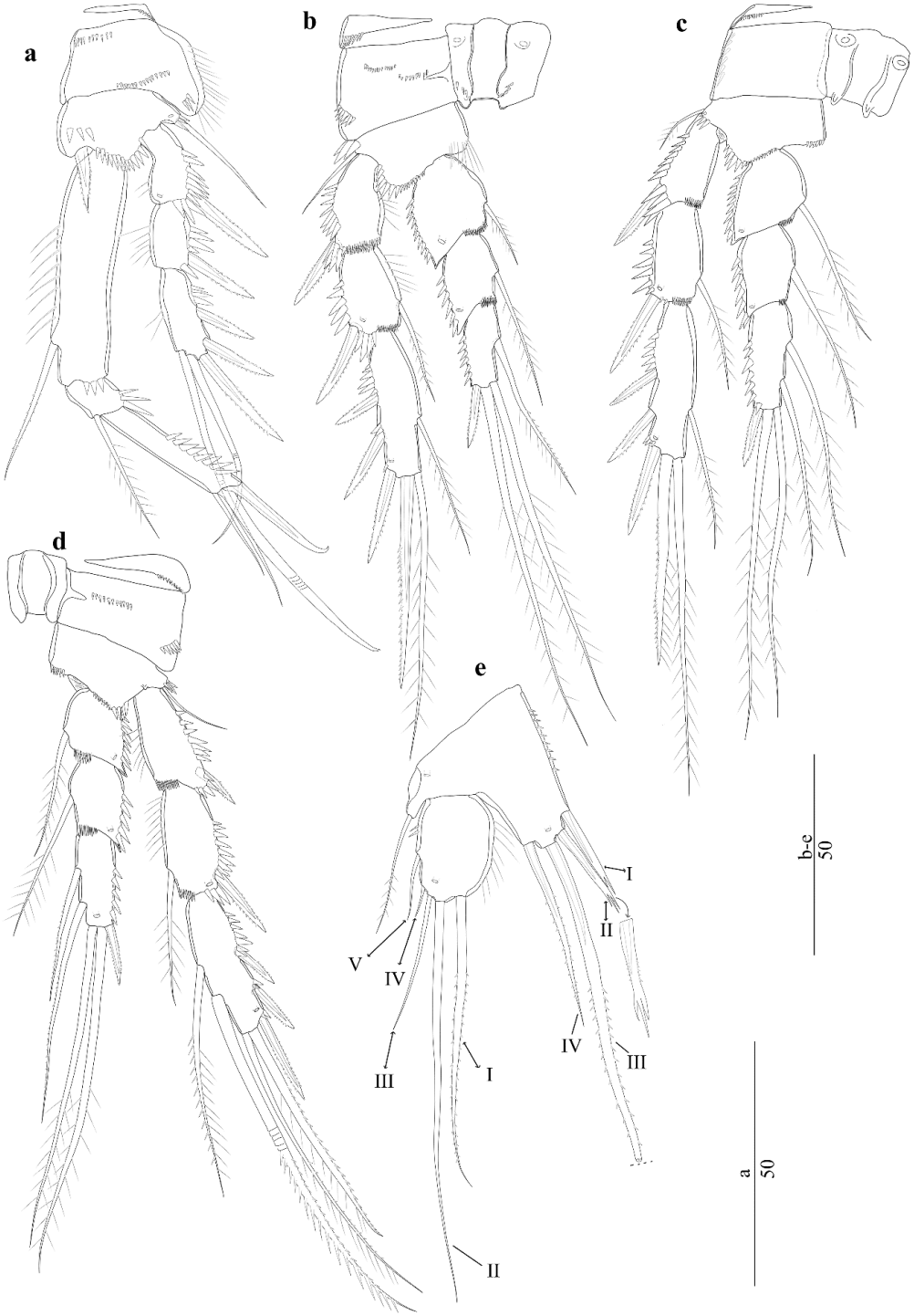


Figure 8. *Ameira venthami* sp. nov. holotype ♀ anterior a) P1; b) P2; c) P3; d) P4; e) P5.

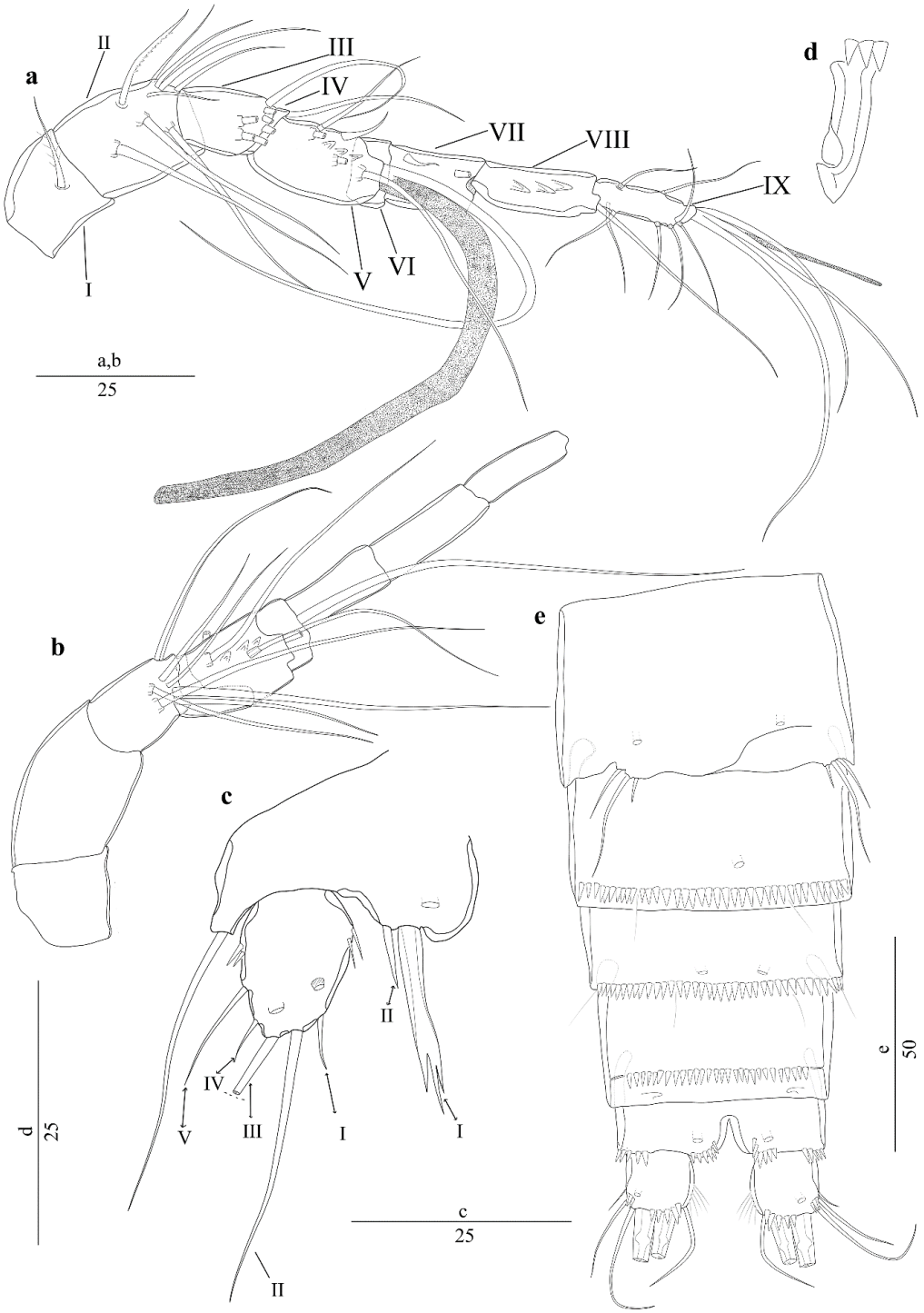


Figure 9. *Ameira venthami* sp. nov. allotype ♂ a) A1; b) A1 ventral; c) P5; d) P1 basis inner spine; e) urosome ventral.

P2–P4 (Figure 8b–d) exp-1,2 covered with robust spinules outer margins, and with a pinnate outer spine. Exp-2 with a plumose inner seta (P2–P4); P2 and P3 exp-3 with three pinnate outer spines, one plumose and one serrate distal seta, and one plumose inner seta. P4 exp-3 with three pinnate outer spines, one spinulose and one plumose distal seta, and one serrate and one plumose inner seta. Enp-1 with a short plumose (P2) or long plumose inner seta (P3, P4); P2 enp-2 with plumose inner seta (P2–P4); enp-3 with one pinnate subapical outer spine (P2–P4), two

long plumose distal setae (P2–P4); with a semi-spinulose inner seta (P2), two plumose inner setae (P3) or two unipinnate inner setae (P4). Pores near distal edge on anterior surface of enp-1–3 (P4) or enp-1,2 (P2), and exp-2,3 (P2–P4).

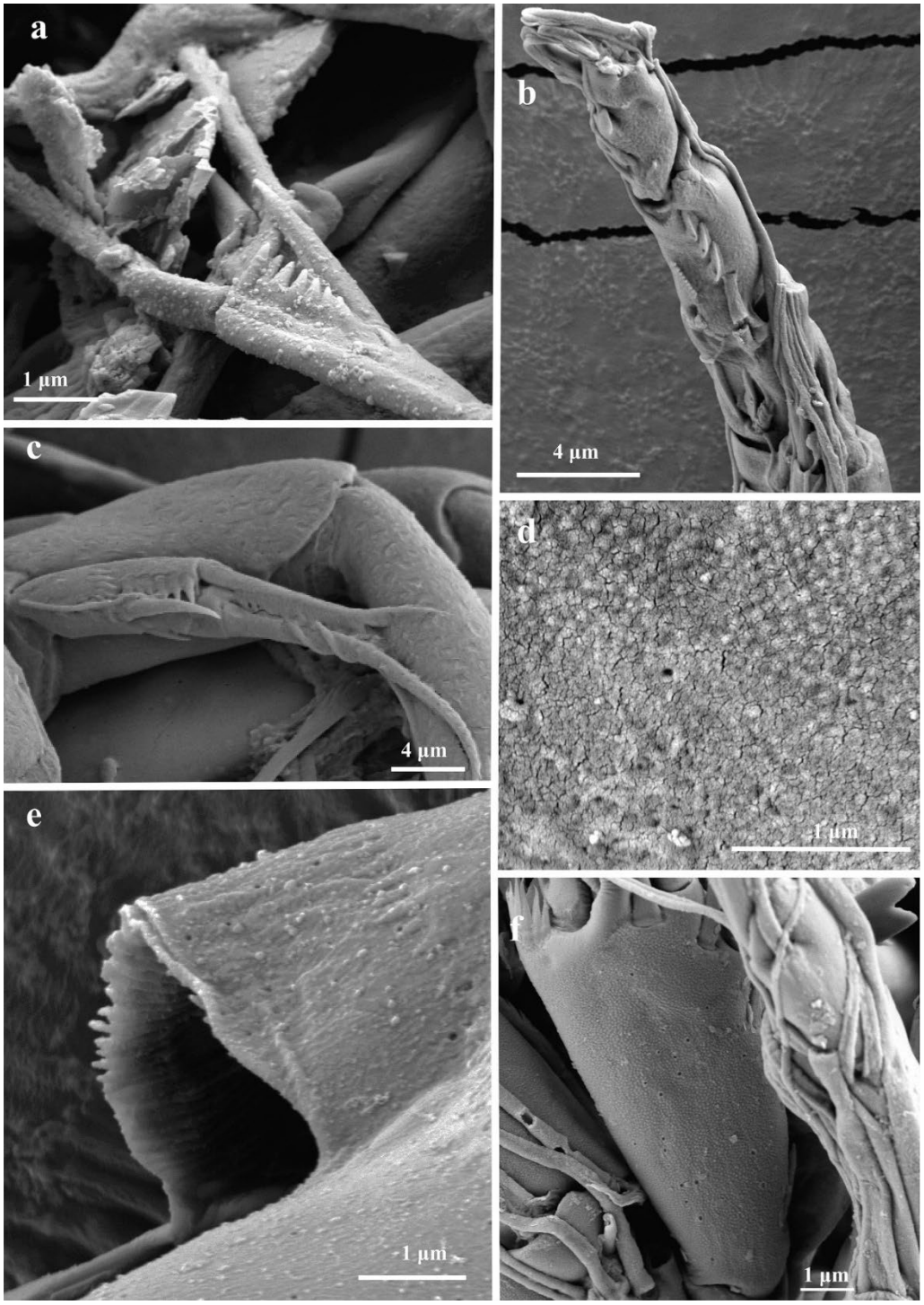


Figure 10. a) *Ameira venthami* sp. nov. ♀ A2 exopod; b) *Ameira parvula* ♂ A1 7th –9th segment; c) *Ameira parvula* ♀ A2 exopod; d) *Ameira parvula* ♀ pitted surface of maxilla in detail; e) *Ameira venthami* sp. nov. ♀ anal operculum; f) *Ameira parvula* ♀ pitted surface of maxilla.

P5 (Figure 8e) baseoendopod triangular and well separated, inner margin with a row of small spinules, with a plumose basal seta, and two pores on anterior surface. Endopodal lobe with four setae (seta I–IV); seta I pinnate, seta II and III apically furcated and spine-like, being seta III the longest seta, seta IV pinnate; exopodal lobe broad, covered with setules on inner margin, with a pore on anterior surface of distal outer edge; with 5 setae; seta I pinnate, seta II longest seta and naked, seta III, V naked, seta IV the shortest and naked, and could be seen hardly.

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.0.032 | 1.1.111 |
| P2 | 0.1.123 | 1.1.121 |
| P3 | 0.1.123 | 1.1.221 |
| P4 | 0.1.223 | 1.1.221 |

Description (male)

Sexual dimorphism in antennule, P1 basis inner spine (Figure 9d), P5, P6, genital segmentation. A1 (Figure 9a, b) 9-segmented, haplocer. Setal formula 1-[1, plumose], 2-[8 + 1, unipinnate)], 3-[7], 4-[1], 5-[4, naked + 1, modified (caudate) + (1+ ae)], 6-[1], 7-[1+ 1, modified (lamellate)], 8-[1], 9-[8+ acrothek]. The inner spine of P1 basis (Figure 9d) hook-like.

P5 (Figure 9c). baseoendopods medially fused, each with 2 setae; inner seta (I) spine-like and apically trifurcated, outer seta (II) small and naked. Exopodal lobe with two pores on anterior surface; with 5 setae; seta I, IV small and naked, seta II long and naked, seta III, V naked; with two spinules on outer edge. P6 (Figure 9e) with three naked setae.

*Ameira nana* Willey, 1935

(Figure 11–13)

https:/zoobank.org/zoobank.org/B55078A0-AB01-47EF-98FB-43D39DA39DED

Synonym *Ameira parvula nana sensu* Willey, 1935

Type locality. Bermuda (Willey, 1935).

Original description

*Ameira parvula* f. *nana* Willey, 1935. Harpacticoid Copepoda from Bermuda. – Part II. *Annals and Magazine of Natural History*, Series 1935.

Material examined

1♀, (dissected on three slides) Mediterranean Sea. St. A7 Göynük Beach, Antalya. 36° 39.667' N; 30° 33.670' E (Deposited at the collection of Turkish Copepod Research Collection reg. no. TCRC-2007/15). 1♀, Cuckmere Haven 13m BCD 50° 44.800 N; 00 ° 08.800′ E 4/7/1993 Leg. Dr David Ventham. (material originally registered as NHMUK reg. no. 2015-770).

Remark

The specific name is designated in accordance with ICZN (1999) article 45.6.4. The subspecific name '*nana*' was previously employed and referred to as 'forma' before 1961. As per article 45.6.4.1, the subspecific name '*nana*' is recognized as a valid nomenclatural designation.

Supplementary description based on the female from Göynük Beach

Body cylindrical, sensilla and pore ornamentations as figured (Figures 11a, b; 12a). Total body length measured from tip of the rostrum to posterior margin of caudal rami 483 μm. Genital double somite rectangular and well fused; with two rows of spinules from lateral to dorsal. Penultimate body smooth. Hyaline frills from cephalothorax to fourth pedigerous somites smooth, while urosomites with narrow frills. Anal somite (Figure 11b) with spinules on dorsolateral; anal operculum with small spinules. Caudal rami with spinules, a pore on dorsal surface, inner margin naked, and a pore distal end of the caudal rami on dorsally (Figure 11c); with 7 setae. Seta I small and naked, located distal outer corner on dorsal; seta II located near distal on lateral, about three times as long as seta I and naked; seta III is quite longer than seta II, and located outer distal corner on ventral; seta IV, V bipinnate, seta VI as long as seta II, and

located inner distal corner; seta VII naked, tri-articulated, and located near inner distal margin dorsally.

Antennule 7-segmented (Figure 12b); setal formula 1-[1, plumose], 2-[9], 3-[9], 4-[2+(1 ae)], 5-[1], 6-[7], 7- [3 + acrothek]. Antenna (Figure 12c), allobasis naked, exopod one segmented with three setae distally and one subapical spinule; outer seta apically spinulose. Endopod with a naked outer seta, one medially pinnate distal seta, five geniculate distal setae and one bipinnate, one unipinnate lateral spines.

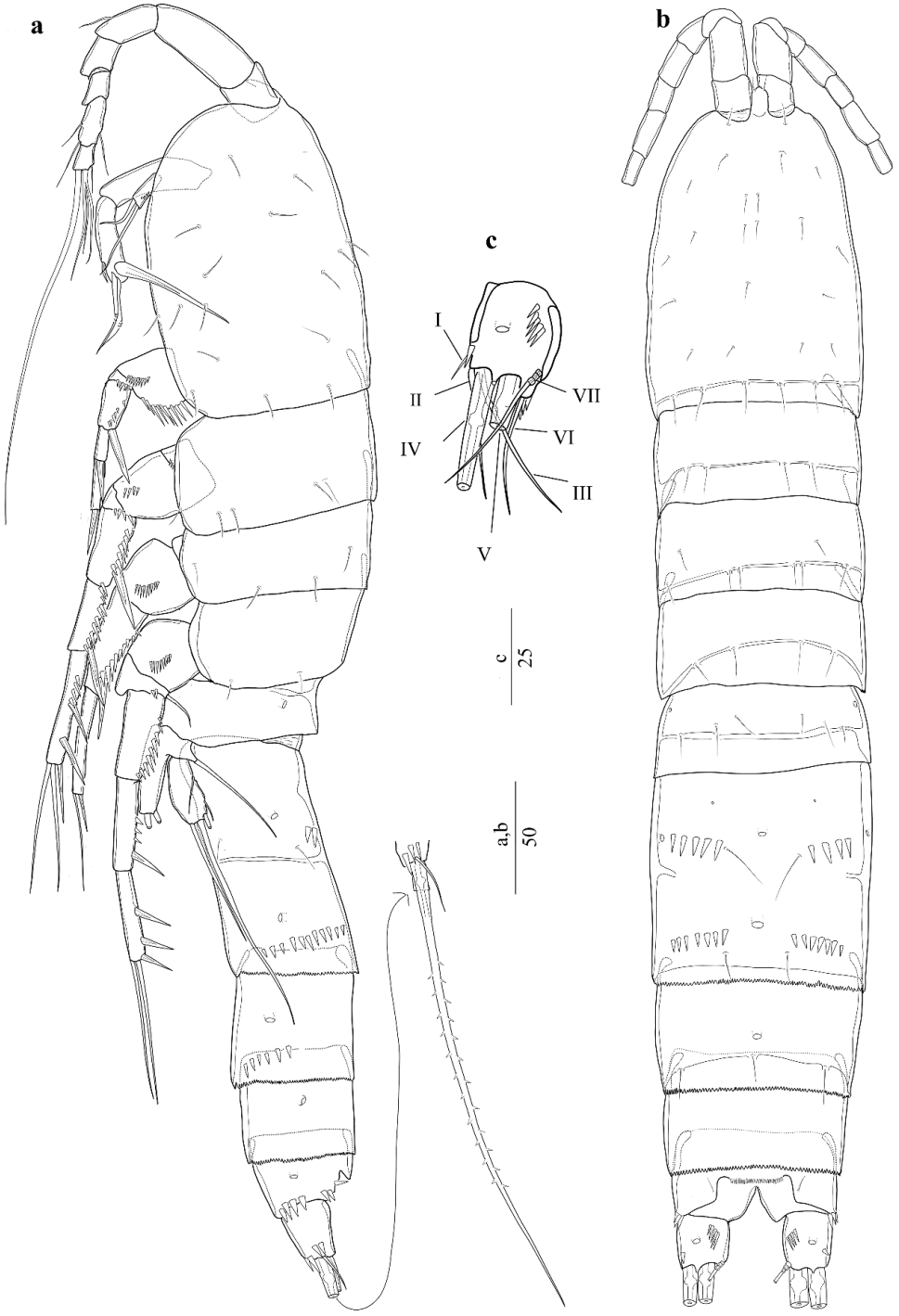


Figure 11. *Ameira nana*. ♀a) habitus lateral; b) habitus dorsal; c) caudal rami dorsal.

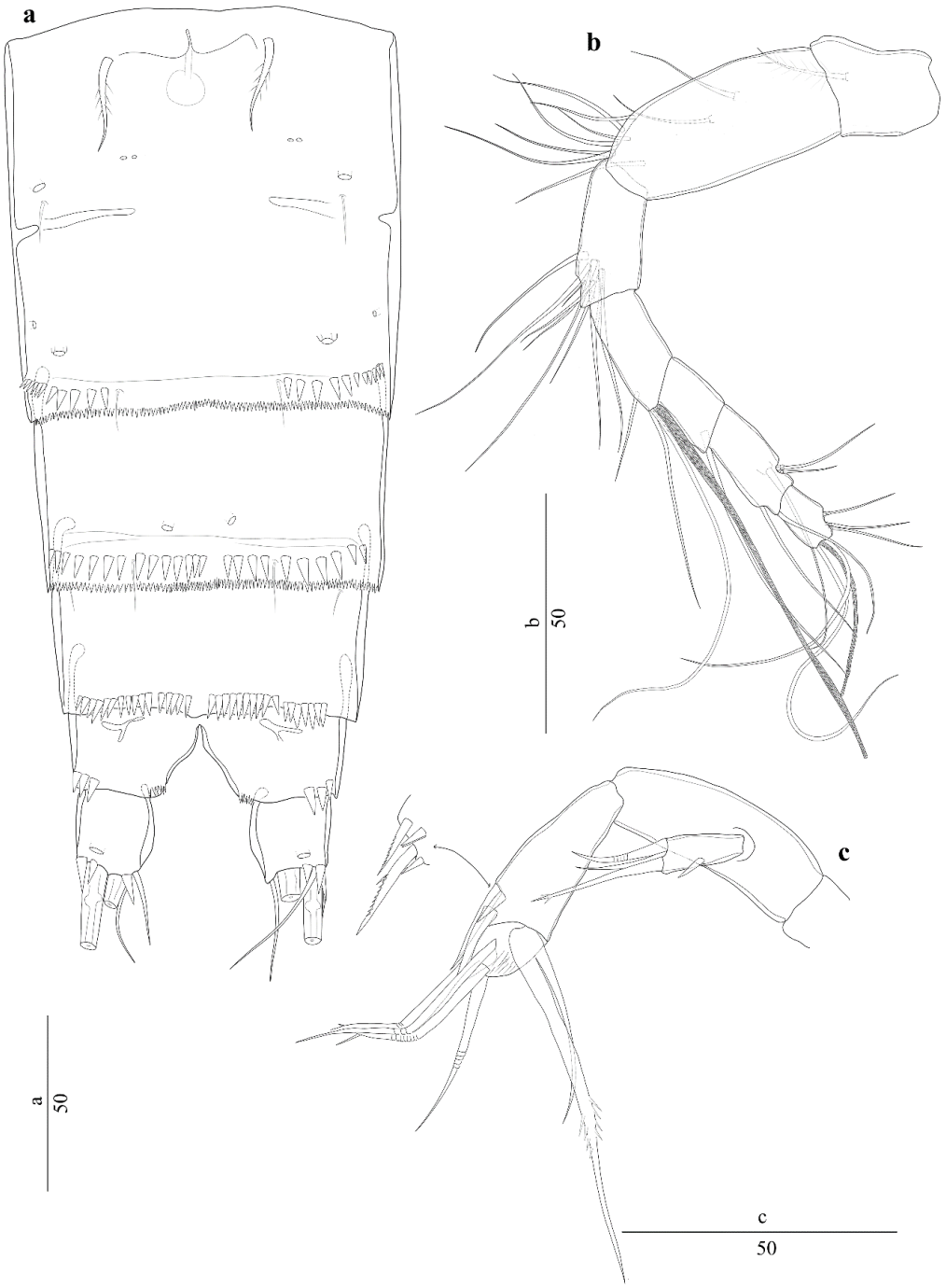


Figure 12. *Ameira nana*. ♀a) abdomen ventral; b) A1; c) A2 posterior, insert anterior part of distal edge.

P1–P4 (Figure 13a–d) with three segmented rami. Coxa trapezoid, anterior surface naked (P1) or a row of spinules (P2–P4) outer edge with spinules (P1–P4). Basis triangular-like; with a naked outer seta and a row of spinules on distal edge (P1, P2, P4), or naked (P3); spinules on inner edge (P4) or naked (P2, P3) or with a pinnate spine (P1). Exp-1 without inner seta (P1–P4). Enp-1,2,3 covered with spinules on outer margin.

P1 (Figure 13a) basis additionally with inner unipinnate spine; exp-1 with a pinnate outer

spine which is elongated to distal end of exp-2. Exp-2 with a bipinnate outer spine, without inner seta. Exp-3 with two geniculate apical setae and three unipinnate outer spines. Enp-1 elongated, reaching distal end of exp-3, relative length of P1 end-1/ P1 exp 0,88; with plumose inner seta and two spinules on distal outer edge. Enp-2 trapezoid, with a naked inner seta apically, enp-3 with a unipinnate outer spine and robust spinules on outer edge, a geniculate distal seta, and a naked slender inner seta.

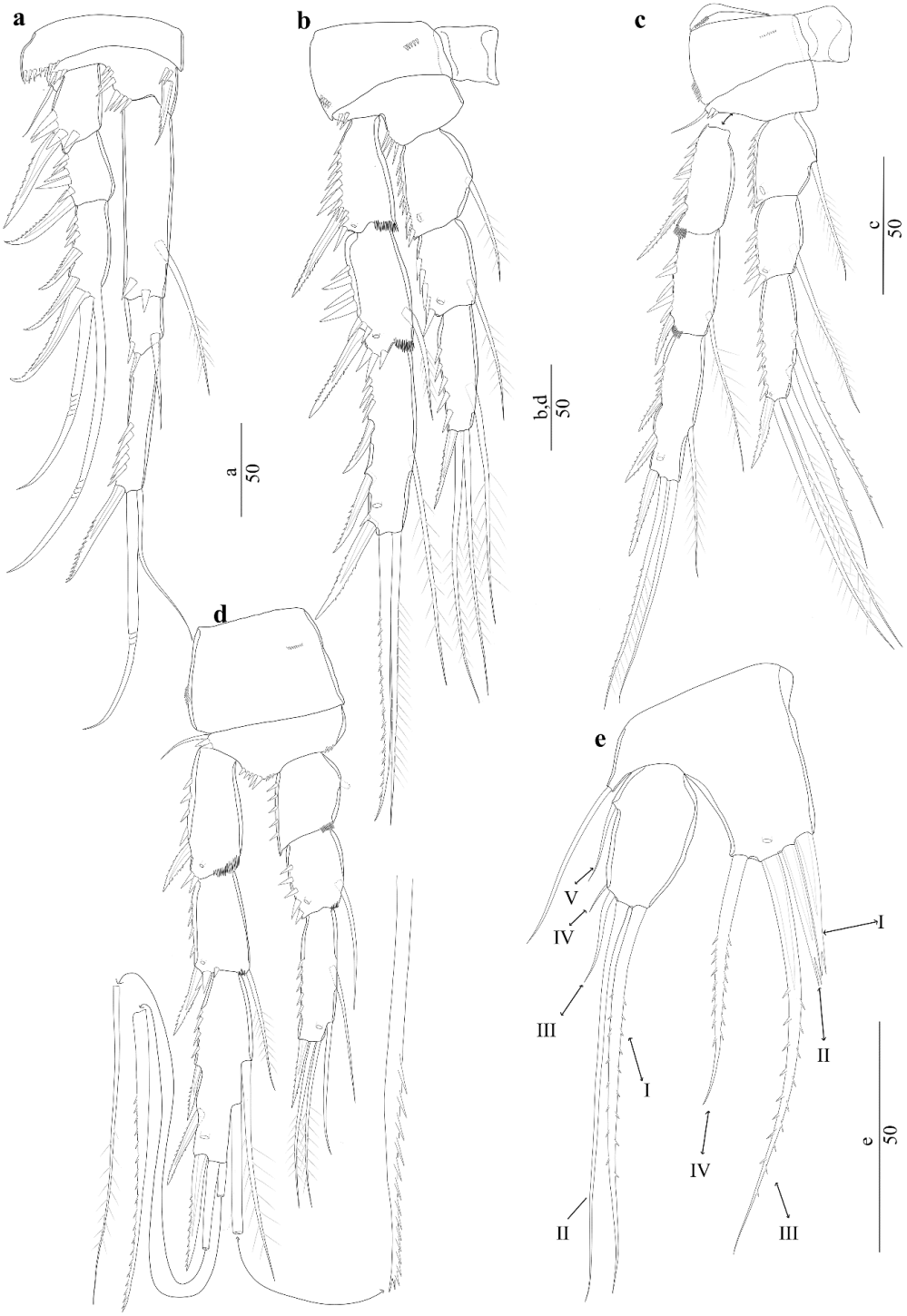


Figure 13. *Ameira nana*. ♀ anterior a) P1; b) P2; c) P3; d) P4; e) P5.

P2–P4 (Figure 13b–d) exp-1,2 covered with spinules on outer edge and a unipinnate outer spine; inner distal edge with spinules. P2 and P3 exp-3 with three bipinnate outer spines, one unipennate and one plumose distal seta, and one plumose inner seta. P4 exp-3 with three bipinnate outer spines, one unipennate and one plumose distal seta, and one plumose as well as one unipinnate inner setae. Enp-1,2 with inner seta (plumose in P2 and P3, broken in P4). P2 enp-3 with one bipinnate subapical outer spine, two plumose distal setae, and one plumose inner seta. P3 enp-3 with one bipinnate subapical spine, two plumose distal setae and two unipinnate inner setae. P4 enp-3 with a bipinnate subapical outer spine, two plumose distal setae and two naked inner setae. Enp-1,2,3 with a pore on anterior surface (P2, P4).

Setal formula of swimming legs:

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.0.113 | 1.1.111 |
| P2 | 0.1.123 | 1.1.121 |
| P3 | 0.1.123 | 1.1.221 |
| P4 | 0.1.223 | 1.1.221 |

P5 (Figure 13e) baseoendopod triangular, basal seta long, slender and naked; endopodal lobe with four setae; bipinnate outer seta (IV), distal seta (Seta III) bipinnate and the longest; two innermost setae (Seta I and II) apically furcated; exopodal lobe with five setae; seta I and II long, slender, seta I bipinnate, and seta II naked, seta III short and slender, seta IV the shortest seta, seta V slender.

### *Ameira wellsi* sp. nov.

https:/zoobank.org/zoobank.org/BFD17EC1-21C7-4D5F-8F78-B4EF4E1F39D1

Original description. Wells and Rao, 1987: 126–127, Figs 106–107

Synonym. *Ameira parvula sensu* Wells and Rao, 1987

Type material

Wells and Rao (1987) provided figures of both female and male specimens. The female specimen illustrated by Wells and Rao (1987: Figures 106a–c, 106g–k, 107a–d) is here designated as the holotype of *A. wellsi* sp. nov. (ICZN Arts 16.4 and 72.5.6). The species can be differentiated by the characters listed in the diagnosis below and those mentioned and illustrated in Wells and Rao (1987) (ICZN Art. 13.1).

Material examined. None.

Type locality

Wells and Rao (1987) collected specimens from various locations on the Andaman and Nicobar Islands between 1973 and 1974. As the basis of illustrations was not specified by Wells and Rao (1987), the type locality includes all respective places of origin (ICZN Art. 73.2.3).

Differential diagnosis

*Ameira*. Penultimate somite with two separate rows of spinules on the medioventrally. Antennary exopod two-segmented; proximal segment rectangular with distal naked seta and with a row of spinules and a large spinule; distal segment small and squarish with two long naked setae. The inner seta of P2–P4 enp-1 and enp-2 small and plumose. P5 baseoendopod with four setae exopod with 5 setae.

Armature formula of the swimming legs:

| | Exopod | Endopod |
|---|---|---|
| P1 | 0.0.023 | 1.1.011 |
| P2 | 0.1.223 | 1.1.120 |
| P3 | 0.1.223 | 1.1.221 |
| P4 | 0.1.323 | 1.1.221 |

Male. P5 baseoendopods medially fused, each with 3 setae; inner seta semispinulose and spine, middle seta minute, outer seta small and naked. Exopodal with 5 setae.

Etymology

The specific name is given in honor of Dr J.B.J.

Wells, who has made significant contributions to copepod taxonomy.

## Discussion

### A Comparative Analysis of Historical Records and Present Observations of *Ameira parvula*

The complexities of copepod morphology, particularly within the genus *Ameira* have historically presented a fascinating yet challenging puzzle. Variations reported in *Ameira parvula* records, such as the number of segments in the antenna exopod, the relative length of the first endopodal segment of the first swimming leg (P1 enp-1) to its exopod, the number of setae on the third exopodal segment of the fourth swimming leg (P4 exp-3), and the number of setae on the mandibular endopod, have elicited rigorous debate and intensive scrutiny.

The taxonomic discourse surrounding *A. parvula* has been subject to extensive debate due to the initial description's limitations and the subsequent efforts to refine its classification. Claus (1866) was the first to describe the species from Nice, France, providing a rudimentary description focusing solely on the antennule, antenna, cephalothorax, mandible, maxilliped and P1 (for further details, refer to the introduction section). Although Claus's (1866) original description lacks the detail necessary for comprehensive comparative analysis, our specimens generally correspond with the features he outlined. Notably, the detailed illustrations provided by Sars (1911) exhibit a remarkable congruence with our samples, suggesting a consistency in the species' morphology over time.

The current state of taxonomic understanding for *A. pa*rvula is hindered by the absence of the type material, which is recognized as a pivotal reference for resolving taxonomic issues within this problematic species. Although it is acknowledged that obtaining new material from the terra typica for a detailed description and illustration would be ideal to address these taxonomic challenges, such an endeavor is currently not feasible under existing conditions. However, a review of the relevant literature published after Claus (1866) reveals a consensus on a suite of characteristics, albeit not exhaustive, that can be utilized to delineate *A. parvula* and differentiate it from other species within the genus. These include: the possession of three-segmented endopods and exopods on P1–P4; the presence of three outer spines on the distal segment of the exopods in P2–P4; a total of five elements on the distal segment of the P1 exopod; the absence of an inner seta on P1 exp-2; the lack of an inner seta on the first segment of exopods P2–P4; the presence of an inner seta on the second segment of exopods P2–P4; the presence of an inner seta on the first segment of endopods P2–P4; bearing four setae on the terminal segment of the P2 endopod, and five setae on the terminal segments of the P3 and P4 endopods; the antenna having a distinct basis; and the caudal rami length-to-width ratio being less than one. Additionally, the length of the P1 enp-1 in relation to the entire exopod is equal to or greater than three. These morphological parameters serve as a provisional framework for identifying *A. parvula* until such time when the lost type material is supplemented by new samples, allowing for a comprehensive reevaluation and potential revision of the species' taxonomic status.

Gurney's (1927) explorations within the Suez Channel have long been considered a significant repository of Harpacticoida records. However, upon re-examination of specimens originally collected from Lake Manzalah, it becomes evident that these specimens do not align with the known morphological characteristics of *A. parvula*, specifically with discrepancies noted in the number of segments of the antenna exopod and the proportional lengths of the P5 and P1 enp-1. Our thorough analysis of this material has indeed led to the identification of three different undescribed species from this locality which also cannot confidently be assigned to the genus

*Ameira*. Based on these findings, we have reserved this material for a detailed examination in a subsequent study.

In earlier research, Vervoort (1962, 1964) documented specimens of *A. parvula* from New Caledonia and Ifaluk Atoll, describing the antenna exopod as one segmented. Subsequent illustrative records by Kunz (1975) and Pallares (1975) agreed with the observation of a single segmented antenna exopod. Contrary to these findings, initial observations by Mielke (1974, 1975) described the antenna exopod as two segmented in German and Norwegian specimens, highlighting variability in morphological characteristics across different populations. Moore's (1976) discussion on the segment number of antennary exopod introduced the hypothesis of potentially overlooked distal segments. Supporting this, Wells and Rao (1987) reported two segmented antenna exopod in Indian specimens of *A. parvula*, along with a consistent presence of eight setae on P4 exp-3, leading to the synonymization of *A. parvula tenuiseta* Willey, 1929 with *A. parvula*. In this study, the antenna exopods of the *A. parvula* specimens examined were also found to have two segments, confirming the two segmented condition. It is noteworthy that in the original description, Claus (1866) depicted the antenna exopod as one segmented; however, we assume that the terminal segment is extremely small and easily overlooked, which likely contributed to the initial one-segmented depiction.

In the discourse of mandibular endopod morphology, a discrepancy emerges when contrasting the observations made by Kunz (1975) and Moore (1976) against those noted by Mielke (1974) and Wells and Rao (1987). The former researchers have observed the mandibular endopod as possessing a setal formula comprising three apical setae in conjunction with a singular lateral seta. Conversely, Mielke (1974) along with Wells and Rao (1987) have documented an additional apical seta, thereby presenting a configuration of four apical setae coupled with one lateral seta. This variance underscores the necessity for a critical evaluation of mandibular endopod setation within the context of the broader morphological discourse. In the material redescribed in this study, we confirm the findings of Kunz (1975) and Moore (1976), having discerned the presence of three apical setae and a single lateral seta on the mandibular endopod.

Additionally, Mielke (1974) has reported the presence of three setae on the mandible basis, in contrast to the findings of Kunz (1975), Moore (1976) and Wells and Rao (1987) who have each observed two setae on the mandible basis. The current examination unequivocally corroborates the presence of two setae in the mandible basis of *A. parvula*. Probably, Mielke's (1974) Spitzbergen material is an undescribed species.

Chang's (2007) redescription of *A. parvula* from South Korea contribute significantly to our understanding of the species. Notably, Chang (2007) observed a two-segmented A2 exopod, similar to specimens in the current study; however, the spinules on the antenna endopod surface were situated more proximally compared to the *A. parv*ula examined here. Moreover, Chang (2007) reported a longer first segment of the endopod in his material relative to the *A. parvula* specimens in the present analysis. Despite these differences, the setae counts and ornamentations of P1 and P4 appear to be consistent across both studies. There is, however, a notable discrepancy in the length of the P1 basis outer setae; in Chang's (2007) specimens these are shorter and do not extend to the distal end of the P1 exp-1 as they do in the specimens of this study. Similarly, the inner seta of P4 enp-1 varies in size, being shorter in Chang's (2007) material, while it extends to the distal end of the third segment in the material examined in this study. Differences are also evident in the female P5 exopod, where the arrangement of spines along the inner margin differs. Chang's (2007) illustrations depict a group arrangement in contrast to the single-row

arrangement observed in the current *A. parvula* specimens. Additionally, the outer seta of the P5 exopod is bare in the specimens examined here whereas Chang's (2007) drawings depict it as plumose. Furthermore, Chang's (2007) P5 exopod illustrations show a more rounded shape, whereas P5 exopod is longer in the specimens examined in this study. Unfortunately, due to the lack of detailed illustrations of the mouthparts, P2-P3, and dorsal and ventral details of the urosome, a comparative analysis of these features is not feasible.

Chang (2007) acknowledged the concordance of his material with Mielke's (1974) and its general compatibility with the Indian population (Wells & Rao 1987), except for a minor difference in the P5 basoendopod setae. However, the Korean and Indian populations differ in several key morphological aspects, such as the length of the P1 endopod first segment, the setae count on the third segment of the P2 endopod, and the setae and spine ornamentation on the male P5 baseoendopod. Given these distinctions, it is plausible to consider that Chang's (2007) specimens may represent a closely related but distinct species from *A. parvula* described in this study. The variation in morphological traits, albeit subtle, may indeed suggest a cryptic diversity within what is currently recognized as a single species, underscoring the need for a more nuanced approach to the taxonomy of this group. Karanovic and Cho (2012) described two new species closely related to *A. parvula* and *A. parvuloides* Lang, 1965, discussing its cosmopolitan nature which corresponds to the fact that many supposed cosmopolitan species actually represent species complexes, with observations suggesting distinctness among the species (Gómez et al. 2012, George 2018, Karaytuğ et al. 2021, Alper et al. 2023).

*Ameira parvula* specimens from Dr Lesya Garlitska's collection, originating from the Cara Sea and Black Sea, exhibited unique characteristics. These specimens, which were collected at depths of 104 to 335 meters (Garlitska et al. 2019), had a P1 enp-1 that was shorter than the exopod distinguishing them from *A. parvula*. Although the number of setae on the swimming legs matched that of *A. parvula*, other features such as the length of P1 enp-1 and the patterns on the anal operculum did not. We have set aside these materials for a more comprehensive analysis in a future study. Currently, these specimens remain unclassified due to their varying morphological traits.

Upgrading *A. parvula* f. *nana* to Species Rank

Willey (1935) described two 'formae' of *A. parvula* from Bermuda: *A. parvula* f. *tenuiseta* and *A. parvula* f. *nana*. *A. nana* is characterized by a short fourth seta on the P5 exopod and a reduced setal formula of the swimming legs. Subsequently, Dinet (1971) provided a detailed redescription of *A. nana* (as *A. parvula nana*) from Marseille, France, covering various aspects such as the swimming legs, antennule, maxilliped, and antenna. Upon a thorough examination of the available literature and the specimens studied in this research, it becomes evident that *A. nana* exhibits distinct differences from other species within the *Ameira* genus.

The distinctions that set *A. nana* apart from *A. parvula* are significant. Notably, *A. nana* possesses an antennule with seven segments, as opposed to *A. parvula*, which has eight segments. Furthermore, the exopod of the antenna in *A. nana* consists of a single segment, whereas in *A. parvula*, it comprises two segments. Another distinguishing feature is the swimming leg setal formula, with *A. parvula* having P2–P4 exp-3 featuring 7-7-8 setae, while *A. nana* exhibits a different setal formula of 6-7-7 for these segments, thus justifying its elevation to species rank.

Establishment of *Ameira wellsi* sp. nov.

Wells and Rao (1987) initially classified *Ameira wellsi* sp. nov. as *A. parvula*, which was found on Andaman and Nicobar Islands in the Indian Ocean. Their research identified specific characteristics: the antenna exopod had two

segments, P2–P4 exp-3 had 7-7-8 setae, and enp-3 displayed 4-5-5 setae in the text. However, in the illustrations, P2 enp-3 appeared with three setae. Another observation was that P1 enp-1 was of the same length as the exopod. In contrast, *A. parvula* had one robust plumose seta and one apically furcated naked seta on the mandibular basis, which differed from *A. wellsi* sp. nov.

Furthermore, distinct setal lengths and ornamentations of the swimming legs can easily distinguishes *A. parvula* from *A. wellsi* sp. nov. Specifically, the inner seta of P2–P4 enp-1 and enp-2 are small and plumose in the new species but long and plumose in *A. parvula*. Additionally, in the male of *A. wellsi*, P5 baseoendopod featured three setae, while in A. *parvula* it has only two setae. Another distinguishing feature is the presence of two separate rows of spinules on the medioventral aspect of the penultimate body somite in *A. wellsi* sp. nov., whereas *A. parvula* has a single row of spinules.

Comparing *A. wellsi* sp. nov. to other species within the genus *Ameira*, it closely resembles *A. longipes* Boeck, 1865, *A. parvula, A. minuta* Boeck, 1865, *A. parvuloides* Lang, 1965, *A. scotti* Sars, 1911, *A. speciosa* Monard, 1935, *A. tenuicornis* T. Scott, 1902, *A. usitata* Klie, 1950, *A. bathyalis* Becker and Schriver, 1979, *A. faroensis* Schriver, 1982, *A. longispina* Gee 2009, *A. zahae* Karanovic and Cho, 2012, and *A. kimchi* Karanovic and Cho, 2012, based on the number of setae in P2–P4 exp-3 (7-7-7(8)) and P2–P4 enp-3 (4-5-5).

Considering these significant morphological differences, we propose that *A. parvula* sensu Wells and Rao, 1987 should be recognized as a distinct species as *Ameira wellsi* sp. nov.

Establishment of *Ameira venthami* sp. nov.

*Ameira venthami* sp. nov. was discovered in the medio-littoral zones along the Aegean and Mediterranean coasts of Türkiye. This new species belongs to the *Ameira* genus by displaying the characteristics: P1 enp-1 is of the same length as the exopod, P1 exp-2 lacks an inner seta, and P1–P4 exp-1 do not have inner setae.

Although *A. venthami* sp. nov. shares the same number of setae on P1–P4 with *A. nana*, several distinguishing features set it apart. These include the number of segments in the A1 (eight in *A. venthami* sp. nov. and seven in *A. nana*), setal and spinular ornamentation, the number of P5 exopod setae (five in *A. venthami* sp. nov. and four in *A. nana*) and the ventral ornamentation of the penultimate body somite.

Furthermore, *A. venthami* sp. nov. appears to be closely related to *A. parvuloides* Lang, 1965. However, it can be distinguished by the setal formula of P2–P4 exp-3 (6-7-7 in *A. venthami* sp. nov. and 6-7-8 in *A. parvuloides*). Additionally, *A. venthami* sp. nov. differs from *A. tenuicornis, A. longispina*, *A. wellsi* sp. nov., and *A. speciosa* (which all have a two-segmented A2 exopod) by having a single segmented A2 exopod.

*Ameira venthami* sp. nov. is also distinguishable from *A. longipes, A. parvula, A. minuta, A. parvuloides, A. scotti, A. speciosa, A. tenuicornis, A. usitata, A. bathyalis, A. faroensis, A. longispina, A. zahae, A. kimch*i, and *A. wellsi* sp. nov. based on the number of setae in P2–P4 exp-3 (6-6-7 in *A. venthami* sp. nov. and 7-7-7(8) in other species).

*Ameira venthami* sp. nov. is predominantly found within interstitial habitats along the Aegean and Mediterranean coasts of Türkiye. It's worth mentioning that in some localities, *A. parvula* and *A. venthami* sp. nov. coexist.

Remarks on the systematic problems surrounding the genus *Ameira* and establishment of *A. mediterranea*

The need for a comprehensive revision of the genus *Ameira* arises from several factors including the presence of incomplete species descriptions, the absence of clear distinguishing features (autapomorphy) defining the genus and an initial lack of a well-defined diagnosis for the genus.

Conroy-Dalton and Huys (1998) noted the existence of two distinct lineages within *Ameira*: the *longipes* group and the *atlantica* group. The

*longipes* group which consists of *A. longipes*, *A. parvula*, *A. minuta*, *A. parvuloides*, *A. scotti*, *A. speciosa*, *A. tenuicornis*, *A. usitata*, *A. bathyalis*, *A. faroensis*, *A. longispina*, *A. zahae* and *A. kimchi*, *A. wellsi* sp. nov. and *A. nana*, featuring traits like i) a smooth anal operculum and short caudal rami, ii) A1 proximal segment short and stout, iii) A2 exopod with one or two segments iv) one or two robust spinules on the outer margin, with a row of spinules on anterior surface, v) mandibular basis with pectinate spine, normal spine and flexible pinnate seta, vi) maxillule coxal endite with two setae and a basis with a discrete, minute endopodal segment, vii) maxilla with a syncoxa, viii) P1 enp-1 either as long as the exopod or longer than the exopod, ix) P2–P4 exp-2 with inner seta, x) P2–P4 enp-1,2 with inner seta, xi) P2–P4 enp-3 with one or two inner setae, xii) generally, female P5 with four baseoendopodal, five exopodal setae and male P5 with two baseoendopodal, five exopodal setae (Conroy-Dalton & Huys 1996, 1998, Gee 2009).

*Ameira nana*, *A. usitata* Klie, 1950, and *A. spinipes* Nicholls, 1940 are separated in the *longipes* group by a seven-segmented antennule. These all share common characteristics within the *longipes* group, P1 enp-1 elongated but not exceeding the exopod, and a one-segmented antenna exopod. Of note, *A. usitata* illustrated by Kunz (1975) displayed the same spine-like inner middle seta on P4 exp-3 as *A. nana*. Differences lie in the setal formula of the distal segments of exopods P2–P4 and the number of setae on P5 (see Table 3). P4 exp-3 inner middle seta is long, unipinnate and strong in *A. usitata* and *A. nana*, but this character is probably convergently evolved in other species (i.e. *Nitocra affinis* Gurney, 1927) of the family Ameiridae. For now, pending further examination of other materials, we propose classifying these species within the genus *Ameira*.

The other linage within the genus is the *atlantica* group: the species *Ameira atlantica atlantica* Noodt, 1958, *A. atlantica mediterranea* Kunz, 1974, and *A. reducta* Petkovski, 1954 all share a reduced setal formula on their swimming legs (see Table 3); however, they can be easily distinguished by the number of segments in antennule (seven-segmented in *A. atlantica atlantica* and *A. atlantica mediterranea*; eight-segmented in the *A. reducta*). This group featuring traits like i) antenna exopod with two setae in the first (exp-1) segment, which features a minute frill on the surface, ii) maxillule coxal endite with one developed element, iii) the P1 endopod is distinctly shorter than exopod, iv) P4 endopod setal formula with 1.1.121, v) P5 baseoendopod shape in male, vi) denticulated or incised hyaline frill on urosomites (Conroy-Dalton & Huys 1996, 1998, Gee 2009). Differences in the number of setae on P5 in females (4:4 in *A. atlantica atlantica* and *A. reducta*, 5:3 in *A. atlantica mediterranea*, 4:4) and males (3:2 in *A. atlantica atlantica*, 1:3 in *A. reducta* and 4:2 in *A. atlantica mediterranea*) *A. atlantica mediterranea* has the most primitive P5 exopodal setae on male and female within the *atlantica* group, and number of robust spinule on A2 exp first segment (with two robust spinules in *A. atlantica mediterranea*, one robust spinule in *A. atlantica atlantica* and *A. reducta*) further distinguish the these species. In line with these observations, we recommend reinstating *A. atlantica mediterranea* and *A. atlantica atlantica* as species, proposing the names *A. mediterranea* Kunz, 1974. and *A. atlantica* Noodt, 1958.

*Ameira pusilla* T. Scott, 1903, redescribed by Bodin (1977), shares some characteristics with the *atlantica* group, such as having a seven-segmented antennule and two-segmented antenna exopod. However, differentiation is possible through the examination of swimming-leg setal formula, *Ameira pusilla* presents the most primitive setal formula on P4 exp-3 (see Table 3) (Conroy-Dalton & Huys 1998).

In the context of swimming-leg setal formula among the species within the genus, *A. lusitanica* Galhano, 1970 deviates from the rest due to the presence of an inner seta on P2–P4 exp-1, which contradicts one of the diagnostic traits of *Ameira*. The absence of an inner seta on P2–P4 exp-1 and

the short caudal rami are shared all species of *Ameira*. Furthermore, *A. lusitanica* features slender swimming legs and long caudal rami, given this combination of traits, we suggest classifying *A. lusitanica* as species *incertae sedis* within Harpacticoida. *Ameira divagans* Kunz, 1963, alongside its subspecies, forms the third group within the genus that necessitates attention and revision due to their reduced swimming-leg setal formula.

Besides this group, other species within the genus need detailed comparison and redescription for especially of the mouthparts. The morphological examination of mouthparts in ameirid taxa can be challenging. However, a comprehensive study will greatly aid in clarifying the polyphyletic status of the genus. As numerous features of the species within the genus *Ameira* are incomparable, taxonomic revision of the other species is challenging and requires a thorough examination, which is beyond the scope of this paper.

## Conclusions

*Ameira parvula* is redescribed based on Brighton material. Through a detailed comparison with *A. parvula* specimens recorded and labeled as *A. parvula* from Turkish shores, it is revealed that the previous *A. parvula* records examined in this study represent two distinct species. One of these species is identified as *A. parvula*, which is morphologically indistinguishable from the Brighton material, while the other is defined as a new species, *A. venthami* sp. nov., which is found along all Turkish coasts except the Black Sea, and in some instances, it coexisted with *A. parvula*. Additionally, Gurney's (1927) Egyptian material (St. Eg1) is determined not to be *A. parvula*, nor do it belong to the genus *Ameira*. This finding is discussed in detail above. Furthermore, specimens recorded as *A. parvula* by Wells and Rao (1987) is redefined as a new species, *A. wellsi* sp. nov., based on the detailed description provided in their article. Lastly, *A. parvula nana* is reinstated as *A. nana*. *A. atlantica mediterranea* is reinstated as *A. mediterranea*. Additionally, *A. lusitanica* is classified as a species of *incertea sedis* within Harpacticoida. All proposed taxonomic changes are briefly given in Table 2 and also discussed in the discussion parts.

For the thorough examination of the genus, it is anticipated that the limits of the genus can be identified through the collection of new material of the species from the type locality, particularly by closely studying the mouthparts, in the absence of type material for several species. Not only *Ameira* but also other genera within the family Ameiridae pose difficulties in making detailed comparisons and necessary taxonomic changes due to imprecise boundaries and insufficient descriptions in the literature. A more integrative approach can clarify the family's systematic status by gathering specimens from type localities and incorporating thorough morphological and molecular research.

Table 2. List of taxonomic changes.

| Taxon | Taxonomic change |
|---|---|
| *Ameira parvula* sensu Gurney, 1927 | *species inquirenda* |
| *Ameira parvula* sensu Bozic, 1955 | *species inquirenda* |
| *Ameira parvula* sensu Pesta, 1959 | *species inquirenda* |
| *Ameira parvula* sensu Vervoort, 1962 | *species inquirenda* |
| *Ameira parvula* sensu Vervoort, 1962 | *species inquirenda* |
| *Ameira parvula* sensu Chislenko, 1976 | *species inquirenda* |
| *Ameira parvula* sensu Chislenko, 1977 | *species inquirenda* |
| *Ameira parvula* sensu Kunz, 1975 | *species inquirenda* |
| *Ameira parvula* sensu Wells and Rao 1987 | *Ameira wellsi* sp. nov. |
| *Ameira parvula nana* Willey, 1935 | *Ameira nana* Willey, 1935. |
| *Ameira atlantica atlantica* Noodt, 1958 | *Ameira atlantica* Noodt, 1958. |
| *A. atlantica mediterranea* Kunz, 1975 | *Ameira mediterranea* Kunz, 1975. |
| *Ameira lusitanica* Galhano, 1970 | *species inquirenda* |

Table 3. List of species within *Ameira* with some taxonomical characters A1 ♀: Female number of segments antennule; A2 exp: number of segments antenna exopod; P1 enp-1/exp: relative length of endopod-1 to exopod; P5♀: number of setae female P5 on exopod: endopod; P5♂: number of setae female P5 on male exopod: endopod; P2 exp; enp: setal formula of P2 exopod 2,3 and endopod 2,3; P3 exp/enp: setal formula of P3 exopod 2,3 and endopod 2,3; P4 exp/enp: setal formula of P4 exopod 2,3 and endopod 2,3. Differences shown in bold.

| Species | A1♀ | A2exp | P1 enp-1/exp | P5♀ | P5 ♂ | P2 | | P3 | | P4 | | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | exp | enp | exp | enp | exp | enp | |
| *A. atlantica* | 7 | 2 | short | **4**:4 | **3**:2 | 1.0**2**3 | 1.0**2**1 | 1.**1**23 | 1.**1**21 | 1.223 | 1.**1**21 | Noodt (1958) |
| *A. mediterranea* **stat. nov.** | 7 | 2 | short | 5:**3** | **4**:2 | 1.0**2**3 | 1.0**2**1 | 1.**1**23 | 1.**1**21 | 1.223 | 1.**1**21 | Kunz (1975) |
| *A. bathyalis* | 8 | 1 | short | **6**:4 | ? | 1.223 | 1.121 | 1.22**1** | 1.221 | 1.223 | 1.221 | Becker and Schriever (1979) |
| *A. confluens* | 8 | 1 | short | 5:4 | 5:4 | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.221 | Ranga Reddy (1984) |
| *A. divagans divagans* | 8 | 2 | long | 5:4 | ? | **0**.023 | 1.121 | 1.023 | 1.**1**21 | 1.223 | 1.1**3**1 | Nicholls (1940), Scheibel (1974) |
| *A. divagans africana* | 8 | 2 | long | 5:4 | **4**:2 | 1.023 | 1.121 | 1.023 | 1.**1**21 | 1.223 | 1.221 | Kunz (1963) |
| *A. divagans pontica* | 8 | 2 | long | 5:4 | ? | **0**.023 | **0?**.121 | **0**.023 | 1.**1**21 | 1.223 | 1.221 | Marinov (1973) |
| *A. faroerensis* | 8 | 1 | short | 5:4 | ? | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.2**1**1 | Schriever (1982) |
| *A. grandis* | 8 | 2 | short | **7:5** | **4:3** | 1.223 | 1.121 | 1.**3**23 | 1.**1**21 | 1.**3**23 | 1.**1**21 | Nicholls (1940) |
| *A. kimchi* | 8 | 1 | long | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | Karanovic and Cho (2012) |
| *A. listensis* | 8 | 1 | short | **6:5** | 5:2 | **0**.023 | 1.121 | **0**.023 | 1.**1**21 | **0**.223 | 1.**1**21 | Mielke (1975) |
| *A. longipes* | 8 | 1 | long | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.221 | Sars (1911) |
| *A. longispina* | 8 | 2 | as long as | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.323 | 1.221 | Gee (2009) |
| *A. minuta* | 8 | 1 | longer | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.221 | Boeck (1865) |
| *A. parascotti* | 8 | - | longer | 5:4 | ? | 1.223 | 1.**2**21 | 1.223 | 1.221 | 1.223 | 1.**1**21 | Chislenko (1977) |
| *A. parvula* | 8 | 2 | longer | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | This paper |
| *A. parvuloides* | 8 | 1 | as long as | 5:4 | 5:2 | 1.**1**23 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | Lang (1965) |
| *A. pusilla* | 7 | 2 | as long as | 5:4 | 5:2 | 1.023 | 1.021 | 1.**1**23 | 1.221 | 1.**3**23 | 1.221 | Bodin (1977) |
| *A. reducta* | 8 | 1 | short | **4**:4 | **3**:**1** | 1.023 | 1.021 | 1.023 | 1.**1**21 | 1.223 | 1.**1**21 | Petkovski (1954) |
| *A. scotti* | 8 | 1 | longer | 5:4 | ? | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.221 | Sars (1911) |
| *A. speciosa* | 8 | 2 | short | 5:4 | **6**:2 | ? | ? | 1.223 | 1.221 | 1.223 | 1.221 | Monard (1935), Lang (1948) |
| *A. spinipes* | 7 | 1 | as long as | 5:4 | **4**:**1** | 1.223 | 1.121 | ?.223 | ?.221 | ?.**3**23 | ?.221 | Nicholls (1940) |
| *A. tenucornis* | 8 | 2 | longer | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | T. Scott (1902), Sars (1911) |
| *A. usitata* | 7 | 1 | as long as | 5:4 | ? | 1.223 | 1.121 | 1.223 | 1.221 | 1.223 | 1.221 | Klie (1950) |
| *A. zahae* | 8 | 1 | longer | 5:4 | 5:2 | 1.223 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | Karanovic and Cho (2012) |
| *A. nana* | 7 | 1 | as long as | 5:4 | 5:**3** | 1.**1**23 | 1.121 | 1.**1**23 | 1.221 | 1.223 | 1.221 | Willey (1935), Dinet (1971) |
| *A. venthami* **sp. nov.** | 8 | 1 | as long as | 5:4 | 5:2 | 1.**1**23 | 1.121 | 1.**1**23 | 1.221 | 1.223 | 1.221 | This paper |
| *A. wellsi* **sp. nov.** | 8 | 2 | as long as | 5:4 | 5:**3** | 1.223 | 1.121 | 1.223 | 1.221 | 1.**3**23 | 1.221 | Wells and Rao (1987) |

**Nomenclature acts.**

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