



Taxonomic revision of the genus *Nannomesochra* Gurney, 1932 (Copepoda, Harpacticoida) with description of three new species

Alp Alper¹ · Süphan Karaytuğ² · Serdar Sak¹

Received: 23 March 2022 / Revised: 22 September 2022 / Accepted: 13 October 2022 / Published online: 31 January 2023
© The Author(s), under exclusive licence to Senckenberg Gesellschaft für Naturforschung 2023

Abstract

A taxonomic revision of the genus *Nannomesochra* Gurney, 1932 was made based on the material collected from a wide range of localities along the Turkish coasts. Detailed morphological examination and comparisons of several specimens as well as the previous descriptions which were assigned to the so-called cosmopolitan species *N. arupinensis* (Brian, 1925) revealed that *N. arupinensis* indeed represents a complex of several closely related morphospecies that can be differentiated from one another by only detailed observations. With this study, *Nannomesochra parvula* (Gurney, 1927) was reinstated and redescribed because of the setation of the swimming legs and the structure of the P5 in female. It has been determined that, according to updated modern keys, the recent inclusion of the monotypic genus *Archeolourinia* Corgosinho & Schizas, 2013 in the Louriniidae Monard, 1927 is not justified since *Archeolourinia shermani* Corgosinho & Schizas, 2013 does not belong to this family but must be assigned to the genus *Nannomesochra* within Canthocamptidae. Therefore, *Archeolourinia* was removed from the family Louriniidae and accepted as junior synonym of *Nannomesochra* keeping *Nannomesochra shermani* (Corgosinho & Schizas, 2013) comb. nov. as a valid species of the genus. As a result of the morphological examination of Turkish material, 3 new species of *Nannomesochra* were discovered and named as *N. gebekumensis* sp. nov., *N. giziri* sp. nov., and *N. erythraiensis* sp. nov. With addition of these species mentioned above, the genus now contains seven valid species, namely, *N. arupinensis*, *N. parvula*, *N. zavodniki* Petkovski & Apostolov, 1974, *N. shermani* comb. nov., *N. gebekumensis* sp. nov., *N. giziri* sp. nov., and *N. erythraiensis* sp. nov. Detailed review of the previous species records is given, indicating that the genus *Nannomesochra* has a worldwide distribution. But it is concluded that almost all of the previous records are unreliable, since they do not contain sufficient information to verify to which *Nannomesochra* species they belong. The phylogenetic position of *Nannomesochra* within Hemimesochrinae Por, 1986 was also evaluated in the study and a generic key within the subfamily is presented. It was concluded that the presence of the three elements on the distal endopodal segment of the P3 endopod in the male can be defined as an autoapomorphy of the genus *Nannomesochra*.

Keywords Species complex · Canthocamptidae · Taxonomy · Turkey

Communicated by S. Gollner

This article is registered in ZooBank under <https://zoobank.org/772258D7-6834-4000-9DD5-4EF219C3858B>

✉ Alp Alper
alpalper80@gmail.com

Süphan Karaytuğ
suphankaraytug@gmail.com

Serdar Sak
serdarsak@gmail.com

¹ Department of Biology, Faculty of Science and Literature, Balıkesir University, Çağış Campus, Balıkesir, Turkey

² Department of Biology, Faculty of Art and Science, Mersin University, Çiftlikköy Campus, Mersin, Turkey

Introduction

The family Canthocamptidae Brady, 1880 is by far the largest family of Harpacticoida G.O. Sars, 1903, comprising in excess of 600 species, being predominantly distributed in freshwater. Representatives of the family can be found in freshwater habitats such as ponds, wetlands, hot springs, glacial melt water, and damp moss. Determining the evolutionary history of the canthocamptids is grossly obstructed by the lack of a coherent scheme of phylogenetic relationships for the family. It has been assumed that the family is almost certainly polyphyletic; therefore, Canthocamptidae is in urgent need of revision and on

the other hand, most of the established genera should be carefully diagnosed on the basis of their apomorphic characters (Boxshall and Jaume 2000; Boxshall and Halsey 2004).

Brian (1923) published *Mesochra arupinensis* as *nomen nudum* in his study on benthic copepods of Rovinj (Croatia). Later, in another study on the harpacticoid copepods of Rovinj, Brian (1925) validly described *Mesochra arupinensis* Brian, 1925 as a new species. On the other hand, Gurney (1927) described *Pseudomesochra parvula* Gurney, 1927 as a new species and created the genus *Pseudomesochra* Gurney, 1927 by monotypy in the same study. Later Gurney (1932) realized that the genus *Pseudomesochra* was preoccupied by *Pseudomesochra* T. Scott, 1902 (family Pseudotachidiidae) and therefore Gurney (1932) created the genus *Nannomesochra* Gurney, 1932 as a replacement name for the genus *Pseudomesochra*. Later Monard (1935a) compared the descriptions of *N. parvula* with that of *Mesochra arupinensis* and finally reached the conclusion that *N. parvula* should be accepted as a junior subjective synonym of *Mesochra arupinensis*. Monard (1935a) also stated that *M. arupinensis* should be located in the genus *Nannomesochra*. So, it was Monard (1935a) who first transferred *M. arupinensis* to the genus *Nannomesochra*. Lang (1936, 1948) agreed with Monard's (1935a) decision and this case has been accepted until now. Currently, the genus *Nannomesochra* contains three valid species (Walter and Boxshall 2022).

During the course of surveys along the Turkish coasts, numerous specimens belonging to the genus *Nannomesochra* were collected from different locations. Detailed morphological comparisons of the populations as well as the descriptions in the literature revealed the presence of several different morphological species, the descriptions of which are given below. This has also provided us to re-evaluate the taxonomic position of the genus and to review the previous records assigned to *N. arupinensis* sensu lato.

Material and methods

Several specimens collected from the Turkish coasts (deposited in the collection of Mersin and Balıkesir Universities, Turkey) were re-examined (see details in the results). Differential interference contrast (DIC) attached binocular microscopes (Olympus BX-50 and BX-53) were used to examine and draw the specimens in detail. An Olympus SZX-12 stereomicroscope was used to dissect selected specimens then dissected parts were mounted on several slides in lactophenol mounting medium. The technique of inserting glass fibers between slide and cover slip was used to prevent the whole specimens and dissected appendages from being squashed by the coverslips and to enable rotation and manipulation, permitting observation from all positions. An ocular micrometer

was used to take measurements. Total body length was measured from tip of rostrum to posterior margin of caudal rami. Illustrations of the specimens were drawn with Photoshop CS2 or Inkscape v0.91 by using a Wacom Cintiq Pro 13 graphic tablet. Scale bars in illustrations are given in μm . SEM examinations were made with a Zeiss SUPRA 55VP (FESEM) scanning electron microscope at the Mersin University Advanced Technology Education, Research, and Application Centre (MEITAM). A protocol described in Kaymak and Karaytuğ (2014) was followed for SEM study. Entellan (Merck) was used for sealing all dissected specimens prepared for light microscopy after examination; undissected whole specimens were preserved in 70% ethanol in small tubes. The descriptive terminology is adapted from Huys et al. (1996). Abbreviations used in the text are as follows: *P1–P6*, first to sixth swimming legs; *ae*, aesthetasc; *enp*, endopod; *exp*, exopod. A cladistic analysis was performed on *Nannomesochra* species. Fifteen morphological characters used in the analysis and their states were listed in Table 1 and the data matrix was given in Table 2. The states of the characters were defined in accordance with the basic principles in the copepod evolution (Huys and Boxshall 1991). Standard coding was used in the matrix: “0” representing a plesiomorphic character state and higher numbers are apomorphies. Unknown values were coded “?”. To construct trees, maximum parsimony (MP) analysis was conducted in PAUP* 4.0a software with a heuristic search option. All material except for the specimens deposited in the Zoology Museum of Adiyaman University (ZMADYU) is incorporated in the collection of Mersin University Biology Department.

Results

Taxonomic account

Order Harpacticoida G.O. Sars, 1903
 Family Canthocamptidae Brady, 1880
 Genus *Nannomesochra* Gurney, 1932

Diagnosis. Canthocamptidae. Body slender and more or less cylindrical, slightly tapering posteriorly, without prominent distinction between prosome and urosome, first thoracic somite fused to cephalosome, forming a cephalothorax.. Urosome 5-segmented in female; comprising fifth pedigerous somite, genital double-somite and three free abdominal somites. Genital double somite with internal trace of subdivision ventrally and (dorso)laterally. Rostrum well developed, bell-shaped, anteroventrally directed, fused with cephalothoracic shield, but defined at base by a suture line. Anal operculum straight, distal margin ornamented with fine setules. Urosome 6-segmented in male; comprising fifth pedigerous somite, genital somite and four free abdominal somites. Caudal rami

Table 1 List of characters used in cladistic analysis (0 is a plesiomorphic state, higher numbers are apomorphic states)

No	Characters
1	A1 segment-2 with nine setae (0); with eight setae (1); unknown (?)
2	A1 segment-3 with six setae (0); with five setae (1); with four setae (2); unknown (?)
3	P1 endopod equal/shorter than exopod (0); endopod longer than exopod (1)
4	P1 enp-2 with one inner seta (0); without inner seta (1)
5	P2 enp-2 with two inner setae (0); with one inner seta (1)
6	P2 exp-2 with one inner seta (0); without inner seta (1)
7	P3 enp-2 with two inner setae (0); with one inner seta (1)
8	P3 exp-2 with one inner seta (0); without inner seta (1)
9	P4 enp-2 with two inner setae (0); with one inner seta (1)
10	P4 exp-2 with one inner seta (0); without inner seta (1)
11	Female P5 exopod with six setae (0); with five setae (1)
12	Female P5 exopod without notch between seta I and II (0); with notch between seta I and II (1)
13	Female P5 exopod without protuberance between seta I and II (0); with protuberance between seta I and II (1)
14	Female P5 baseoendopodal lobe not reaching distal margin of exopod (0); reaching to distal margin of exopod (1); extends beyond distal margin of exopod (2)
15	Caudal rami without a spinular row near base of the seta VII (0); with a spinular row near base of the seta VII (1)

with seven setae, seta II difficult to observe. Antennule short; 7-segmented in female, furnished with aesthetasc on 4th and 7th segments; indistinctly 9-segmented and haplocer, furnished with aesthetasc on 5th and 9th segments in male. Antenna biramous; allobasis with two abexopodal setae; endopod 1-segmented; exopod 1-segmented with two setae. Mandible with well-developed gnathobase; palp represented by a segment with 5 setae. Maxillule with well-developed praecoxal arthrite; exo- and endopod incorporated into basis. Maxilla with two syncoxal endites; allobasis represented by claw. Maxilliped prehensile with syncoxa and basis; endopod with claw and a small seta. P1 with both rami 3-segmented. P2–P4 with 3-segmented exopods and 2-segmented endopods in female; endopod P3 2-segmented in male, second segment with modified inner spine. P5 confluent in both sexes; exo- and endopodal lobes in female with 5–6 and 4 setae respectively; in male endopodal lobe with 2 setae. Female P6 with by 2 setae. Male P6 with 1 seta. Sexual dimorphism in body ornamentation, antennule, endopod of P3, P5 and P6.

Type species. *Pseudomesochra parvula* Gurney, 1927 = *Nannomesochra parvula* (Gurney, 1927) (by monotypy).

Other species. *N. arupinensis* (Brian, 1925), *N. zavodniki* Petkovski & Apostolov, 1974, *N. shermani* (Corgosinho & Schizas, 2013) comb. nov., *N. gebekumensis* sp. nov., *N. giziri* sp. nov., *N. erythraiensis* sp. nov.

Species inquirendae. *Mesochra arupinensis* sensu Brian (1928a, 1928b); *Pseudomesochra parvula* sensu Willey (1930); *Mesochra arupinensis* = *Mesochra armoricana* sensu Monard (1935b); *Nannomesochra arupinensis* sensu Jakubisiak (1938); *Nannomesochra arupinensis* sensu Noodt (1953); *Nannomesochra arupinensis* sensu Vervoort, 1964; *Nannomesochra arupinensis* sensu Apostolov and Marinov (1988).

Unverifiable records: Tunisia (Monard 1935a; Lang 1936); Algeria (Monard 1937); Greece (Monard 1937); Teneriffe (Noodt 1955a); Turkey (Noodt 1955b); Ireland (Roe 1960); Indian Ocean, Aldabra (Wells and McKenzie 1973); Bulgaria (Apostolov 1977); San Diego, USA (Thistle 1982); Italy

Table 2 Data matrix used in the PAUP analysis of *Nannomesochra* species. The character numbers refer to the character list given in Table 1

No Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>N. arupinensis</i>	?	?	1	0	0	0	1	0	1	0	1	0	0	1	0
<i>N. shermani</i> comb. nov.	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0
<i>N. parvula</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	2	1
<i>N. giziri</i> sp. nov.	1	2	0	0	0	0	0	0	0	0	1	1	0	2	0
<i>N. gebekumensis</i> sp. nov.	0	0	0	1	1	1	0	1	1	1	1	0	0	0	0
<i>N. erythraiensis</i> sp. nov.	1	2	0	0	0	1	1	1	1	1	0	0	0	0	1
<i>N. zavodniki</i>	?	?	0	0	0	1	1	1	1	1	0	0	1	0	0

(Ceccherelli and Mistri 1990); Australia (Halse et al. 2000); United Kingdom (Ventham 2011); Tanzania (Callens et al. 2012); Brazil (Sarmiento and Santos 2012). No illustrations.

Nannomesochra arupinensis (Brian, 1925)

Original description. *Mesochra arupinensis* Brian, 1925: p.20, Figs. 8–16.

Mesochra arupinensis sp.n. *nomen nudum* (Brian, 1923): p.130.

Material examined. None

Remarks. *N. arupinensis* was first published by Brian (1923) as *nomen nudum* under the name of *Mesochra arupinensis* in his study on benthic copepods of Rovinj (Croatia). Later, in another study on the harpacticoid copepods of Rovinj, Brian (1925) described *Mesochra arupinensis* as a new species. Unfortunately, the type material of *N. arupinensis* sensu Brian (1925) cannot be traced but the detailed comparisons of the original descriptions (Brian, 1925) with those of the successive records revealed that the following combination of the characters easily differentiate *N. arupinensis* sensu Brian (1925) from other species considered valid of the genus in this study: i) the presence of 6 setae on the third exopod segment of P4 in female; ii) the structure of female P5, i.e. baseopodal lobe not exceeds the exopod; iii) the structure of male P5, i.e. the triangle shape of baseopodal lobe which exceeds the exopod; iv) the structure of male P3 enp-2. The unusual shape and setation of the male P3 enp-2 are unique within the genus; the modified inner seta on the enp-2 cannot be identified on the figure provided by Brian (1925) but the small/reduced element on the anterior surface of the enp-2 may represent the modified seta. Nevertheless, the P3-enp is very different from that of other species in the genus. Other minor differences compared to those of valid species are summarized in Table 3.

Nannomesochra parvula (Gurney, 1927)

Original description. *Pseudomesochra parvula* Gurney, 1927: p.543, Fig. 153 (A–L).

Synonym. *Nannomesochra arupinensis* (Brian, 1925) sensu Alper et al. (2010).

Material examined. Two ♀♀ (one ♀ dissected on six slides), collected from washings of macroalgae *Cystoseira* sp., *Corallina* sp., *Halopteris* sp. and *Laurencia* sp., 16 April 2007. Seven ♀♀ in alcohol, collected from washings of macroalgae *Cystoseira* sp., *Corallina* sp., *Halopteris* sp. and *Laurencia* sp., 23 February 2008. All material collected from the intertidal zone at rocky shore of Gebekum (36.7639833° N, 27.7450000° E), Datça, Muğla/Turkey.

Redescription of the female

Body (Fig. 1a, b) cylindrical, gradually tapering posteriorly; without clear distinction between prosome and urosome; first thoracic somite fused to cephalosome, forming a cephalothorax. Total body length: 498 µm. Greatest width measured

at posterior margin of cephalothorax: 124 µm. Surface ornamentation of somites as figured (Figs. 1a, b and 4a). Hyaline frills of somites smooth.

Rostrum (Fig. 1c) bell shaped, defined at base; bears two sensilla.

Antennule (Fig. 1d) 7-segmented. Segment-1 ornamented with rows of spinules near posterior margin and a row of robust spinules at distal margin; with a seta at distal corner. Segment-2 with nine setae. Segment-3 rectangular, with six setae. Segment-4 bears one seta and an aesthetasc fused basally to a seta. Segments -5 and -6 are similar in length, with one and two setae respectively. Segment-7 bears five setae and an apical acrothek consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[9]-3[6]-4[1+(1+ae)]-5[1]-6[2]-7[5+acrothek].

Antenna (Fig. 2a). Coxa ornamented with a row of spinules as figured. Allobasis with two abexopodal setae. Exopod 1-segmented, rectangular; armed with two apical setae. Endopod with two lateral robust pinnate spines; distal margin ornamented with spinules as figured; apical armature consists of two pinnate spines, two geniculate setae, and one pinnate spine fused basally to a seta.

Labrum (Fig. 2b) large, with bilateral extensions medially. Anterior surface with long spinules subdistally, posterior surface with a row of spinules bi-laterally.

Mandible (Fig. 2c) with well-developed gnathobase that bears a pinnate seta at dorsal corner; cutting edge with series of teeth. Palp 1-segmented, exopod and endopod incorporated into basis, armature consisting of three pinnate setae laterally and two elements (one pinnate spine and one seta) apically.

Maxillule (Fig. 2d). Praecoxa with spinules laterally. Praecoxal arthrite well-developed, with a row of small spinules on posterior surface, with one seta on anterior surface, with nine elements around distal margin. Coxa ornamented with spinular row as figured. Coxal endite bears one pinnate spine and one bare seta. Endopod and exopod incorporated into basis, armature consisting of four setae laterally and, one pinnate spine and three bare setae apically.

Maxilla (Fig. 2e). Syncoxa with two endites; each bears three spines apically, two of which with tubular extensions as figured. Allobasis forming spinous claw, slightly curved distally; accessory armature represented by two setae. Endopod reduced, represented by two setae.

Maxilliped (Fig. 2f and g) subchelate. Syncoxa and basis ornamented with spinular rows as figured. Endopod 1-segmented; armed with long claw, slightly curved apically and with one small accessory seta.

P1–P4 (Fig. 3a, b, c and d). Praecoxae well developed, ornamented with spinules along distal margin. Intercostal sclerites wider than long. Coxae rectangular; ornamented with row of spinules as figured (P1, P2) or unornamented (P3, P4). Bases ornamented with large spinules along distal margin; with a tube-pore as figured; with one inner seta and one outer

Table 3 Morphological comparison of *Nannomesochra* species (uk: male unknown, N/A: data not available; **: see description)

	<i>N. parvula</i>	<i>N. giziri</i> sp. nov.	<i>N. gebekamensis</i> sp. nov.	<i>N. arupinensis</i>	<i>N. shermani</i> comb. nov.	<i>N. zavodniki</i>	<i>N. erythraensis</i> sp. nov.
P1 (♂)							
Length of endopod relative to exopod	Endopod as long as exopod	Endopod as long as exopod	Endopod as long as exopod	Endopod longer than exopod	Endopod longer than exopod	Endopod as long as exopod	Endopod as long as exopod
Length of Emp-1 inner seta relative to endopod	Extends to approximately the end of endopod	Extends well beyond the end of endopod	Extends to approximately the middle of Emp-3	Extends to approximately the end of Emp-2	Extends to approximately the end of endopod	Extends to approximately the end of Emp-2	Extends to approximately the end of endopod
Length of Emp-1 relative to exopod	Extends to approximately the middle of Exp-2	Extends to approximately the end of Exp-2	Extends to approximately the end of Exp-2	Extends to approximately the end of Exp-2	Extends to approximately the end of Exp-2	Extends to approximately the middle of Exp-2	Extends to approximately the end of Exp-2
Emp-2, number of inner seta	1	1	0	1	1	1	1
Emp-3, ratio of maximum length to maximum breadth	~2.5	~4.5	~2	~3	~3.4	~3	~3.5
P2 (♀)							
Length of endopod relative to exopod	Extends to approximately the end of Exp-2	Extends to approximately the end of Exp-2	Extends to approximately the middle of Exp-2	N/A	Extends to approximately the middle of Exp-2	Extends to approximately the middle of Exp-2	Extends to approximately the end of Exp-2
Emp-2, number of inner seta(e)	2	2	1	N/A	2	2	2
Emp-2, ratio of maximum length to maximum breadth	~2.7	~2	~1.8	N/A	~2.5	~2.5	~2.4
Exp-2 – Exp-3, number of inner seta	1–1	1–1	0–0	N/A	1–1	0–0	0–0
Exp-3, apical armature (inner/outer)	Long seta with outer spinules and inner setules/long seta with outer spinules	Long seta with outer spinules and inner setules/ Long seta with outer spinules and inner setules	Short, delicate seta/pinnate spine	N/A	Long seta with outer spinules and inner setules/long spiniform seta with outer spinules and inner setules	Long naked seta/ spiniform seta with outer spinules	Long naked seta/ spiniform seta with robust outer spinules
P3 (♀)							
Emp-2, number of inner setae	2	2	2	N/A	1	1	1
Emp-2, inner sub-distal seta	Long, plumose	Long, plumose	Short, serrated apically	N/A	-	-	-
Exp-2 – Exp-3, number of inner seta(e)	1–2	1–2	0–1	N/A	1–2	0–1	0–1
Exp-3, apical armature (inner/outer)	Long seta with outer spinules and inner setules/long seta with outer spinules	Long seta with outer spinules and inner setules/long seta with outer spinules	Short, delicate seta/bipinnate spine	N/A	Long seta with outer spinules and inner setules/long seta with outer spinules	Long seta with outer spinules/spiniform seta with outer spinules	Long seta with outer spinules/- spiniform seta with robust outer spinules
P3 (♂)							
Emp-2, modified inner element	uk	Spine, tip in form of crochet-hook	Spine, tip in form of toggle harpoon	Thorn-like spine	uk	uk	Blunt tipped spine
P4 (♀)							
	2	2	1	1	1	1	1

Table 3 (continued)

	<i>N. parvula</i>	<i>N. giziri</i> sp. nov.	<i>N. gebekamensis</i> sp. nov.	<i>N. arupinensis</i>	<i>N. shermani</i> comb. nov.	<i>N. zavodniki</i>	<i>N. erythraensis</i> sp. nov.
Exp-2, number of inner seta(e)	1–2	1–2	0–1	1–2	1–2	0–1	0–1
Exp-2 – Exp-3, number of inner seta(e)	Extends to approximately the middle of Exp-2	Extends beyond the end of Exp-1	Extends to approximately the middle of Exp-2	Extends beyond the end of Exp-1	Extends beyond the end of Exp-1	Extends beyond the end of Exp-1	Extends to approximately the end of Exp-1
Length of endopod relative to exopod	~1.4	~2.2	~2.6	N/A	~2	~2.9	~2.8
Exp-3, ratio of the length of inner seta serrated apically to Exp-3							
Exp-3, apical armature (inner/outer)	Very long seta with outer spinules and inner setules/very long seta with outer spinules and inner setules	Long seta with outer spinules and inner setules/long seta with outer spinules and inner setules	Short, delicate seta/pinnate seta	Long pinnate seta/long pinnate seta	Long seta with outer spinules and inner setules/long seta with outer spinules and inner setules	Long pinnate seta/long pinnate seta	Long bipinnate seta /spiniform seta with robust outer spinules
P5 (♀)							
Number of setae on baseoendopod and exopod	4–5	4–5	4–5	4–5	4–5	4–6	4–6
Length of baseoendopodal lobe relative to exopod	Extends beyond distal margin of exopod	Extends beyond distal margin of exopod	Not reaching distal margin of exopod	Reaching to distal margin of exopod	Not reaching distal margin of exopod	Not reaching distal margin of exopod	Not reaching distal margin of exopod
Baseoendopodal lobe, spinular ornamentation on distal margin	Present	Present	Present	Absent	Absent	Absent	Absent
Baseoendopodal lobe, spinular ornamentation on surface	Present (delicate spinules)	Present (delicate spinules)	Present (large spinules)	Absent	Absent	Present (delicate spinules)	Present (delicate spinules)
P5 (♂)							
Number of setae on baseoendopod and exopod	uk	2–6	2–5(6)**	2–5	uk	uk	2–5(6)**
Length of baseoendopodal lobe relative to exopod	uk	Reaching to distal margin of exopod	Not reaching distal margin of exopod	Extends beyond distal margin of exopod	uk	uk	Not reaching distal margin of exopod
Baseoendopodal lobe, spinular ornamentation on surface	uk	Present (delicate spinules)	Present (large spinules)	Absent	uk	uk	Present (delicate spinules and microspinules as figured)
Caudal rami							
Spinular row near base of seta VII	Present	Absent	Absent	N/A	Absent	Absent	Present
Ratio of length of seta V to seta IV	~2.1	~1.6	~1.35	~2.8	N/A	~2.25	~2.2

seta (P1) or with one outer seta (P2–P4). P1–P4 with 3-segmented exopods; outer margin of exopodal segments ornamented with strong spinules. Exp-1 with naked inner margin (P1–P4). Exp-2 without (P1) or with one inner seta (P2–P4). Exp-3 with two geniculate setae and two outer spines (P1) or with one inner seta, two long apical setae and three outer spines (P2) or with two inner setae, the medial one long and plumose, the sub-distal one short and serrated apically; two apical long setae and three outer spines (P3–P4). Endopod 3-segmented (P1) or 2-segmented (P2–P4); outer margin of endopodal segments ornamented with spinules. Enp-1 with one inner seta, serrated apically (P1, P2, P4); or with one inner bare seta (P3). Enp-2 with one inner seta (P1) or with two inner setae serrated apically, two apical setae (inner one minute, outer one long and plumose) and one outer pinnate spine (P2) or with two inner setae (medial one short and serrated apically, sub-distal one long and plumose), two apical setae (inner one short, outer one long and plumose) and one outer pinnate spine (P3–P4). Enp-3 with one inner naked seta and two apical long, pinnate setae (P1).

Setal formula of swimming legs:

	Exopod	Endopod
P1	0.0.022	1.1.120
P2	0.1.123	1.221
P3	0.1.223	1.221
P4	0.1.223	1.221

P5 (Fig. 4a) fused medially, forming a bilobate plate with medial incision, bearing a pore and a row of fine spinules on anterior surface. Endopodal lobe extending beyond distal margin of exopod, armed with four pinnate setae. Exopods roundish, armed with five setae (seta-III shortest, spiniform). Outer basal seta with a flagellum.

Caudal rami (Fig. 4a, b and c) slightly wider than long; with a tube-pore at outer distal corner dorsally; with seven setae. Seta I naked; seta II delicate bifid at tip; seta III naked, inserted at outer distal corner. Seta IV and V inserted terminally, with a fracture plane. Seta VI naked. Seta VII located dorsally, tri-articulated at base. A spinular row is present near base of seta VII.

Remarks. As mentioned in the “Introduction” section, *N. parvula* was synonymized of *M. arupinensis* and *M. arupinensis* transferred to the genus *Nannomesochra* by Monard (1935a). Lang (1936, 1948) agreed with Monard’s (1935a) decision. This case has accepted until now. Some Turkish material of *Nannomesochra* (named and redescribed in detail above as *Nannomesochra parvula*) examined in this study is morphologically almost identical with Gurney’s (1927) original description of *N. parvula*. Comparisons between two species were revealed that *N. parvula* differs from *N. arupinensis* by the combination of the following characters: i) P1 endopod equal

to exopod in length ii) female P2–P4 bears 5,5,5 and 6,7,7 setae on the distal segments of endo- and exopods respectively; iii) baseoendopodal lobe of female P5 extends beyond distal margin of exopod; iv) seta III on female P5 exopod is short, spiniform; v) spinular row is present near base of seta VII on caudal rami. Other minor differences compared to *N. arupinensis* and other species of the genus are summarized in Table 3. Because of the characters listed above *N. parvula* should be considered as a valid species.

Nannomesochra zavodniki Petkovski & Apostolov, 1974

Original description. *Nannomesochra zavodniki* Petkovski & Apostolov, 1974: *Fragmenta Balcanica*, 10, 1–8, Figs. 1–3.

Material examined. None.

Remarks. *N. zavodniki* was originally described from a single female, collected between the algae and stones on Marjan Beach near Split, Croatia (Petkovski and Apostolov 1974), and has not been reported since then. *N. zavodniki* can be distinguished from the other species of the genus except *N. erythraiensis* sp. nov. by the combination of the following characters: i) female P5 exopod bears six setae; ii) female P2–P4 bears 5,4,4 and 5,6,6 setae on the distal segments of endo- and exopods respectively. *N. zavodniki* morphologically differs from *N. erythraiensis* sp. nov. by the combination of the following characters: i) the inner seta of P1 enp-1 extends to approximately the end of enp-2; ii) P1 enp-1 extends to approximately the middle of exp-2; iii) P2 endopod extends to approximately the middle of exp-2; iv) P4 endopod extends beyond the end of exp-1; v) female P5 exopod with a protuberance between seta I and II; vi) caudal rami without a spinular row near base of seta VII. Other minor differences compared to those of valid species are summarized in Table 3.

Nannomesochra shermani (Corgosinho & Schizas, 2013) comb. nov.

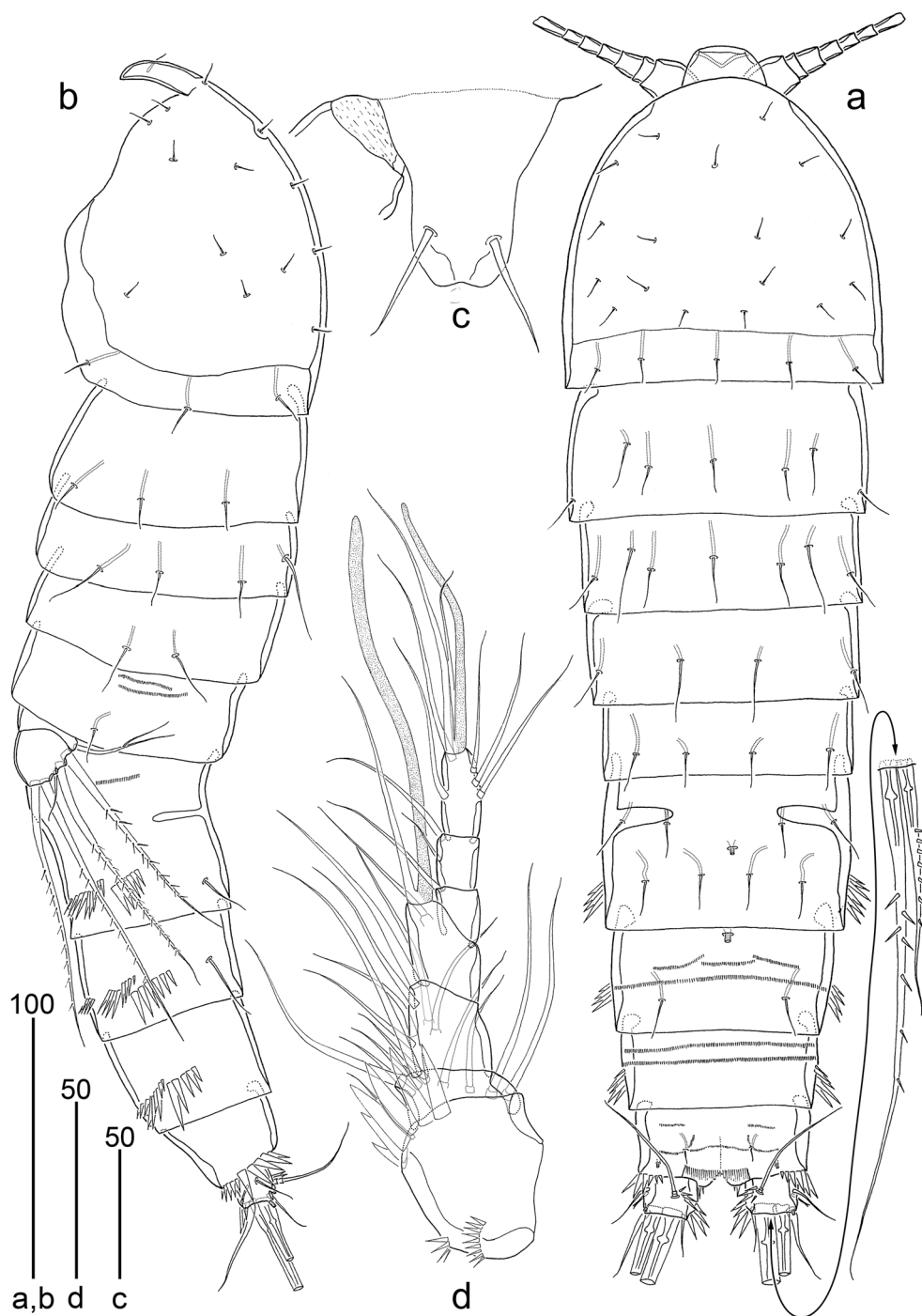
Original description. *Archeolourinia shermani* Corgosinho & Schizas, 2013 Figs. 1–4.

Synonym. *Archeolourinia shermani* Corgosinho & Schizas, 2013.

Material examined. None

Remarks. In their study from mesophotic coral ecosystems in southwestern Puerto Rico, Corgosinho and Schizas (2013) described *Archeolourinia shermani* as a new genus and a new species. As noted by Karaytuğ et al. (2021), the inclusion of the monotypic genus *Archeolourinia* in the Louriniidae is not justified. Therefore *A. shermani* is now removed from Louriniidae and transferred to the genus *Nannomesochra* within the family Canthocamptidae. *N. shermani* comb. nov. can be distinguished from the other species of the genus by the combination of the following characters: i) female P5

Fig. 1 *N. parvula*, female. **a** Habitus, dorsal; **b** Habitus, lateral; **c** Rostrum, dorsal; **d** Antennule, dorsal



exopod bears five setae; ii) baseoendopodal lobe of female P5 not reaching distal margin of exopod; iii) female P2–P4 bears 5,4,4 and 6,7,7 setae on the distal segments of endo- and exopods respectively. Other minor differences compared to those of valid species are summarized in Table 3.

***Nannomesochra gebekumensis* sp. nov.**

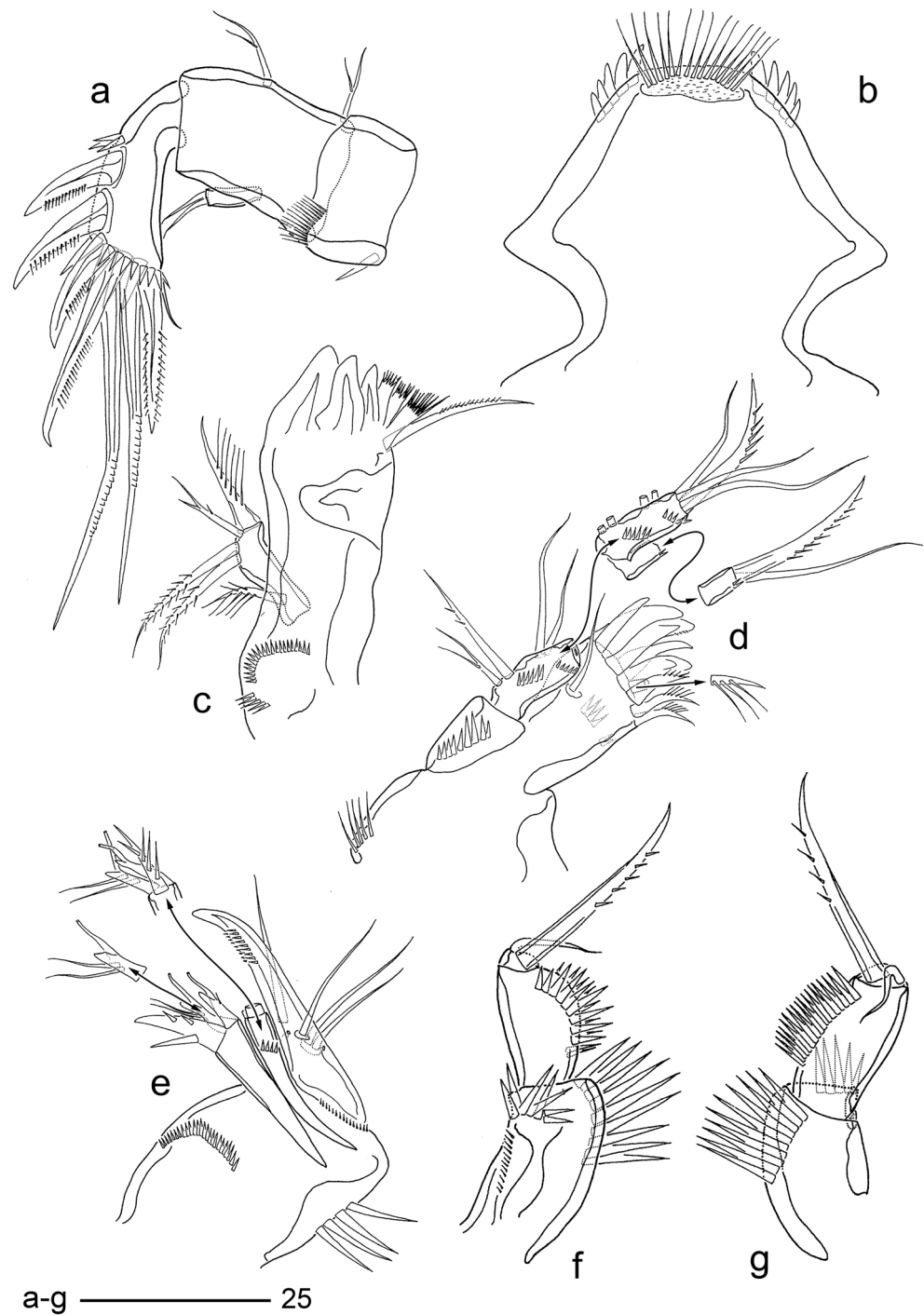
<https://zoobank.org/4630FD02-B646-4A31-A6F9-E2FC4A8BBFAE>

Synonym. *Nannomesochra* sp. sensu Alper et al. (2010).

Type locality. Turkey, Muğla province, from intertidal zone at rocky shore of Gebekum/Datça (36.7639833° N, 27.7450000° E).

Type material. Holotype, ♀, collected from washings of macroalgae *Cystoseira* sp., *Corallina* sp., *Halopteris* sp. and *Laurencia* sp., 16 April 2007; dissected on eight slides (catalogue number: ZMADYU 2007/273). Paratype, ♂, 23 February 2008, dissected on seven slides (catalogue number: ZMADYU 2008/096).

Fig. 2 *N. parvula*, female. **a** Antenna; **b** Labrum; **c** Mandible; **d** Maxilule; **e** Maxilla; **f** Maxilliped, anterior; **g** Maxilliped, posterior



Additional material examined. One ♀ (dissected on six slides) and one ♂ in alcohol, collected from the type locality on 16 April 2007. Three ♀♀, collected from the type locality on 23 February 2008. One ♀ and one ♂ preserved in alcohol; collected from interstitial habitat at Bademlibük beach, İzmir province, Turkey (38.6213333° N, 026.3577778° E), 24 May 2012.

All material collected by S. Sak, A. Alper and S. Sönmez.

Description of the female

Body (Fig. 5a, b) cylindrical, gradually tapering posteriorly; without clear distinction between prosome and urosome; first thoracic somite fused to cephalosome, forming a cephalothorax. Total body length 513 µm. Greatest width measured at posterior margin of cephalothorax: 102 µm. Surface ornamentation of somites as figured (Figs. 5a, b and 9a).

Fig. 3 *N. parvula*, female. Swimming legs. **a** P1; **b** P2; **c** P3; **d** P4



Rostrum (Fig. 6a) bell shaped, defined at base; bears two sensilla.

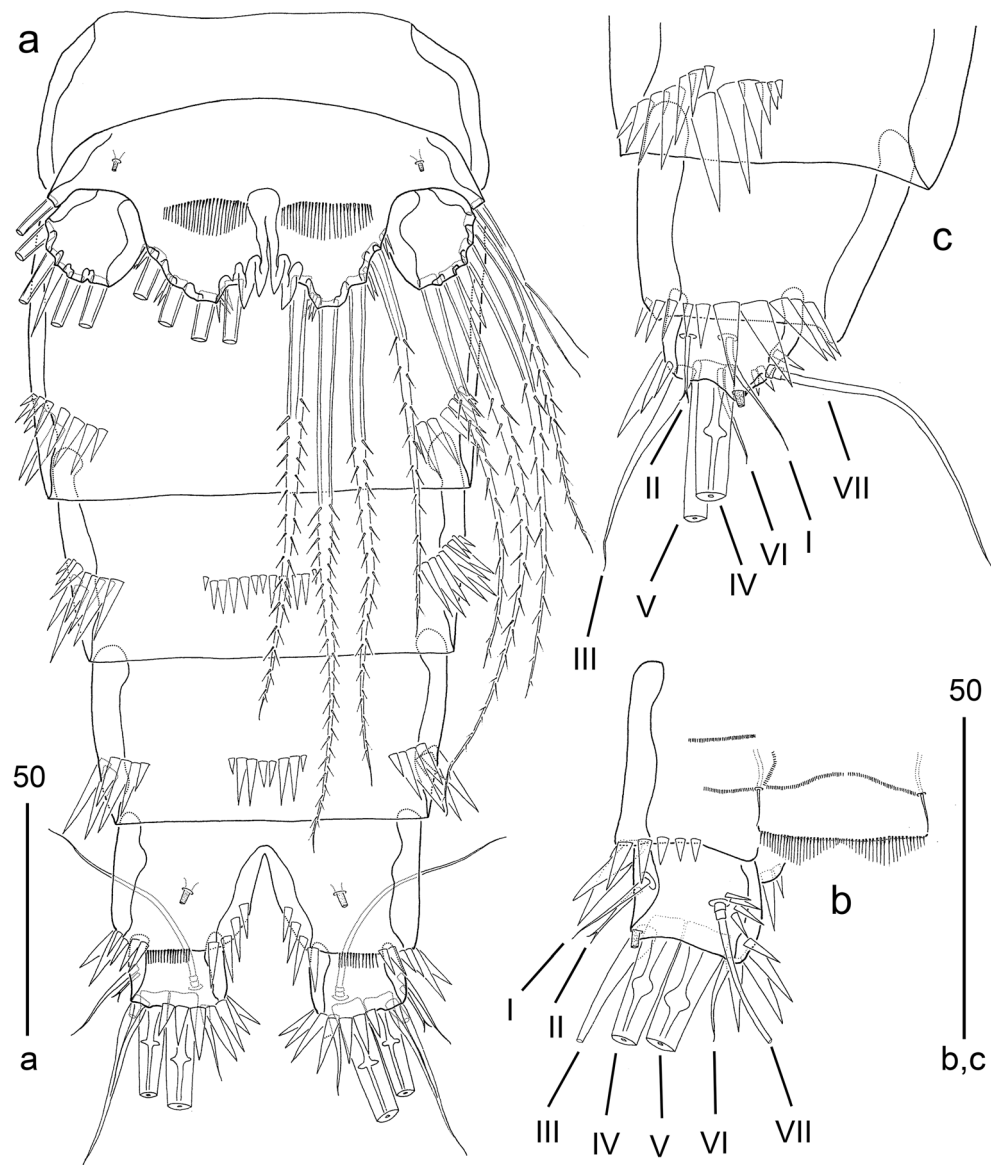
Antennule (Fig. 6b) 7-segmented. Segment-1 ornamented with rows of spinules near posterior margin and a row of robust spinules at distal margin; with a seta at distal corner. Segment-2 with nine setae. Segment-3 rectangular, with six setae. Segment-4 bears one seta and an aesthetasc fused basally to a seta. Segments-5 and -6 are similar in length, with one and two setae respectively. Segment-7 bears five setae and with an apical acrothek consisting of an aesthetasc and

two setae. Armature formula: 1[1]-2[9]-3[6]-4[1+(1+ae)]-5[1]-6[2]-7[5+acrothek].

Antenna (Fig. 6c, d). Allobasis with two abexopodal setae. Exopod 1-segmented, rectangular; armed with two apical setae. Endopod with two lateral robust pinnate spines; distal margin ornamented with spinules as figured, apical armature consists of two pinnate spines, two geniculate setae, and one pinnate spine fused basally to a seta.

Labrum (Fig. 7a) large. Anterior surface with long spinules subdistally, posterior surface with a row of small

Fig. 4 *N. parvula*, female. **a** Urosome and P5, ventral; **b** Left caudal ramus, dorsal; **c** Left caudal ramus, lateral



spinules subdistally and with large row of spinules bilaterally.

Mandible (Fig. 7b, c) with well-developed gnathobase that bears a pinnate seta at dorsal corner; cutting edge with series of teeth. Palp 1-segmented, exopod and endopod incorporated into basis, armature consisting of three pinnate setae laterally and two elements (one pinnate spine and one seta) apically.

Maxillule (Fig. 7d). Praecoxa with spinules laterally. Praecoxal arthrite well-developed; with a row of small spinules on posterior surface, with one seta on anterior surface, with nine elements around distal margin. Coxa ornamented with spinular row as figured. Coxal endite bears one spine and one seta. Endopod and exopod incorporated into basis, armature consisting of four setae laterally and, one spine and three setae apically.

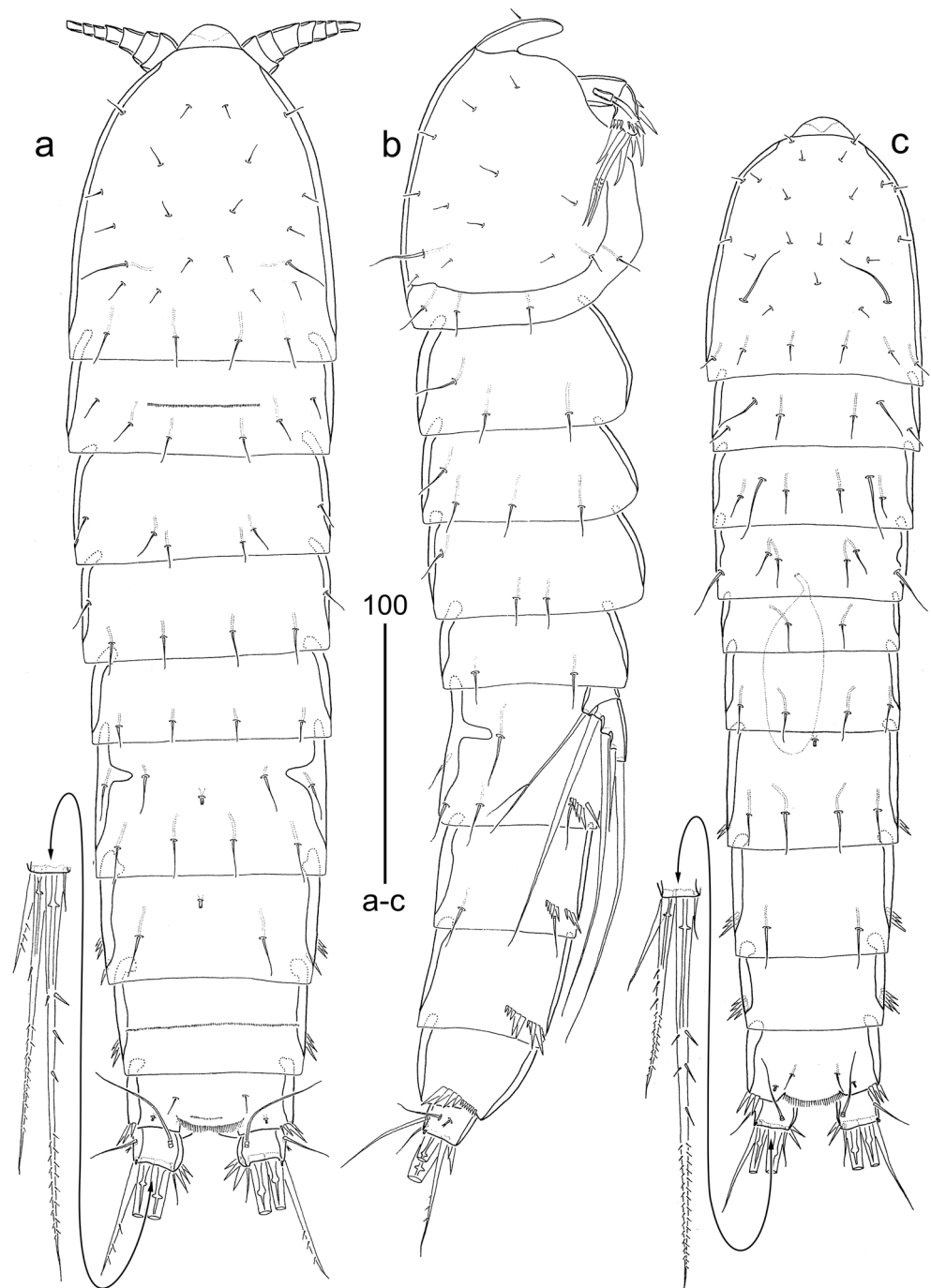
Maxilla (Fig. 7e). Syncoxa with two endites; each bears three spines apically, two of which with tubular extensions

as figured. Allobasis forming spinous claw, slightly curved distally; accessory armature represented by two setae. Endopod reduced, represented by two setae.

Maxilliped (Fig. 7f, g) subchelate. Syncoxa and basis ornamented with spinular rows as figured. Endopod 1-segmented; armed with long claw, slightly curved apically and, with one small accessory seta.

P1–P4 (Fig. 8a, b, c, and d). Praecoxae well developed, ornamented with spinules along distal margin. Intercoxal sclerites rectangular (P1) or squarish (P2–P4). Coxae rectangular; ornamented with row of spinules as figured (P1, P2) or unornamented (P3, P4). Bases ornamented with large spinules along distal margin; with a tube-pore as figured; with one inner seta and one outer seta (P1) or with one outer seta (P2–P4). P1–P4 with 3-segmented exopods; outer margin of exopodal segments ornamented with strong spinules. Exp-1 and exp-2 naked (P1–P4). Exp-3 with two geniculate

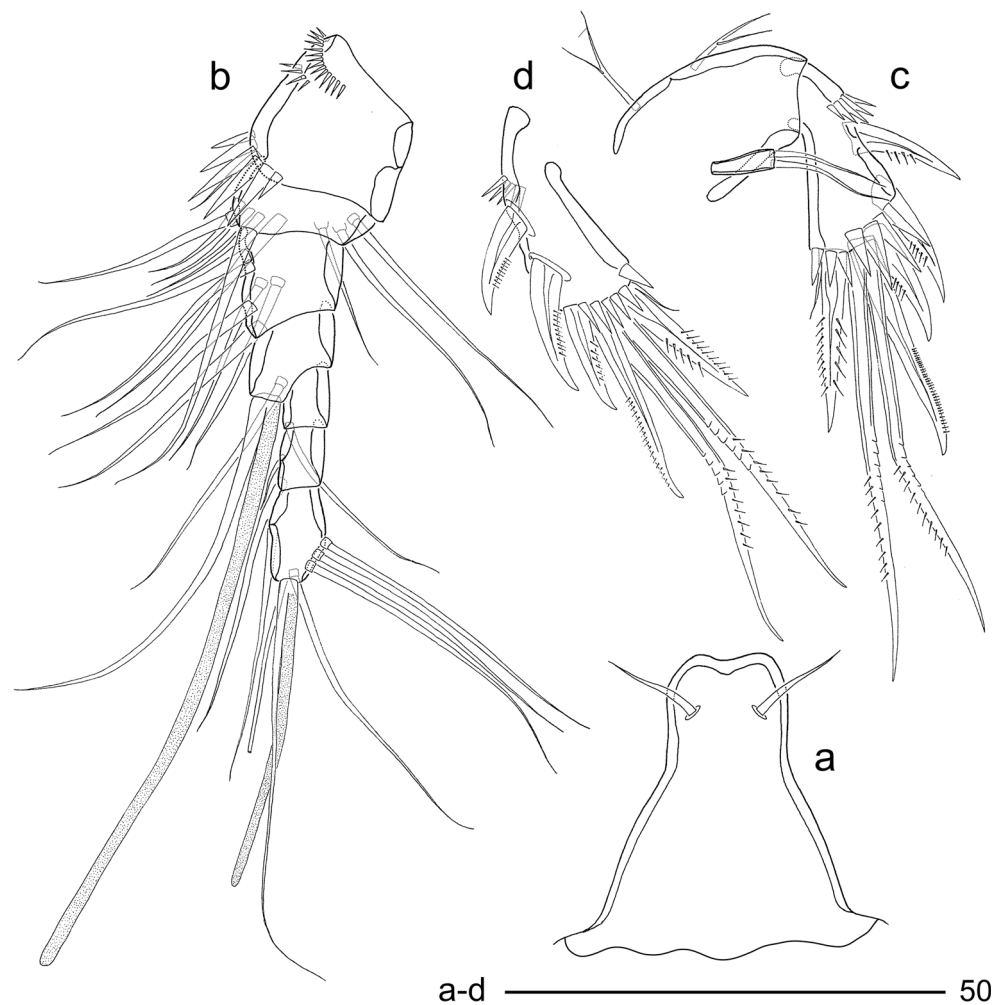
Fig. 5 *N. gebekumensis* sp. nov., habitus. Female. **a** Dorsal; **b** Lateral. Male. **c** Dorsal



setae apically and two outer spines (P1) or with 2 apical elements (inner a minute seta, outer a pinnate spine) and 3 outer spines (P2) or with one inner seta serrated apically, two apical elements (inner a minute seta, outer a pinnate spine) and three outer spines (P3) or with one inner long seta serrated apically, two apical setae (inner one minute, outer one long) and three outer spines (P4). Endopod 3-segmented (P1) or 2-segmented (P2–P4); outer margin of endopodal segments ornamented with spinules. Enp-1 with one inner seta, serrated apically (P1–P4). Enp-2 without

inner seta (P1) or with one inner setae serrated apically, two apical setae (inner one short, outer one long) and one outer pinnate spine (P2) or with two inner setae serrated apically (proximal one long, distal one short), two distal setae serrated apically (inner one minute; outer one long) and one outer pinnate spine (P3) or with one inner seta, serrated apically, two distal setae (inner one minute; outer one long and serrated apically) and one outer pinnate spine (P4). Enp-3 with one inner minute seta serrated apically and two apical, long, geniculate setae (P1).

Fig. 6 *N. gebekumensis* sp. nov., female. **a** Rostrum, dorsal; **b** Antennule, dorsal; **c** Antenna; **d** Endopod of antenna



Setal formula of swimming legs:

	Exopod	Endopod
P1	0.0.022	1.0.120
P2	0.0.023	1.121
P3	0.0.123	1.221
P4	0.0.123	1.121

P5 (Fig. 9a) fused medially, forming a bilobate plate with medial incision, bearing a pore and a spinule row on anterior surface. Endopodal lobe not reaching distal margin of the exopod, armed with four pinnate setae. Exopods ovoid, armed with five setae (seta-III shortest, naked).

P6 and genital field (Fig. 7h). P6 represented by a small plate armed with two setae. Copulatory pore located medially, flanked by two secretory tube-pores.

Caudal rami (Fig. 9a, b and c) slightly wider than long; with a tube-pore at outer distal corner dorsally; with seven setae. Seta I naked; seta II delicate, bifid. Seta III inserted at outer distal corner. Seta IV and V inserted terminally; with a fracture plane. Seta VI naked. Seta VII located dorsally, tri-articulated at base.

Description of the male

Body (Fig. 5c) smaller than female. Total body length: 436 μm . Greatest width measured at posterior margin of cephalothorax: 83 μm . Surface ornamentation of somites as figured (Figs. 5c and 10c).

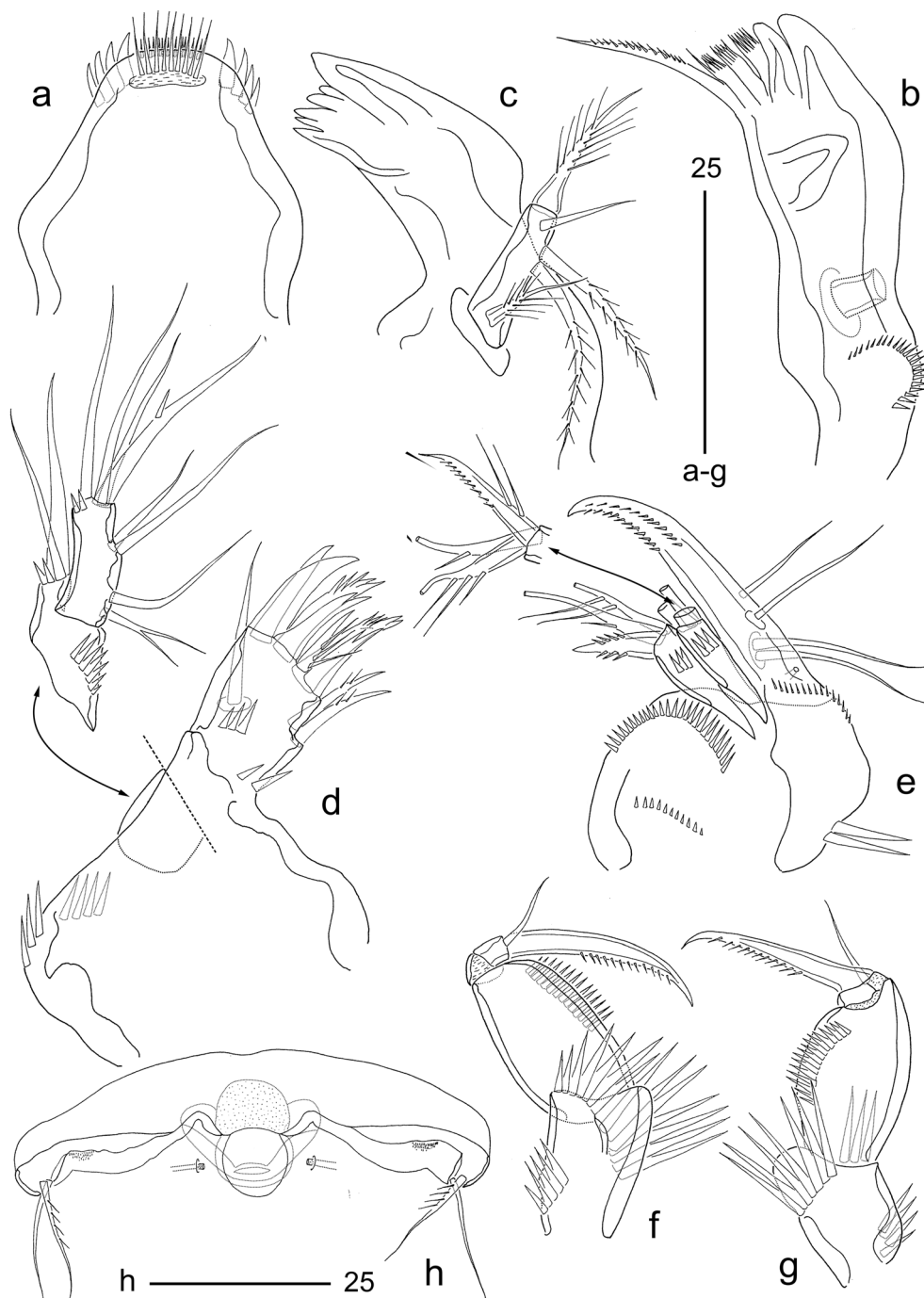
Sexual dimorphism in body size, sensillar and spinular ornamentation of somites, antennule, Enp-P3, P5, P6.

Antennule (Fig. 10a) haplocer, 9-segmented. Segment-5 with an aesthetasc, fused basally to a seta. Segment-9 with an apical acrothek, consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[9]-3[1]-4[2]-5[4+(1+ae)]-6[1]-7[0]-8[2]-9[4+acrothek].

P3 endopod (Fig. 10b); segment-1 rectangular, longer than female; ornamented with spinules along outer margin, with one inner seta which is shorter than the female. Segment-2 outer margin naked, with two setae apically and with one inner robust, modified spine as figured.

P5 (Fig. 10c) fused medially, forming a bilobate plate with deep medial notch. Endopodal lobe not reaching distal margin of the exopod, armed with two setae. Exopods ovoid. Right exopod with five setae; seta-IV shortest. Left exopod with six elements; the innermost is extra and modified as figured.

Fig. 7 *N. gebekumensis* sp. nov., female. **a** Labrum; **b** Mandible, anterior; **c** Mandible, posterior; **d** Maxillule; **e** Maxilla; **f** Maxilliped, anterior; **g** Maxilliped, posterior; **h** P6 and genital area



P6 (Fig. 10c) fused, forming a bilobate, single plate; armed with 1 pinnate seta.

Variation. In the other male paratype collected from the type locality, the modified innermost extra seta of exp-P5 was observed in the right leg instead of the left leg.

Etymology. The specific epithet “gebekumensis” refers to the type locality.

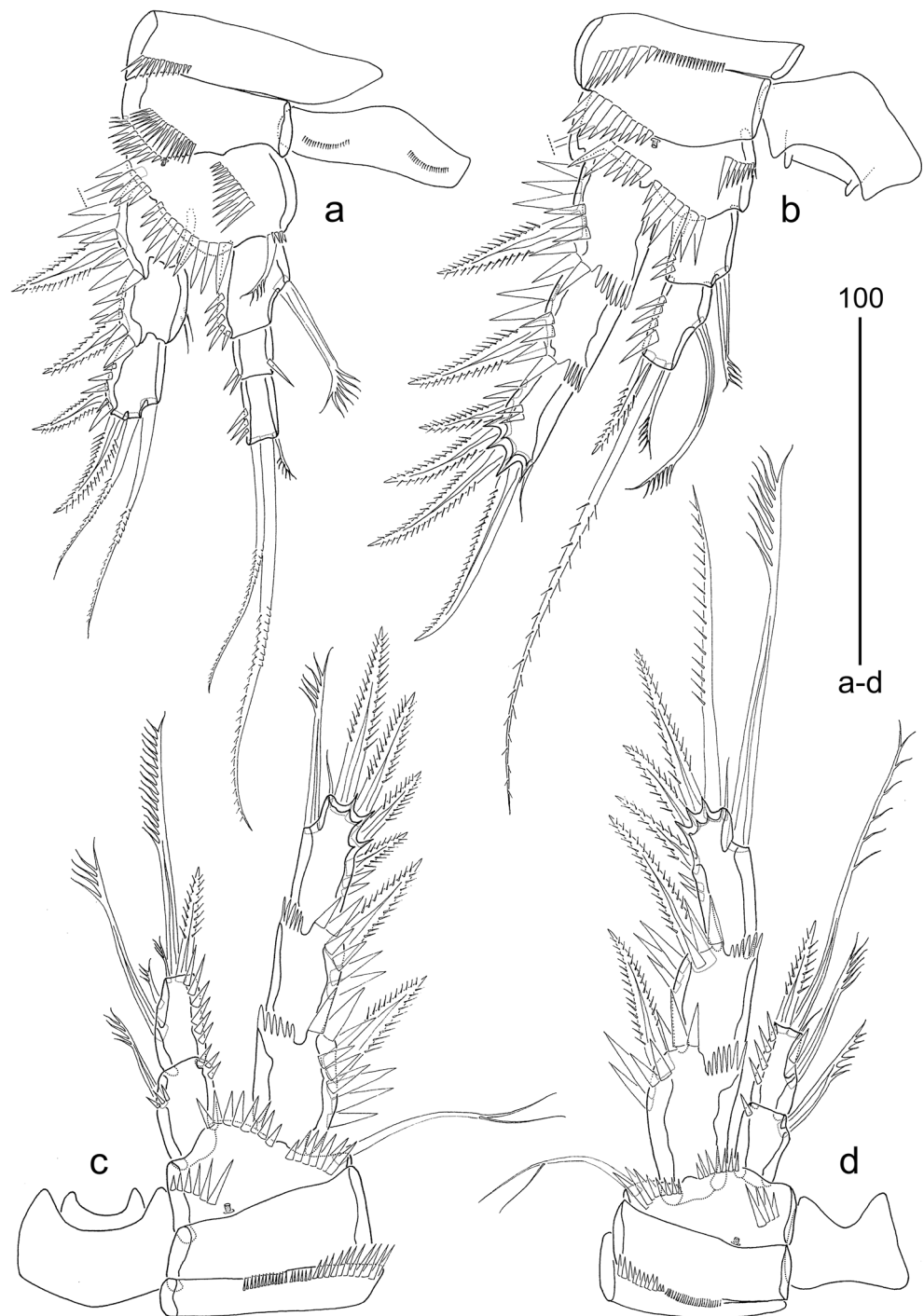
Remarks. The new species morphologically differs from other members of the genus by the combination of the following characters: i) female P5 exopod bears five setae; ii) baseoendopodal lobe of female P5 not reaching

distal margin of exopod; iii) inner margin of P1 enp-2 is naked, which is unique in the genus; iv) female P2–P4 bears 4,5,4 and 5,6,6 setae on the distal segments of endo- and exopods respectively; v) male P3 enp-2, the tip of inner spine modified in form of toggle harpoon. Other minor differences compared to those of valid species are summarized in Table 3.

***Nannomesochra giziri* sp. nov.**

<https://zoobank.org/195A4F4F-DD9C-4B1C-AD0F-7516044F6D5A>

Fig. 8 *N. gebekumensis* sp. nov., female. Swimming legs. **a** P1; **b** P2; **c** P3; **d** P4



Type locality. Turkey, Antalya province, from interstitial habitat at Phaselis Beach (36.5270667° N, 30.5514500° E).

Type material. Holotype, ♀, collected on 13 April 2007, dissected on four slides (catalogue number: ZMADYU 2007/274). Paratype, ♂, dissected on four slides (catalogue number: ZMADYU 2012/197); collected from interstitial habitat at Gündoğan Beach, Muğla province, Turkey (37.1306944° N, 27.3450278° E), 20 May 2012.

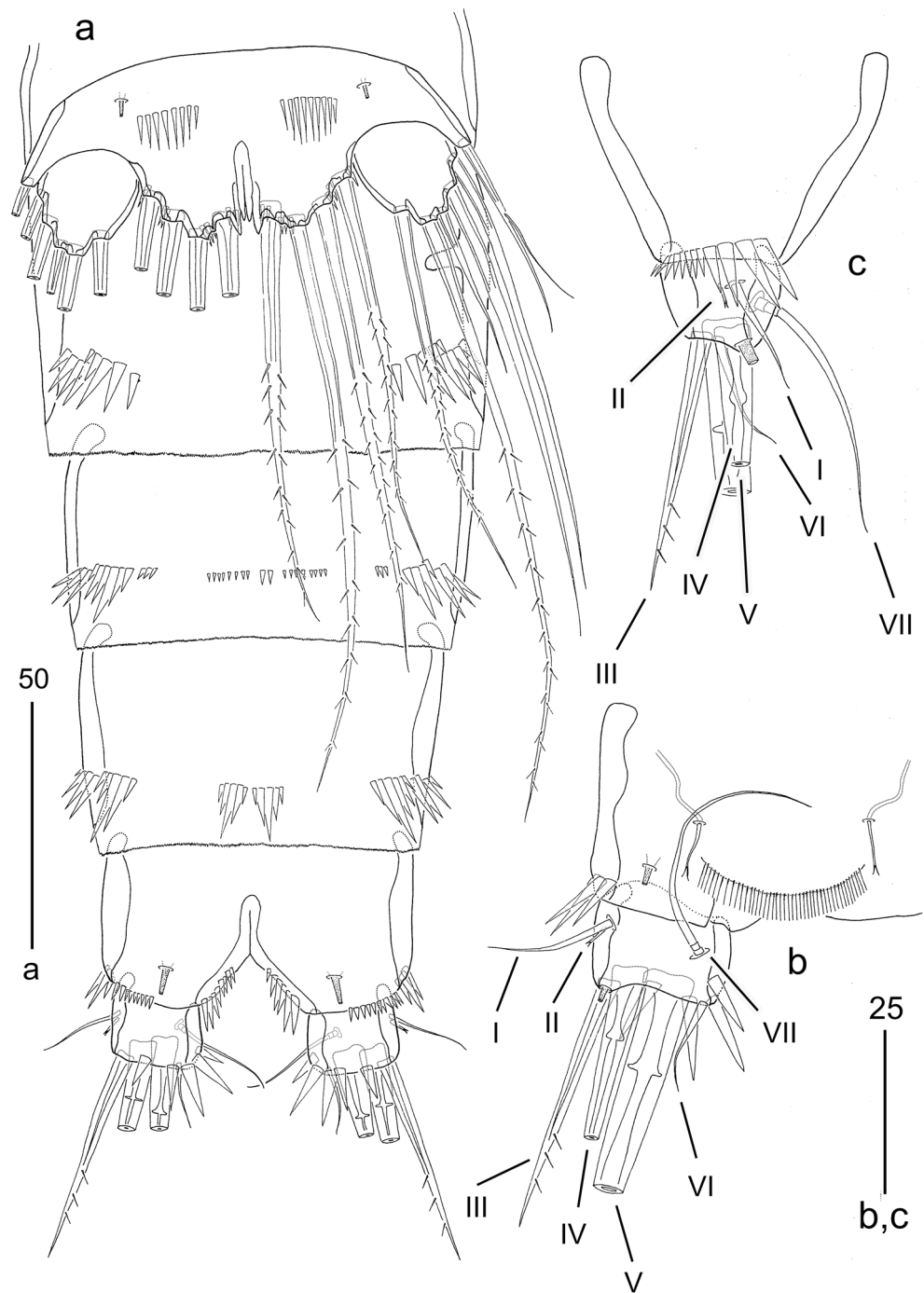
All material collected by S. Sak, A. Alper and S. Sönmez.

Description of the female

Body (Fig. 11a, b) cylindrical, gradually tapering posteriorly; without clear distinction between prosome and urosome; first thoracic somite fused to cephalosome, forming a cephalothorax. Total body length: 440 µm. Greatest width measured at posterior margin of cephalothorax: 124 µm. Surface ornamentation of somites as figured (Figs. 11a, b and 13c).

Rostrum (not illustrated) bell shaped, defined at base; bears two sensilla.

Fig. 9 *N. gebekumensis* sp. nov., female. **a** Urosome and P5, ventral; **b** Left caudal ramus, dorsal; **c** Left caudal ramus, lateral

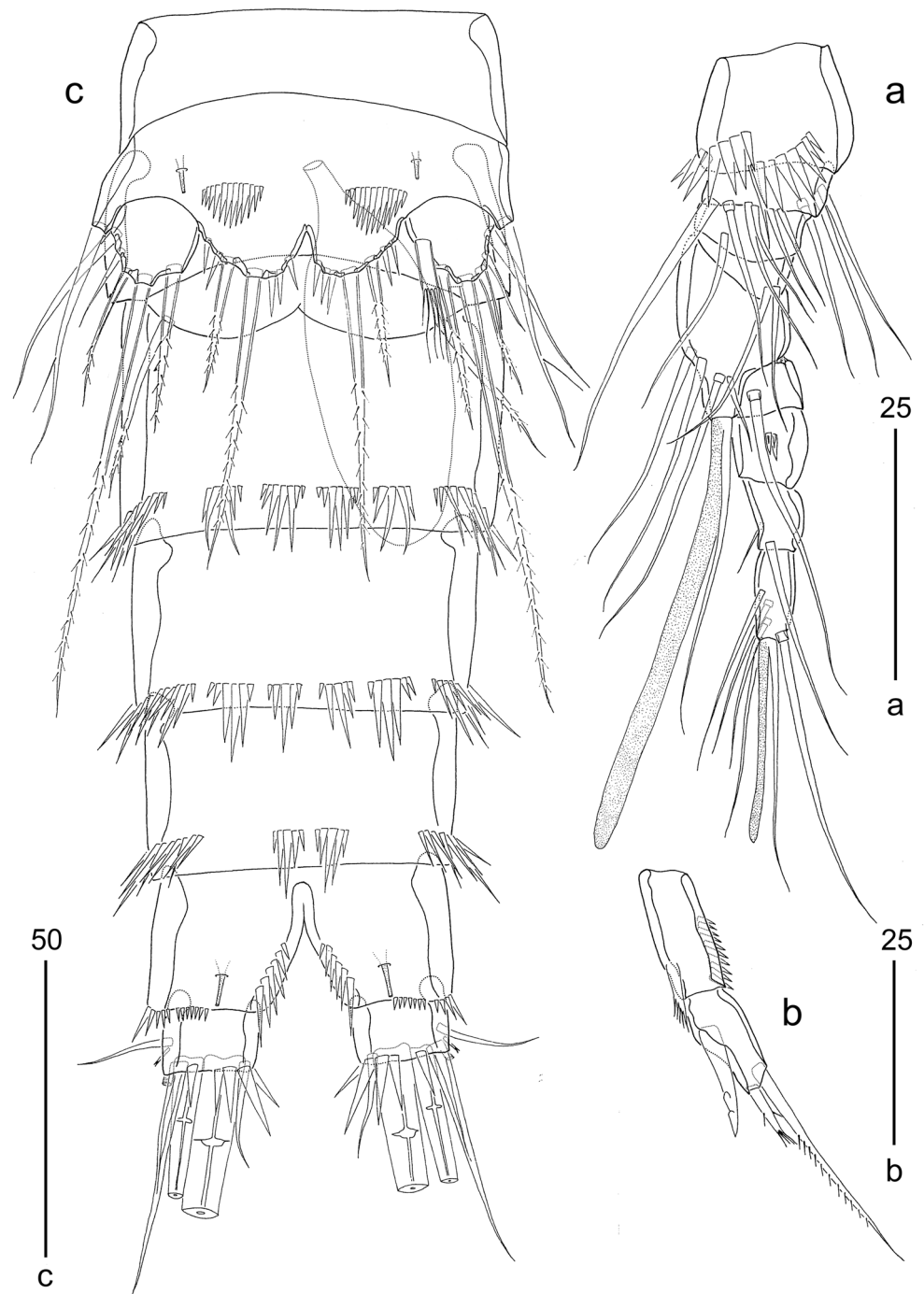


Antennule (Fig. 13a) 7-segmented. Segment-1 ornamented with rows of spinules near posterior margin and a row of robust spinules at distal margin; with a seta at distal corner. Segment-2 with eight setae. Segment-3 rectangular, with four setae. Segment-4 bears an aesthetasc fused basally to a seta. Segments -5 and -6 are similar in length, with one and two setae respectively. Segment-7 bears five setae and with an apical acrothek, consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[8]-3[4]-4[(1+ae)]-5[1]-6[2]-7[5+acrothek].

Antenna, labrum, mandible, maxillule, maxilla and maxilliped (not illustrated) similar to that of *N. parvula*.

P1–P4 (Fig. 12a, b, c and d). Praecoxae well developed, ornamented with spinules along distal margin. Intercoxal sclerites wider than long. Coxae rectangular; ornamented with row of spinules as figured (P1, P2) or unornamented (P3, P4). Bases ornamented with large spinules along distal margin; with a tube-pore as figured; with one inner seta and one outer seta (P1) or with one outer seta (P2–P4). P1–P4 with 3-

Fig. 10 *N. gebekumensis* sp. nov., male. **a** Antennule, ventral; **b** P3 endopod; **c** Urosome, P5 and P6, ventral



segmented exopods; outer margin of exopodal segments ornamented with strong spinules. Exp-1 with naked inner margin (P1–P4). Exp-2 without (P1) or with one inner seta (P2–P4). Exp-3 with two geniculate setae and two outer spines (P1) or with one inner seta, two long apical setae and three outer spines (P2) or with two inner setae, medial one long and plumose, the sub-distal one short and serrated apically; two apical long setae and three outer spines (P3–P4). Endopod 3-segmented (P1) or 2-segmented (P2–P4); outer margin of

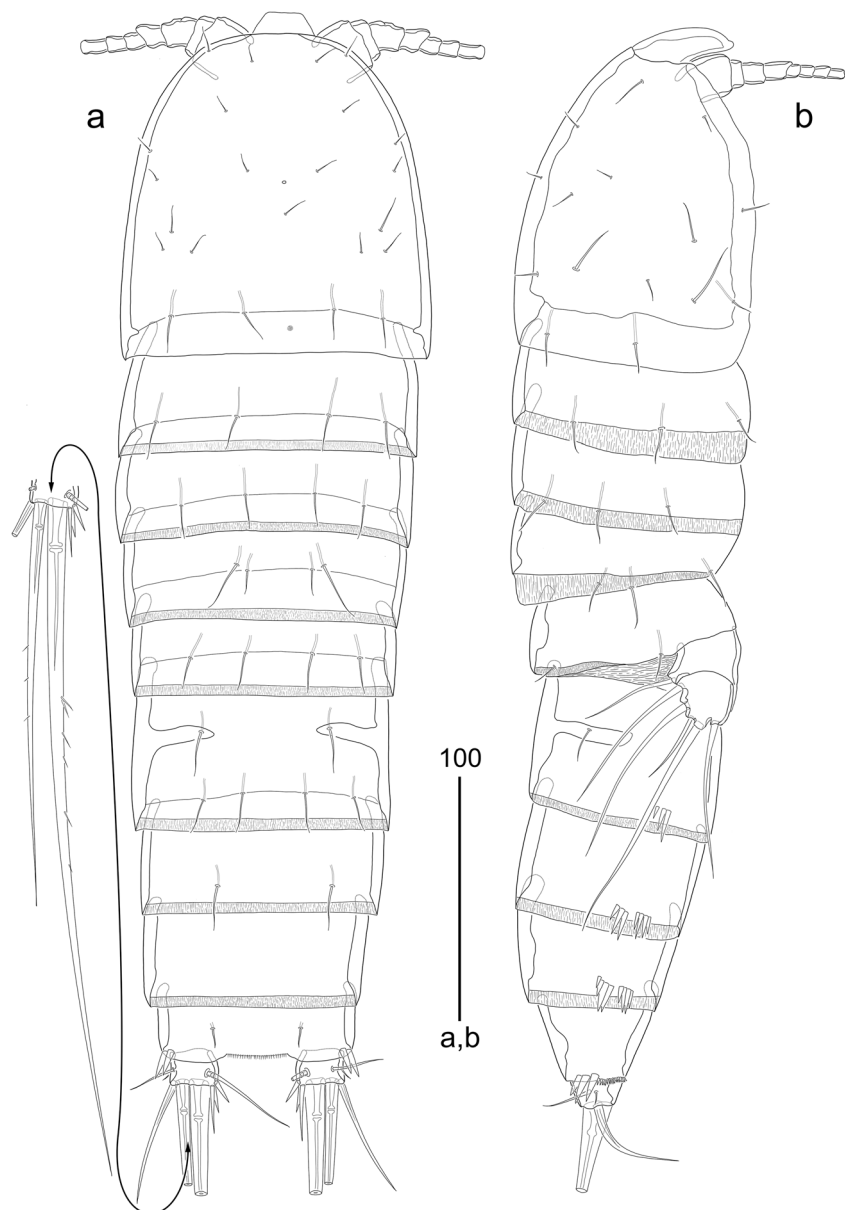
endopodal segments ornamented with spinules. Enp-1 with one inner seta, serrated apically (P1–P4). Enp-2 with one inner seta (P1) or with two inner setae serrated apically, two apical setae (inner one minute, outer one long and plumose) and one outer pinnate spine (P2) or with two inner setae (medial one short and serrated apically, sub-distal one long and plumose), two apical setae (inner one short, outer one long and plumose) and one outer pinnate spine (P3–P4). Enp-3 with one inner naked seta and two apical long, pinnate setae (P1).

Setal formula of swimming legs:

	Exopod	Endopod
P1	0.0.022	1.1.120
P2	0.1.123	1.221
P3	0.1.223	1.221
P4	0.1.223	1.221

P5 (Fig. 13b) fused medially, forming a bilobate plate with medial incision; bearing a pore and a spinule row on anterior surface. Endopodal lobes extends beyond distal margin of the exopod; armed with four pinnate setae. Exopods squarish, with notch between seta I and II; armed with five setae (seta-III shortest, naked).

Fig. 11 *N. giziri* sp. nov., female. Habitus. **a** Dorsal; **b** Lateral



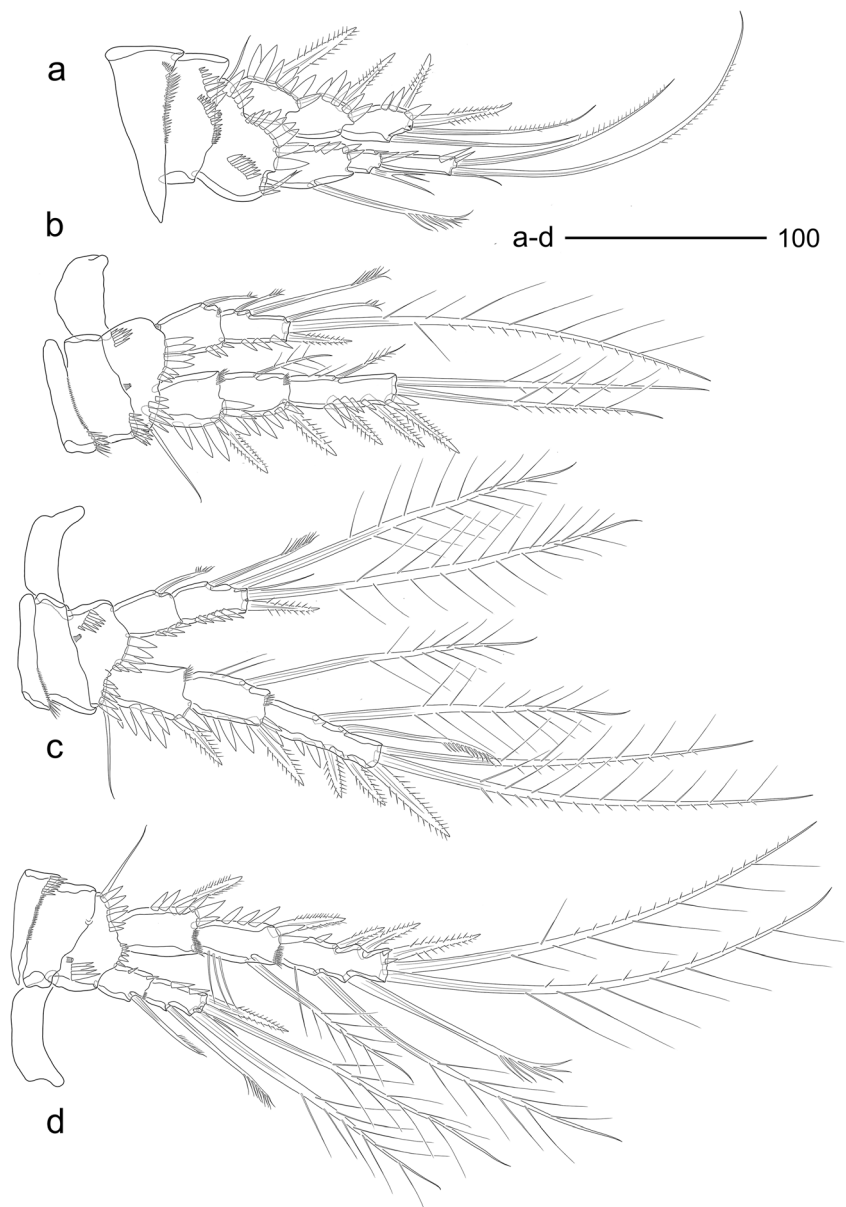
P6 (Fig. 13c) represented by a small plate, armed with two setae.

Caudal rami (Figs. 11a,b, 13c) slightly wider than long; with a tube-pore at outer distal corner dorsally; with seven setae. Seta I naked; seta II delicate, bifid. Seta III inserted at outer distal corner. Seta IV and V inserted terminally; with a fracture plane. Seta VI naked. Seta VII located dorsally, tri-articulated at base.

Description of the male

Body (Fig. 14a, b) smaller than female. Total body length: 418 μm . Greatest width measured at posterior margin of cephalothorax: 106 μm . Surface ornamentation of somites as figured (Figs. 14a, b and 16a, c and d). Sexual dimorphism in body size, sensillar and spinular ornamentation of somites, antennule, P3, P5 and P6.

Fig. 12 *N. giziri* sp. nov., female. Swimming legs. **a** P1; **b** P2; **c** P3; **d** P4



Antennule (Fig. 15a, b and c) haplocer, 9-segmented. Segment-1 ornamented with spinules as figured. Segment-5 with an aesthetasc fused basally to a seta. Segment-9 with an apical acrothek, consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[9]-3[1]-4[2]-5[4+(1+ae)]-6[1]-7[0]-8[2]-9[4+acrothek].

P3 (Fig. 15d) endopod 2-segmented; enp-1 rectangular, longer than in female; ornamented with spinules along outer margin, with one inner seta. Enp-2 without spinular ornamentation along outer margin; armed with one inner spine, tip in form of crochet-hook, and with two setae apically (inner one short, naked; outer one long and plumose, fused basally to segment). Inner sub-distal seta of exp-3 naked.

P5 (Fig. 16a, b) fused medially, forming a bilobate plate, bearing two pores and a spinule row on anterior surface; lobes

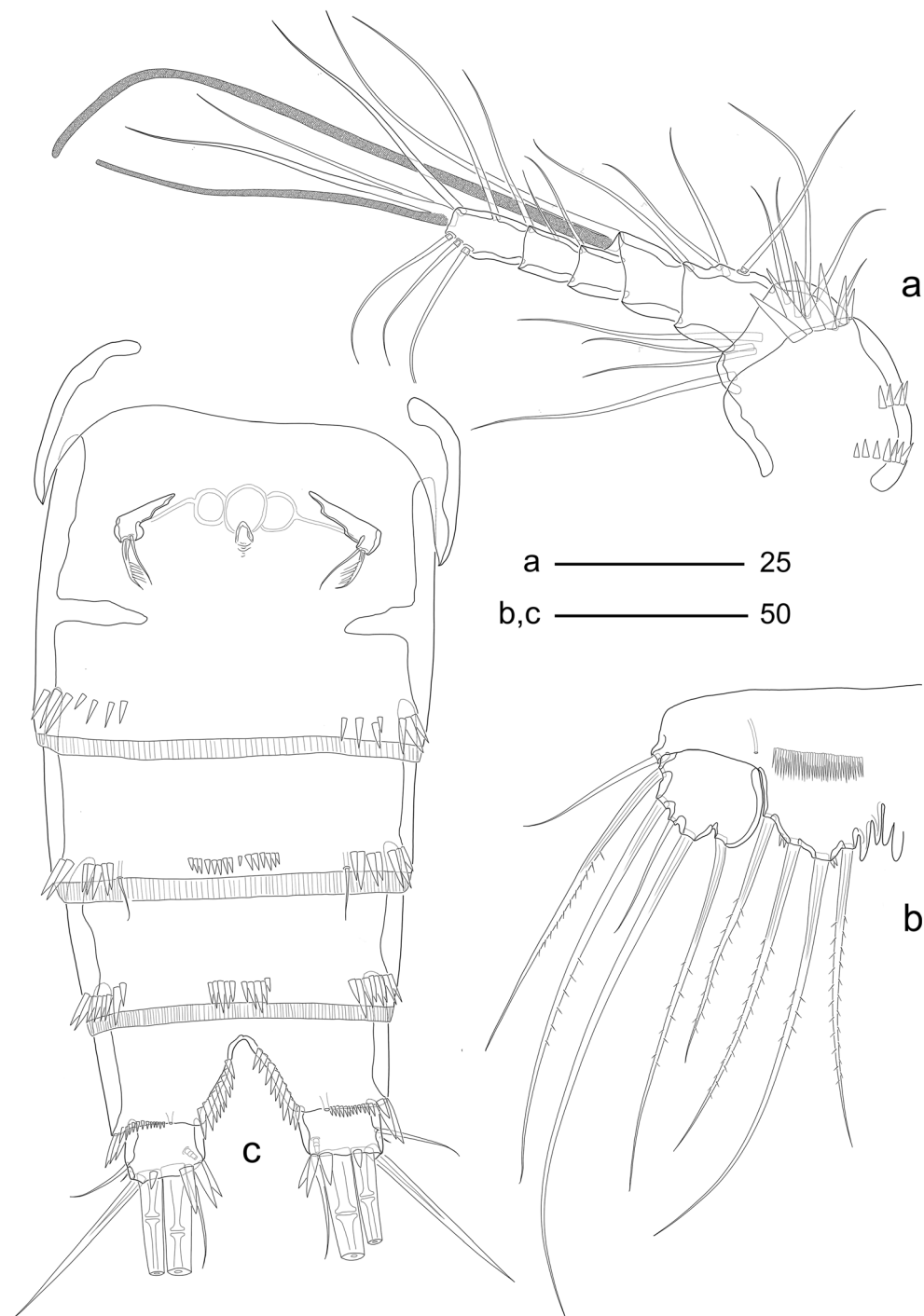
are not as prominent as in *N. gebekumensis* sp. nov. Endopodal lobe not extending beyond distal margin of the exopod, armed with two pinnate setae. Exopods squarish, with six setae (seta V shortest).

P6 (Fig. 16a) fused with somite, armed with 1 naked seta.

Etymology. The new species is named in honour of Prof. Dr. Murat Gizir (Mersin University).

Remarks. The new species can be distinguished from the other species of the genus except *N. parvula* by the combination of the following characters: i) female P5 exopod bears five setae; ii) female P2–P4 bears 5,5,5 and 6,7,7 setae on the distal segments of endo- and exopods respectively; iii) male P3 enp-2, the tip of inner spine modified in form of crochet-hook. *N. giziri* sp. nov. morphologically differs from *N. parvula* by the combination of the following characters: i)

Fig. 13 *N. giziri* sp. nov., female.
a Antennule, dorsal; **b** P5; **c**
 Urosome and P6, ventral



female A1, segment -2 and -3 with eight and four setae respectively; ii) the inner seta of P1 enp-1 extends well beyond end of the endopod; iii) P1 enp-1 extends to approximately end of the exp-2; iv) female P5 exopod with a notch between seta I and II; v) caudal rami without a spinular row near base of the seta VII. Other minor differences compared to those of valid species are summarized in Table 3.

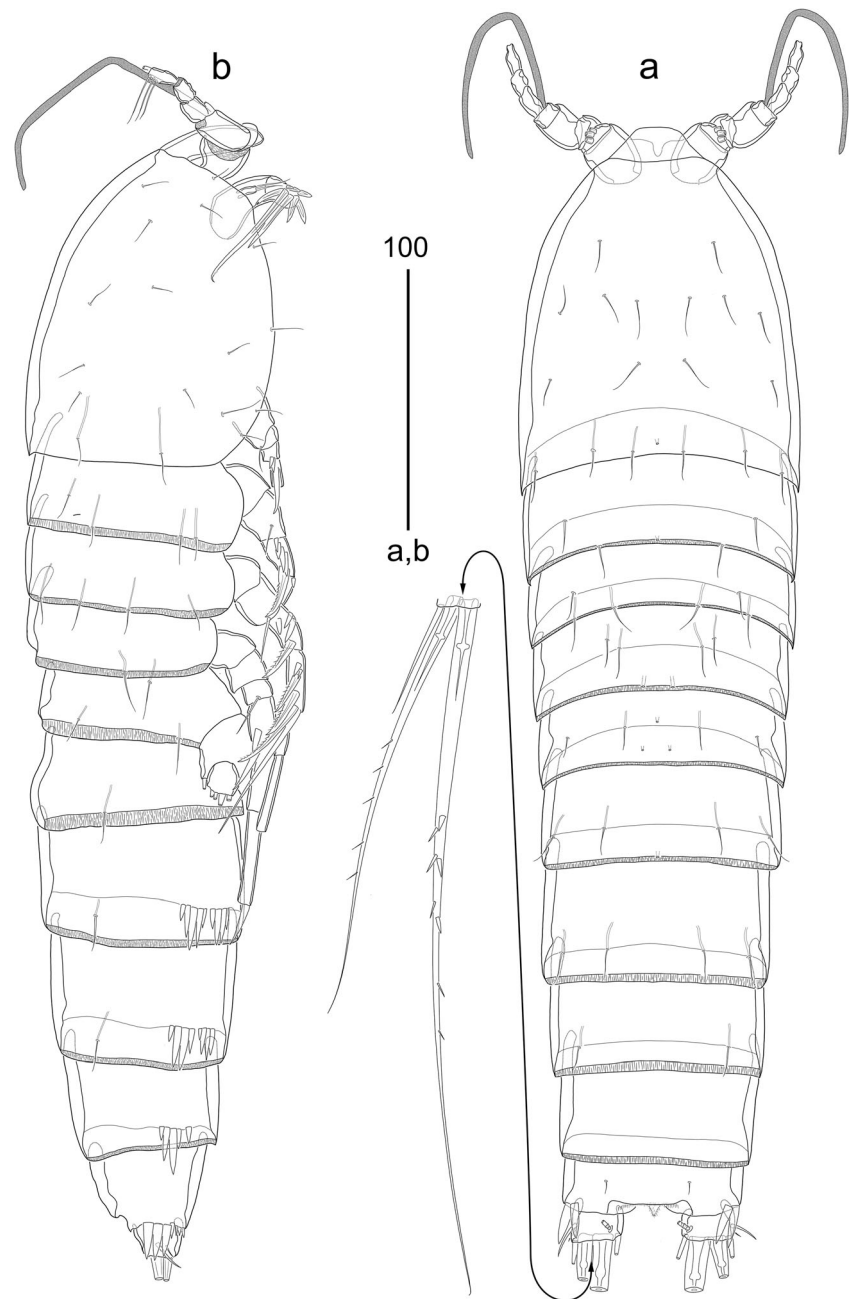
***Nannomesochra erythraiensis* sp. nov.**

<https://zoobank.org/3C3CACEC-0CEC-4C12-8E62-2C53FCC90858>

Type locality. Turkey, İzmir province, from interstitial habitat at Ildır village/Çeşme (38.3472222° N, 26.4505000° E).

Type material. Holotype, ♀, collected on 24 May 2012, dissected on seven slides (catalogue number: ZMADYU

Fig. 14 *N. giziri* sp. nov., male. Habitus. **a** Dorsal; **b** Lateral



2012/198). Paratype, ♂, collected on 24 May 2012, dissected on five slides (catalogue number: ZMADYU 2012/199).

Additional material examined. Three ♀♀ and one ♂, preserved in alcohol, collected from type locality, 24 May 2012. One ♀, preserved in alcohol; collected from Aydın province, Turkey; collected from washings of macroalgae from Pygela Beach (37.9012222° N, 27.2725556° E), 23 May 2012. Two ♀♀, preserved in alcohol; collected from İzmir province, Turkey; collected from washings of macroalgae from Pırlanta Beach (38.2851389° N, 26.2514722° E), 24 May 2012. One ♂, preserved in alcohol; collected from Mersin province,

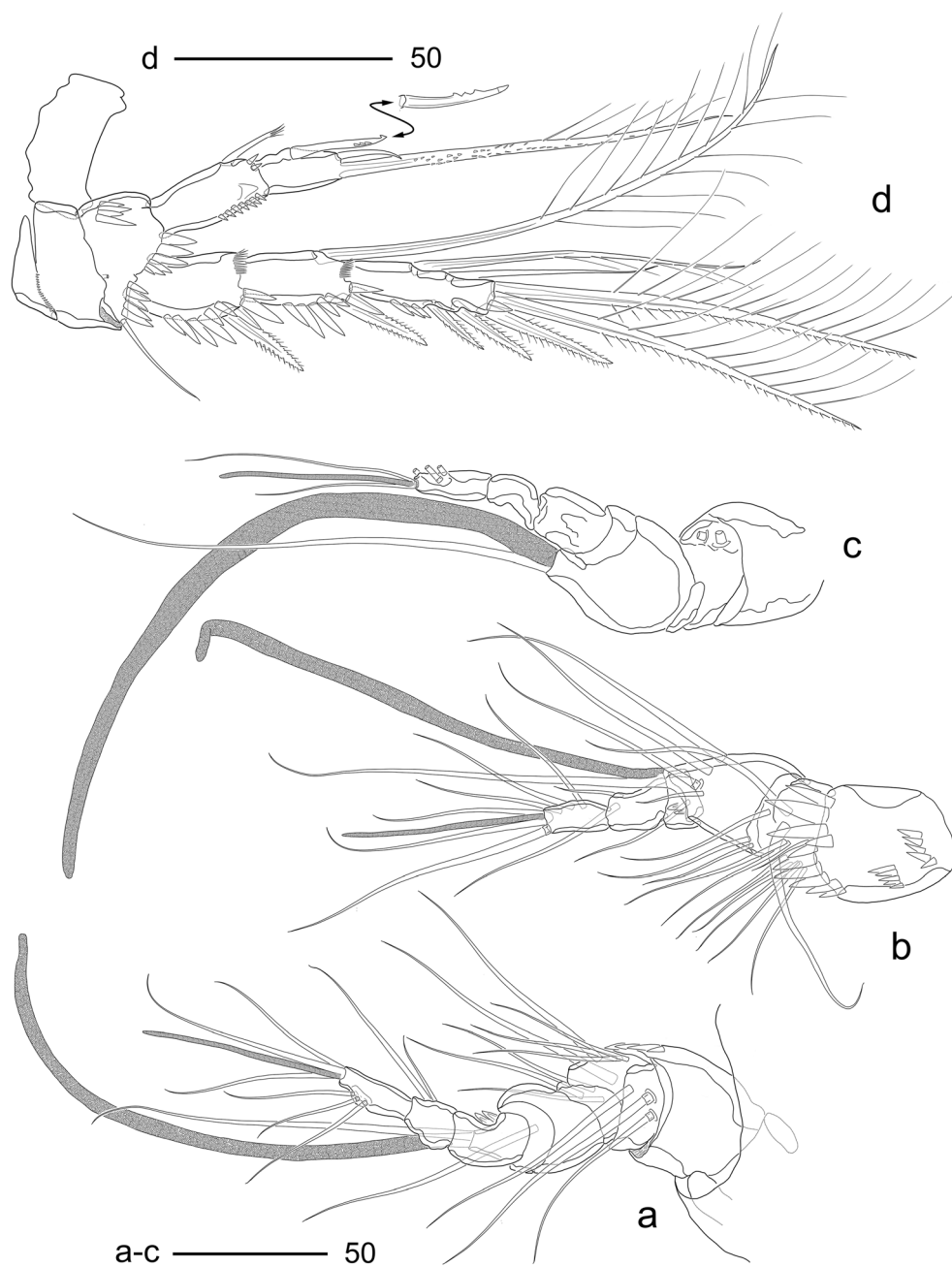
Turkey; from interstitial habitat in front of Eskur-2 Estates (36.1552500° N, 33.4424667° E), 28 August 2007. One ♂, preserved in alcohol; collected from Adana province, Turkey; from interstitial habitat in front of Yonca Estates (36.5825278° N, 35.4061667° E), 09 July 2006.

All material collected by S. Karaytuğ, S. Sak, A. Alper and S. Sönmez.

Description of the female

Body (Figs. 17a, b and 18a, b) cylindrical, gradually tapering posteriorly; without clear distinction between prosome and urosome; first thoracic somite fused to cephalosome,

Fig. 15 *N. giziri* sp. nov., male. Antennule. **a** Dorsal; **b** Ventral; **c** Ventro-lateral. **d** P3



forming a cephalothorax. Total body length: 668 μm . Greatest width measured at posterior margin of cephalothorax: 172 μm . Surface ornamentation of somites as figured (Figs. 17a, b and 19a, b).

Rostrum (Figs. 17c and 18d) bell shaped, defined at base; bears two sensilla.

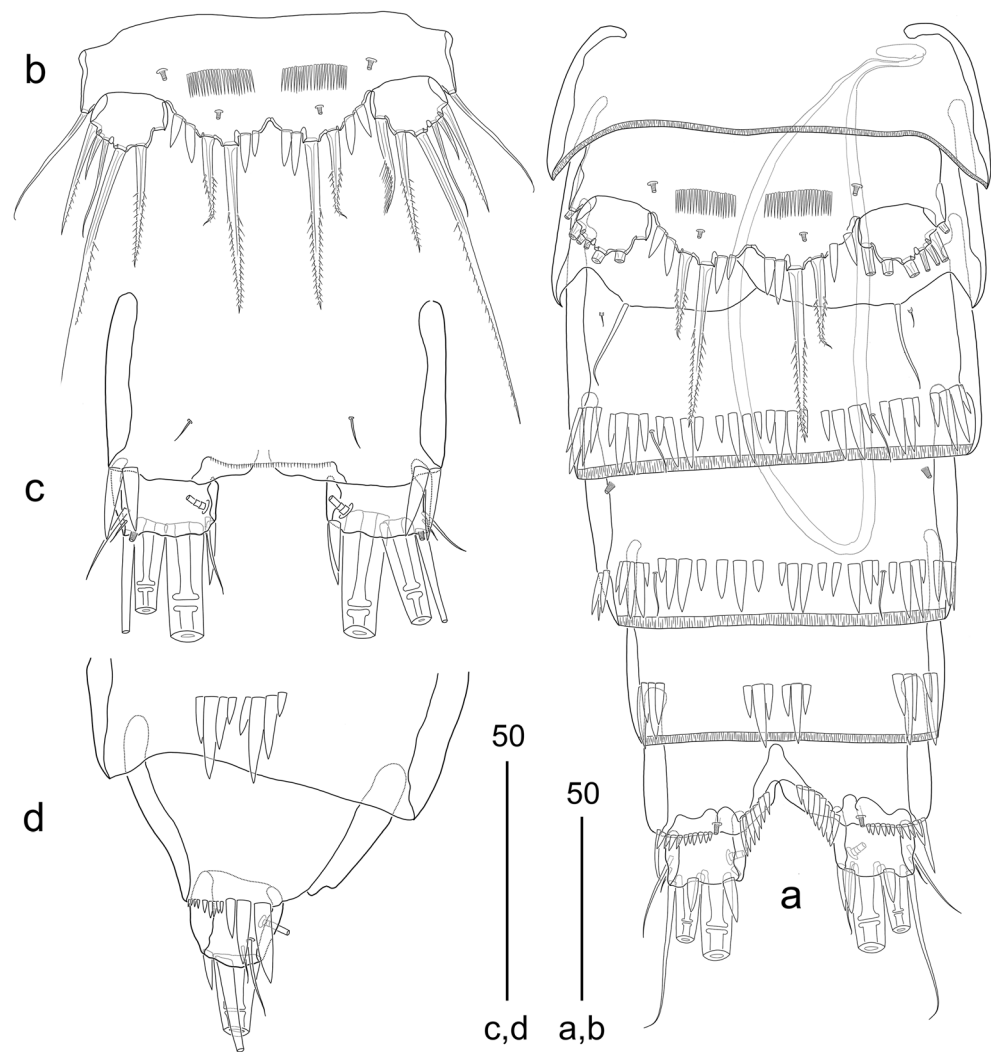
Antennule (Figs. 17c and 18c, d) 7-segmented. Segment-1 ornamented with rows of spinules near posterior margin and a row of robust spinules at distal margin; with a seta at distal corner. Segment-2 with eight setae. Segment-3 rectangular, with four setae. Segment-4 bears one seta and an aesthetasc

fused basally to a seta. Segments-5 and -6 are similar in length, with one and two setae respectively. Segment-7 bears five setae and an apical acrothek consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[8]-3[4]-4[1+(1+ae)]-5[1]-6[2]-7[5+acrothek].

Antenna (Figs. 17d and 18e), labrum, mandible, maxillule, maxilla (not illustrated) and maxilliped (Figs. 17e and 18e), similar to that of *N. parvula*.

P1–P4 (Fig. 20a, b, c and d). Praecoxae well developed, ornamented with spinules along distal margin. Intercoxal sclerites wider than long. Coxae rectangular; ornamented with row

Fig. 16 *N. giziri* sp. nov., male. **a** Urosome, P5 and P6, ventral; **b** P5. Anal somite. **c** Dorsal; **d** Lateral



of spinules as figured (P1, P2) or unornamented (P3, P4). Bases ornamented with large spinules along distal margin; with a tube-pore as figured; with one inner seta and one outer seta (P1) or with one outer seta (P2–P4). P1–P4 with 3-segmented exopods; outer margin of exopodal segments ornamented with strong spinules. Exp-1 and exp-2 without inner seta (P1–P4). Exp-3 with two setae apically and two outer spines (P1) or two apical setae (inner one naked, outer one spinulose) and 3 outer spines (P2) or with one inner seta serrated apically, two apical setae (inner one long, outer one spinulose) and three outer spines (P3, P4). Endopod 3-segmented (P1) or 2-segmented (P2–P4); outer distal margin of first endopodal segments ornamented two with spinules except for P4. Enp-1 with one inner seta, serrated apically (P1–P4). Enp-2 with one inner seta (P1) or with two inner setae serrated apically, two apical setae (inner one short, outer one long) and one outer pinnate spine (P2) or with one inner seta serrated apically, two distal setae (inner one short, outer one long) and one outer pinnate spine (P3, P4). Enp-3 with one inner short seta serrated apically, and two apical long setae (P1).

Setal formula of swimming legs:

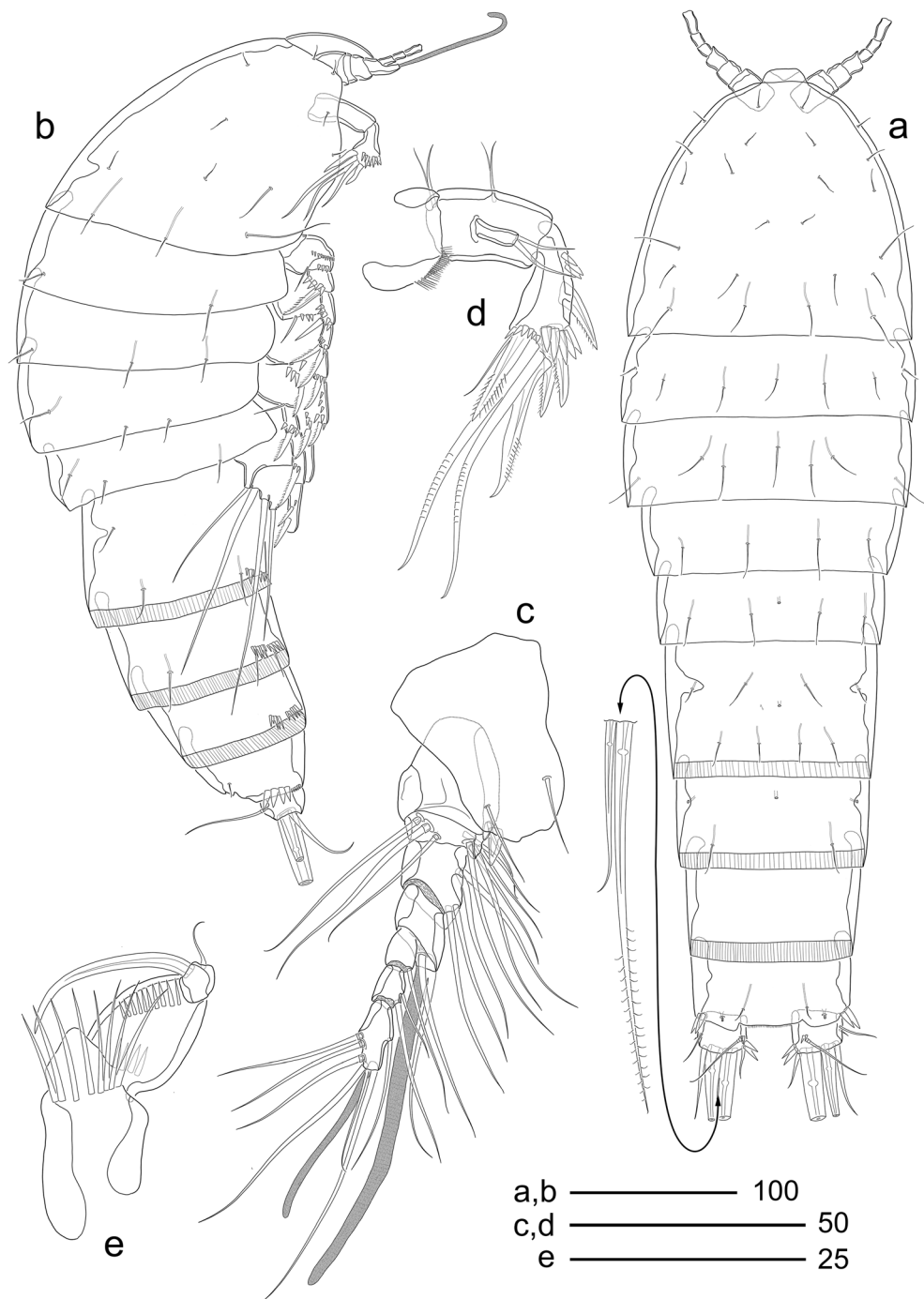
	Exopod	Endopod
P1	0.0.022	1.1.120
P2	0.0.023	1.221
P3	0.0.123	1.121
P4	0.0.123	1.121

P5 (18f and Figs. 19c) fused medially, forming a bilobate plate with pronounced medial incision than in *N. parvula*, *N. gebekumensis* sp. nov. and *N. giziri* sp. nov. Endopodal lobes not reaching distal margin of the exopod, armed with four pinnate setae. Exopods squarish, armed with six setae (seta-IV shortest, naked).

P6 (Fig. 19a, b) represented by small plate fused to genital segment, armed with two setae.

Caudal rami (Figs. 17a, b, 18g and 19a, b) slightly wider than long; with a tube-pore at outer distal corner dorsally; with seven setae. Seta I naked, seta II delicate bifid at tip, seta III naked, inserted at outer distal

Fig. 17 *N. erythraiensis* sp. nov., female. **a** Habitus, dorsal; **b** Habitus, lateral; **c** Rostrum and antennule, dorsal; **d** Antenna; **e** Maxilliped



corner. Seta IV and V inserted terminally; with a fracture plane. Seta VI naked. Seta VII located dorsally, tri-articulated at base. A spinular row is present near base of seta VII.

Description of the male

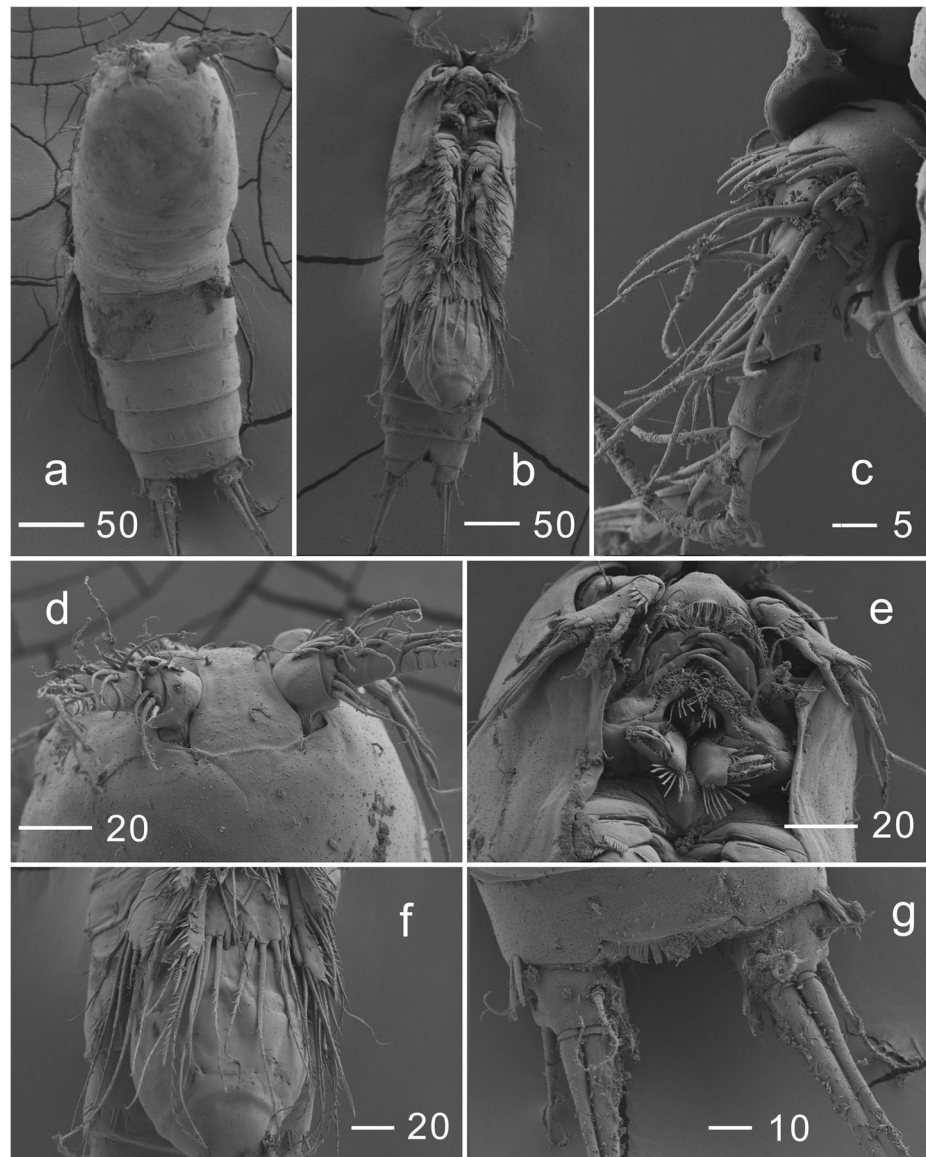
Body (Figs. 21a, b and 22a) smaller than female. Total body length: 524 μm . Greatest width measured at posterior margin of cephalothorax: 109 μm . Surface ornamentation of somites as figured (Figs. 19e, 21a, b, 22c, d). Sexual

dimorphism in body size, sensillar and spinular ornamentation of somites, antennule, P2, P3, P5 and P6.

Antennule (Figs. 21c and 22b) haplocer, 9-segmented. Segment-1 ornamented with spinules as figured. Segment-5 with an aesthetasc fused basally to a seta. Segment-9 with an apical acrothek, consisting of an aesthetasc and two setae. Armature formula: 1[1]-2[9]-3[1]-4[2]-5[4+(1+ae)]-6[1]-7[0]-8[2]-9[5+acrothek].

P2 enp-2 distal margin as figured (Fig. 20e). Inner seta longer than in female.

Fig. 18 *N. erythraiensis* sp. nov., female. **a** Habitus, dorsal; **b** Habitus, ventral; **c** Antennule, ventral. **d** Antennules and rostrum, dorsal; **e** Antennae and oral region, ventral; **f** P5 and egg sac, ventral; **g** Anal operculum and caudal rami, dorsal



P3 (Fig. 19d) endopod 2-segmented; enp-1 rectangular, longer than female; ornamented with spinules along outer margin, with one inner seta. Enp-2 without spinular ornamentation along outer margin, with one inner, robust spine as figured and with two setae apically (inner one short, naked; outer one long, fused basally to segment). Exopod-3 inner seta shorter than in female.

P5 (Figs. 19e and 22c) fused medially, forming a bilobate plate; medial notch more pronounced than in *N. giziri* sp. nov. Endopodal lobe not reaching distal margin of the exopod, armed with two pinnate setae. Exopods squarish; with asymmetrical armature, similar to that of *N. gebekumensis* sp. nov.: Right exopod with five setae; seta-IV shortest. Left exopod with six elements; the innermost is extra and modified as figured.

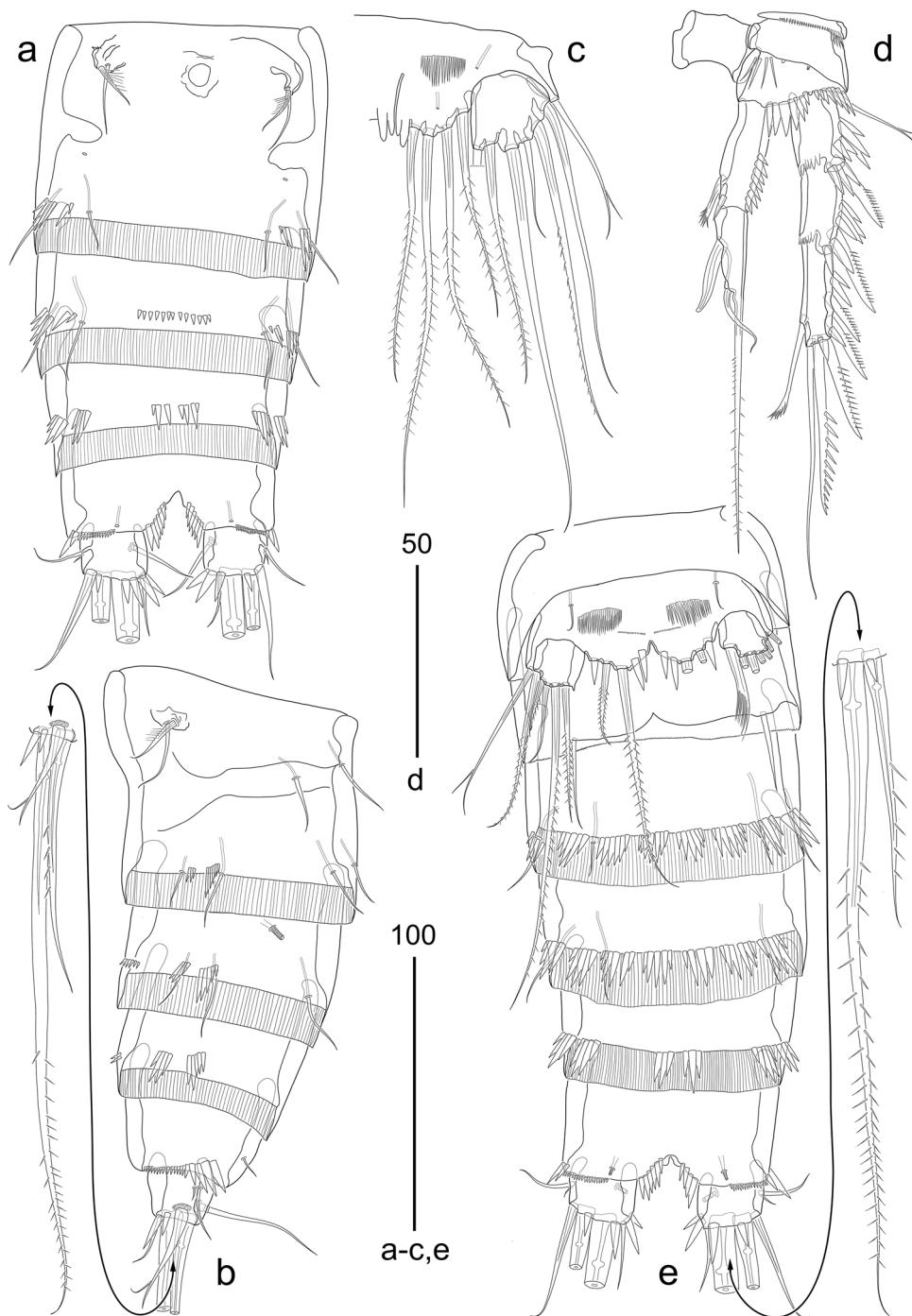
P6 (Fig. 19e) fused with somite, forming a bilobate single plate; armed with 1 naked seta.

Etymology. The specific name refers to “erythrai” which is the historical name of Ildır village (İzmir, Turkey).

Remarks. The new species can be distinguished from the other species of the genus except *N. zavodniki* by the combination of the following characters: i) the presence of six setae on the female P5 exopod; ii) P2–P4 bears 5,4,4 and 5,6,6 setae on distal segments of endo- and exopods respectively; iii) male P3 enp-2, the tip of inner spine is blunt. *N. erythraiensis* sp. nov. morphologically differs from *N. zavodniki* by the combination of the following characters: i) the inner seta of P1 enp-1 extends to approximately end of the endopod ii) P1 enp-1 extends to approximately end of the exp-2; iii) P2 endopod extends to approximately end of the exp-2; iv) P4 endopod extends to approximately end of the exp-1; v) female P5 exopod without a protuberance between seta I and II; vi) the caudal rami with a spinular row near base of the seta VII on. Other minor differences compared to those of valid species are summarized in Table 3.

A cladistic analysis was performed on *Nannomesochra* species. The resulted cladogram is shown in Fig. 23. The

Fig. 19 *N. erythraiensis* sp. nov. Female. **a** Abdomen and P6, ventral; **b** Abdomen and P6, lateral; **c** P5. Male. **d** P3; **e** Urosome, P5 and P6, ventral

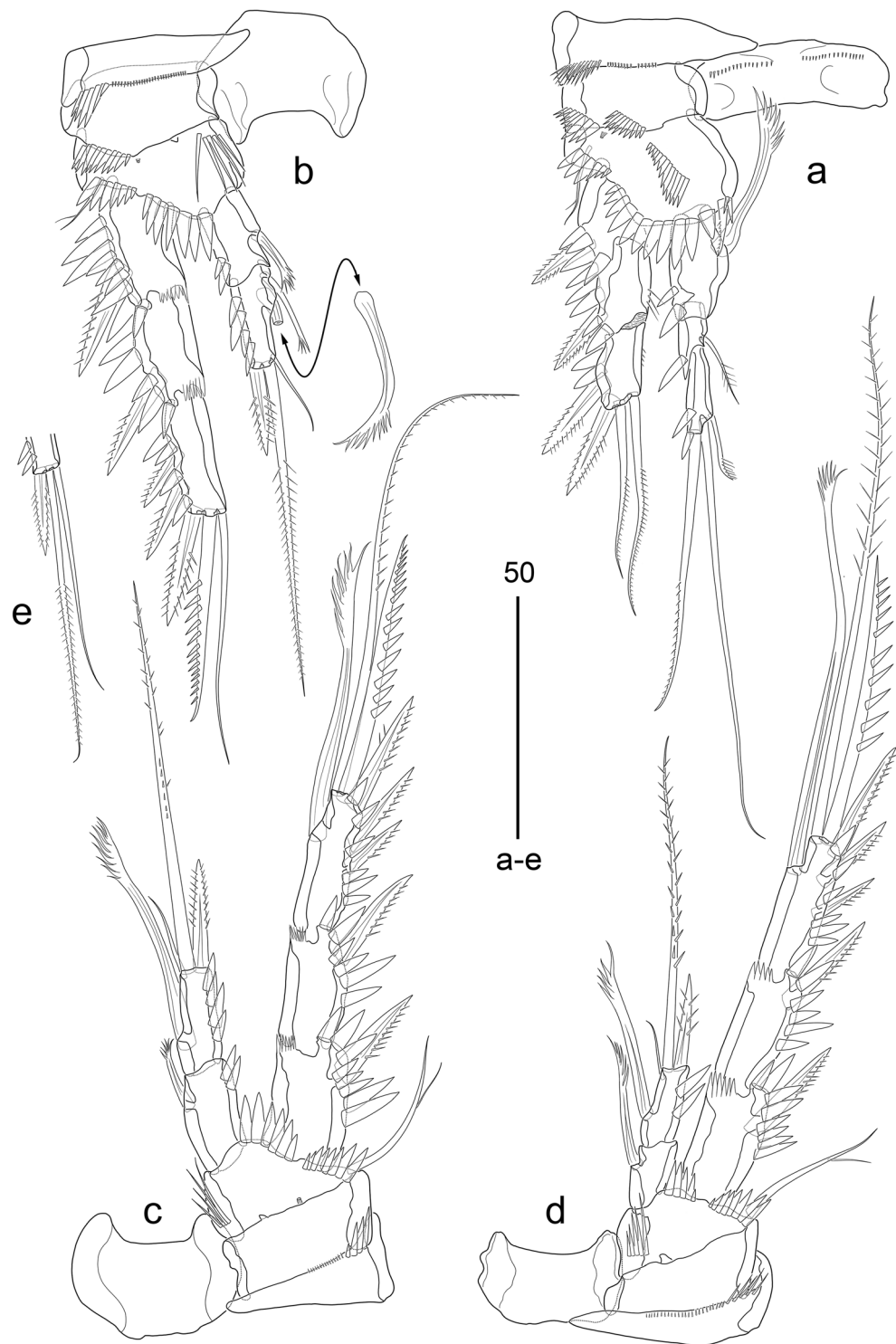


length of the tree is 23, and the consistency index (CI) and retention index (RI) are 0.7391 and 0.6842, respectively. As a result of the analysis, the genus is divided into two groups. *N. parvula* and *N. giziri* sp. nov. are grouped together and formed one of the main groups. The other main group consists of the remaining 5 species and is divided into two subgroups. *N. gebekumensis* sp. nov., *N. erythraiensis* sp. nov. and *N. zavodniki* are clustered in one of the subgroups, while *N. arupinensis* and *N. shermani* comb. nov. are clustered in the other sub-group.

Discussion

A detailed examination and comparison of the material used in this study as well as the examination of *Nannomesochra* literature showed that the large variation previously attributed generally to *N. arupinensis* sensu lato in fact indicates a complex of closely related morphospecies. As a result, seven different morphologically closely related species, three of which being new to science, were recognized and considered valid: *N. arupinensis*; *N. parvula*; *N. zavodniki*; *N. shermani* comb. nov.;

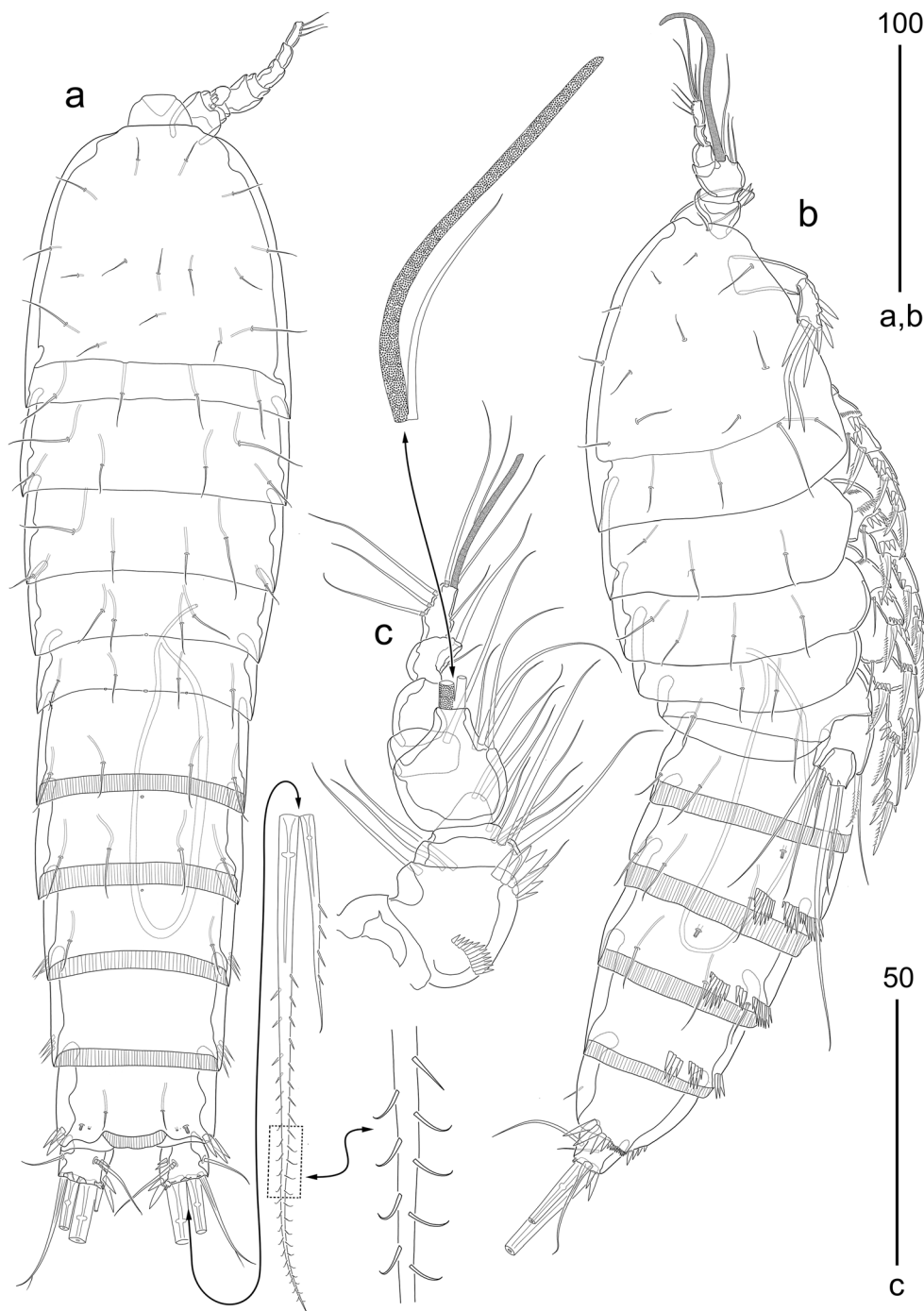
Fig. 20 *N. erythraiensis* sp. nov., female. Swimming legs. **a** P1; **b** P2; **c** P3; **d** P4. Male. **e** P2 endopod, tip of distal segment



N. gebekumensis sp. nov.; *N. giziri* sp. nov. and *N. erythraiensis* sp. nov. The differences between *Nannomesochra* species are summarized in Table 3. In addition, each species considered valid as well as their synonyms and doubtful records/descriptions are discussed in the respective remarks section in detail above. All other records assigned to *N. arupinensis* sensu lato are reviewed below.

Brian (1928a) reported *Mesochra arupinensis* from the islands of Rhodes, Stampalia, Gyalı, and Symi in the Aegean Sea but did not specify the exact locality of the material on which the description (Brian 1928a: p.22, figs. 96–99) was made. Brian (1928a) examined female and male specimens but provided only the illustrations of the male P2, P3-enp, P5 and the ventral view of the urosome which may

Fig. 21 *N. erythraiensis* sp. nov., male. **a** Habitus, dorsal; **b** Habitus, lateral; **c** Antennule



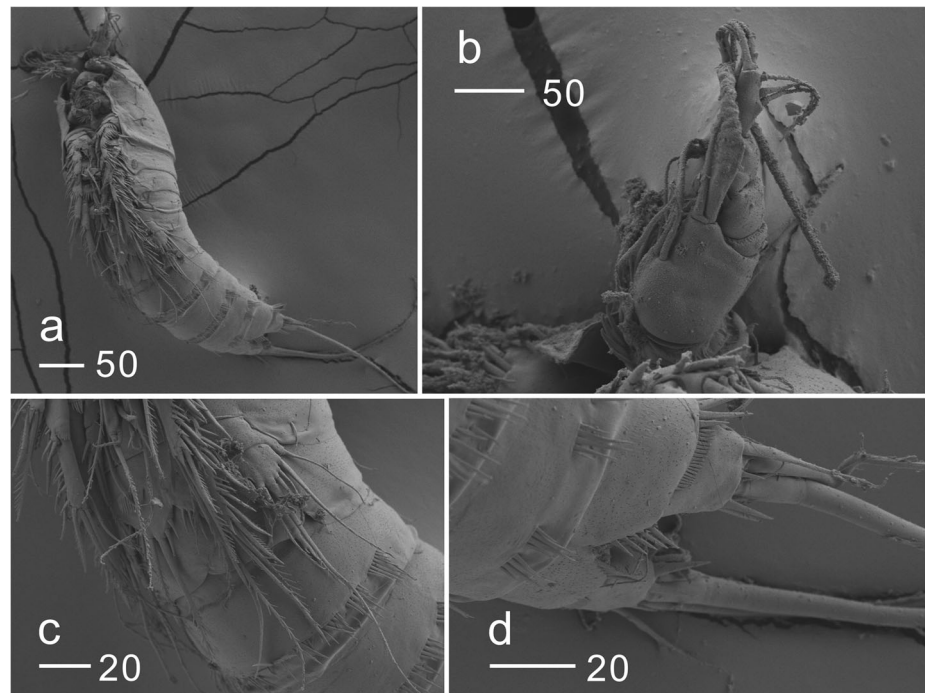
belong to a different species in terms of the structures of P5 and P3-emp in the male.

Wiley (1930) reported *Pseudomesochra parvula* from the brackish Mangrove Lake (Bermuda). The material was collected (June 21, 1928) among intertidal algae attached to roots of mangrove trees in the southern arm of Fairyland Creek, near Agar's Island. Unfortunately, the description and the illustrations provided by Wiley (1930) are incomplete, only the figures of antennule, P2, P3-emp of the female and the antennule, P3-emp and P5 of the male were provided. The

female characteristics of the Bermuda population generally matches with *N. parvula*, unfortunately the male of *N. parvula* sensu Gurney (1927) is not known in order to make a final decision. This Bermuda population also may represent another distinct species considering the isolated position of Mangrove Lake in the North Atlantic Ocean.

Monard (1935b) reported *Mesochra arupinensis* in the study of the marine harpacticoid fauna of Roscoff (France), this species being morphologically closely related to *N. parvula* and *N. giziri* sp. nov. Monard (1935b) figured only the P5 of the

Fig. 22 *N. erythraiensis* sp. nov., male. **a** Habitus, ventrolateral; **b** Antennule, ventral; **c** P5, ventrolateral; **d** caudal rami, ventrolateral



female which strongly resembles the P5 of *N. giziri* sp. nov. on the basis of the inner lobe of baseoendopod not exceeding the exopod (in *N. parvula*, this lobe exceeds the exopod) but no further comparisons can be made since the figure lack other minor details such as setal ornamentations. On the other hand, in the descriptive part of the paper Monard (1935b) wrote that the total number of setae/spines on the terminal exopodal segments of the P2–P4 is 6,7,6 but 6,7,7 in *N. parvula* and *N. giziri* sp. nov., and the total number of setae/spines on the terminal endopodal segments of the P2–P4 is 6,5,4 but 5,5,5 in *N. parvula* and *N. giziri* sp. nov. Monard's (1935b) material can certainly be assigned to the genus *Nannomesochra* on the basis of the fused baseoendopod in the midline in the female and a 1-segmented antennary exopod with two setae (Monard 1935b, p. 60), but it cannot be verified at species level.

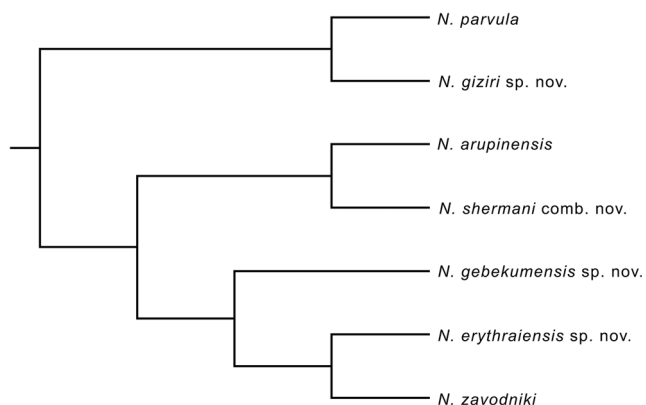


Fig. 23 Cladogram generated by the PAUP analysis of the character matrix presented in Table 2

Therefore, it is considered as *species inquirenda*. In the same paper, Monard (1935b) also described *Mesochra armoricana* as new to science but later it was accepted as a synonym of *N. arupinensis* by Lang (1948) who did not provide a clear justification about the synonymy. Lang's (1948) action was also simply followed by other authors (Marcus and Por 1961; Vervoort 1964; Apostolov and Marinov 1988). The male of this species was partially described by Marcus and Por (1961). But, Wells (2007) rightly removed the species from the synonymy and placed it again in the genus *Mesochra*.

In the study of the Romanian Black Sea harpacticoids, Jakubisiak (1938) determined *Nannomesochra arupinensis* and provided only the illustration of the male P3-enp which is insufficient to confirm the specific identity of this Black Sea population.

Noodt (1953) collected six females and three males from the Fastensee (Lake Fasten), a brackish Lake on the northwest side of Fehmarn, Kiel Firth, Germany. This species morphologically mostly resembles *N. parvula* and *N. giziri* sp. nov. on the basis of setation of the female P2 and P5. They all have an inner seta on the P2 enp-2 and have 6 setae on the terminal exopod segment of P2. The other characteristics of the German material generally matches well *N. parvula* and *N. giziri* sp. nov. but descriptions of Noodt (1953) are devoid of minor details such as the ventral spinular pattern on the urosome and dorsal spinules on the caudal rami which are important to separate *N. parvula* from *N. giziri* sp. nov.

Vervoort (1964) reported one female specimen of *Nannomesochra arupinensis* on the basis of the material originated from the alga *Microdictyon* collected at 35–40 ft. depth in the lagoon of Paugob Canoe House at Falarik Islet in the

Ifaluk Atoll in the Pacific Ocean. Ifaluk specimens morphologically mostly resembles *N. parvula* and *N. giziri* sp. nov. on the basis of setation of the female P2 and P5 (a fine distal seta on the terminal endopod segment of P3 and P4 possibly overlooked by Vervoort (1964)). They all have an inner seta on the P2 enp-2 and have 6 setae on the terminal exopod segment of P2. The first segment of the antennule is not a real segment but the base of the antennule, it is highly possible that the second segment drawn by Vervoort (1964) represent the first and second segment. It is possible that Vervoort (1964) overlooked the separation line of these two segments, because of imaging quality of the microscope at that time. Considering the male has not been described and the isolated position of the Ifaluk Atoll in Pacific Ocean, it would not be surprising if this Ifaluk population also represented another distinct species.

Apostolov and Marinov (1988) provided the illustration of *Nannomesochra arupinensis* from the Bulgarian coast. The setal formula of the swimming legs given by Apostolov and Marinov (1988) indicates that Bulgarian material resembles *N. parvula*. Yet, the descriptions are devoid of minor details such as the ventral spinular pattern on the urosome and dorsal spinules on the caudal rami.

Alper et al. (2010) reported *N. arupinensis* from the Turkish coast. This material was reexamined and now verified as *N. parvula*.

Other reports of *N. arupinensis* from Salambo, Tunisia (Monard 1935a); Castiglione, Italy (Monard 1937); Tenerife in the Canary Islands, Spain (Noodt 1955a); Sea of Marmara, Turkey (Noodt 1955b); Lough Ine of County Cork, Ireland (Roe 1960); Aldabra, Indian Ocean, Seychelles (Wells and McKenzie 1973); Gulf of Bourgas, Bulgaria (Apostolov 1977); San Diego, USA (Thistle 1982); Valleys of Comacchio and Lesina lagoon, Italy (Ceccherelli and Mistri 1990); Lake McLeod (Blue Holes), western Australia (Halse et al. 2000); East Sussex, United Kingdom (Ventham 2011); Porto de Galinhas coral reefs, northeastern Brazil (Sarmiento and Santos 2012) and *Nannomesochra* sp. from Zanzibar, Tanzania (Callens et al. 2012) do not contain description or sufficient information, therefore these reports cannot be verified at species level and are considered as unverified records.

The characters used in the cladistic analysis of *Nannomesochra* species in this study were selected by considering the data available in the original descriptions of the previously published species. Although microcharacters such as sensillar and microspinular ornamentations on the body somites and appendages are considered important in the current harpacticoid phylogeny (Galassi et al. 2011; Karanovic et al. 2018), unfortunately, they could not be included in the character set (Tables 1 and 2) since they cannot be discerned from the illustrations or descriptions. Therefore, basic characters such as the armature of swimming legs were mostly used in the analysis. The other characters used in the analysis were related to A1 and furcal rami, as well as the shape and armature of the female P5 (Table 1).

As a result of the cladistic analysis, the genus was divided into two major groups (Fig. 23). *N. parvula* and *N. giziri* sp. nov. were grouped together and took place in the first group. One of the significant characters connecting the two species and separating them from the other species in the genus is the length of the female P5 baseoendopodal lobe. A baseoendopodal lobe extending beyond the distal margin of the exopod (character 14 in Tables 1 and 2) is considered a synapomorphy for *N. parvula* and *N. giziri* sp. nov. In contrast, the presence of only one seta, i.e. the reduction of one seta on the inner margin of the P4 endopod (character 9 in Tables 1 and 2) is considered here as a synapomorphy for all remaining *Nannomesochra* species, whilst *N. parvula* and *N. giziri* sp. nov. retain the plesiomorphic state (the presence of two setae). The presence of a notch between seta I and II on the female P5 (character 12 in Tables 1 and 2) is an autoapomorphy for *N. giziri* sp. nov.

The second major group was divided into two sub-groups. The first sub-group consisted of *N. gebekumensis* sp. nov., *N. erythraiensis* sp. nov. and *N. zavodniki*. The bare inner margin of P2–P4 (characters 6, 8 and 10 in Tables 1 and 2) is defined as synapomorphies for this sub-group. The presence of a protuberance between seta I and II on female P5 (character 13) is an autoapomorphy for *N. zavodniki*. The P1 enp-2 with bare inner edge and the P2 enp-2 with one inner seta (characters 4 and 5 in Tables 1 and 2) are autoapomorphies for *N. gebekumensis* sp. nov. The presence of a spinular row near the base of the seta VII on the caudal rami (character 15 in Tables 1 and 2) is considered as an autoapomorphy for *N. erythraiensis* sp. nov.

The other sub-group includes *N. arupinensis* and *N. shermani* comb. nov. which are characterized by longer P1 endopods (character 3 in Tables 1 and 2) than in other species of the genus. A baseoendopodal lobe reaching the distal edge of the exopod (character 14 in Tables 1 and 2) is considered as an autapomorphy for *N. arupinensis*.

Phylogenetic position of *Nannomesochra* within Hemimesochrinae

Gurney (1927) put some reservations about the monophyletic status of the genus by stating that none of the differences may have had a generic value for *Pseudomesochra* (= *Nannomesochra*). On the other hand, Gurney (1927) assumed that the justification for treating *Pseudomesochra* as sufficiently distinct genus within the family Canthocamptidae may be justified by the peculiar/characteristic structure of the female P5. Since Gurney (1927), several new genera have been added to the family Canthocamptidae and the family was divided into two subfamilies Canthocamptinae Brady, 1880 and Hemimesochrinae Por, 1986 (Wells 2007). The genus *Nannomesochra* belongs to the Hemimesochrinae and seems to be phylogenetically closely related to *Bathycamptus* Huys & Thistle, 1989, *Pusillargillus* Huys & Thistle, 1989 and *Heteropsyllus* T. Scott, 1894. However, *Nannomesochra* can easily be distinguished from *Bathycamptus* by its fifth pair of

legs with medially fused baseoendopods in the female and a 2-segmented P3 endopod with three elements (two elements apically and a modified inner seta) on the distal segment in the male (3-segmented with an apophysis on the middle segment in *Bathycamptus*). Within the subfamily, the 2-segmented P3 endopod is only found in the males of *Nannomesochra*, *Pusillargillus* and *Heteropsyllus* and can be considered as a synapomorphy of the three genera. *Pusillargillus* can easily be differentiated from *Nannomesochra* in having a 5-segmented antennule

and a 2-segmented P1-enp in the female, and *Pusillargillus* bears an apophysis on the outer distal corner and three setae (two setae apically and an unmodified inner seta) on the second segment of the male P3 endopod. *Heteropsyllus* differs from *Nannomesochra* by having an antennary allobasis with a 1-segmented trisetose exopod and a 5-segmented antennule in the female and *Heteropsyllus* bears an apophysis on anterior side and four setae (two setae apically and two unmodified inner seta) on the second segment of the male P3 endopod.

A key to subfamily Hemimesochrinae

1. Antennary exopod with 1 seta *Dahlakia*
 Antennary exopod with 2 setae 2
 Antennary exopod with 3 setae 7
2. P1-enp 1-segmented. P2–P4 endopod absent *Isthmiocaris*
 P1-enp 2-segmented 3
 P1-enp 3-segmented 4
3. Baseoendopod and exopod of P5 not fused in female; exopod with 5 setae *Pusillargillus*
 Baseoendopod and exopod of P5 fused in female; exopod with 4 setae *Boreolimella*
4. P2 and P3 endopod 3-segmented *Poria*
 P2 and P3 endopod 2-segmented 5
5. Male P3 endopod 2-segmented *Nannomesochra*
 Male P3 endopod 3-segmented 6
6. Antennule 6-segmented; sexual dimorphism in P1–P2. *Psammocamptus*
 Antennule 7-segmented; no sexual dimorphism in P1–P2 *Bathycamptus*
7. P4 endopod absent *Perucamptus*
 P4 endopod 2-segmented 8
8. Antennule 6-segmented *Mesopsyllus*
 Antennule 5-segmented 9
9. P1 endopod 3-segmented *Heteropsyllus*
 P1 endopod 2-segmented *Hemimesochra*

A key to the species of the genus *Nannomesochra*

1. P1 enp-2 with 1 inner seta, P2 enp-2 with 1 inner setae *N. gebekumensis* sp. nov.
 P1 enp-2 with 1 inner seta, P2 enp-2 with 2 inner setae 2
2. Female, P5 exp with 6 setae 3
 Female, P5 exp with 5 setae 4
3. Female, caudal ramus without a spinular row near base of seta VII. P5 exp roundish, with protuberance between seta I and II.
 A2 exp with two setae unequal in length *N. zavodniki*
 Female, caudal ramus with a spinular row near base of seta VII. P5 exp squarish, without protuberance between seta I and II.
 A2 exp with two setae equal in length *N. erythraiensis* sp. nov.
4. Female, P3–P4 enp-2 with 4 setae 5
 Female, P3–P4 enp-2 with 5 setae 6
5. Female, P5 baseoendopodal lobe triangular, reaching to distal margin of the exopod *N. arupinensis*
 Female, P5 baseoendopodal lobe not triangular, not reaching distal margin of the exopod *N. shermani* comb. nov.
6. Female, caudal ramus with a spinular row near base of seta VII. The length of distal seta on the inner margin of P4 exp-3 equal/shorter than the segment. P5-exp without a notch between seta I and II; seta III spiniform. *N. parvula*
 Female, caudal ramus without a spinular row near base of seta VII. The length of distal seta on the inner margin of P4 exp-3 longer than the segment. P5-exp with a notch between seta I and II; seta III slender. *N. giziri* sp. nov.

Acknowledgements Results included in this paper partly originated from a PhD thesis by the senior author. We are grateful to Dr. Serdar Sönmez for his effort during the sampling period of the material. We would also like to thank the anonymous reviewers for their constructive criticism and valuable comments that improved the manuscript.

Funding information This study was funded by Balikesir University Research Fund (grant number 2007/12) and the Scientific and Technological Research Council of Turkey (grant numbers 106T590 and 111T576).

Declarations

Conflict of interest The authors declare no competing interests.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the Agriculture and Forestry Ministry's General Directorate of Nature Conservation and National Parks, Turkey.

Data availability All data generated or analyzed during this study are included in this published article.

Author contribution A.A., S.K., and S.S. designed research and conducted samplings. S.S. and S.K. contributed illustrations of the specimens. A.A. performed digital editing of the illustrations/SEM photos. The first draft of the manuscript was written by S.K., A.A., and S.S. All authors read and approved the manuscript.

References

- Alper A, Karaytuğ S, Sak S (2010) Interstitial and phytal Harpacticoida (Crustacea: Copepoda) inhabiting the mediolittoral zone of the Datça–Bozburun Peninsulas (Muğla, Turkey). *SDÜ J Sci* 5:16–28
- Apostolov A (1977) Harpacticoides nouveaux de la mer Noire et de la faune Bulgare. *Acta Zool Bulgar* 7:8–21
- Apostolov A, Marinov T (1988) Copepoda. Harpacticoida. Fauna Bulgaria, Aedibus Academiae Scientiarum Bulgariae, Bulgaria
- Boxshall G, Halsey S (2004) An Introduction to Copepod Diversity. The Ray Society, London
- Boxshall G, Jaume D (2000) Making waves: the repeated colonization of fresh water by copepod crustaceans. *Adv Ecol Res* 31:61–79. [https://doi.org/10.1016/S0065-2504\(00\)31007-8](https://doi.org/10.1016/S0065-2504(00)31007-8)
- Brady GS (1880) A monograph of the free and semi-parasitic Copepoda of the British Islands. Ray Society, London
- Brian A (1923) Elenco di copepodi marini bentonici proveniente da Rovigno e descrizione di una n. varietà di *Parathalestris clausi* Norm. *Monit Zool Ital* 34:126–135
- Brian A (1925) Descrizione di forme nuove di Copepodi arpacticoidi raccolti a Rovigno. *Monit Zool Ital* 34:15–24
- Brian A (1928a) Descrizione di specie nuove o poco conosciute di copepodi bentonici del mare Egeo. *Boll Mus Zool Anat Comp R Univ Genova* 7:1–37
- Brian A (1928b) I Copepodi bentonici marini. *Arch Zool Ital* 12:293–343
- Callens M, Gheerardyn H, Ndarog SG, De Troch M, Vanreusel A (2012) Harpacticoid copepod colonization of coral fragments in a tropical reef lagoon (Zanzibar, Tanzania). *J Mar Biol Assoc UK* 92:1535–1545. <https://doi.org/10.1017/S0025315411001597>
- Ceccherelli VU, Mistri M (1990) Ecological and zoogeographical study of some Mediterranean associations of brackish water harpacticoids. *Ital J Zool* 57:73–81
- Corgosinho P, Schizas N (2013) *Archeolourinia shermani*, a new genus and species of Louriniidae (Copepoda: Harpacticoida) from a Caribbean mesophotic zone. *J Mar Biol Assoc UK* 93:651–657. <https://doi.org/10.1017/S0025315412001336>
- Galassi DM, De Laurentiis P, Fiasca B (2011) Systematics of the Phyllognathopodidae (Copepoda, Harpacticoida): re-examination of *Phyllognathopus viguieri* (Maupas, 1892) and *Parbatocamptus jochenmartensi* Dumont and Maas, 1988, proposal of a new genus for *Phyllognathopus bassoti* Rouch, 1972, and description of a new species of *Phyllognathopus*. *ZooKeys* 104:1–165. <https://doi.org/10.3897/zookeys.104.763>
- Gurney R (1927) Zoological Results of the Cambridge Expedition to the Suez Canal, 1924. XXXIII. Report on the Crustacea:—Copepoda (littoral and semi-parasitic). *Trans Zool Soc Lond* 22:451–577
- Gurney R (1932) British Freshwater Copepoda. Volume 2. Ray Society, London
- Halse S, Shiel R, Storey A, Edward D, Lansbury I, Cale D, Harvey M (2000) Aquatic invertebrates and waterbirds of wetlands and rivers of the southern Carnarvon Basin, Western Australia. *Rec West Aust Mus* 61:217–265. <https://doi.org/10.18195/issn.0313-122x.61.2000.217-265>
- Huys R, Thistle D (1989) *Bathycamptus eckmani* gen. et spec. nov. (Copepoda, Harpacticoida) with a review of the taxonomic status of certain other deepwater harpacticoids. *Hydrobiologia* 185:101–126
- Huys R, Boxshall G (1991) Copepod evolution. The Ray Society, London
- Huys R, Gee J, Moore C, Hamond R (1996) Marine and brackish water harpacticoid copepods. Part 1. In: Barnes RSK, Crothers JH (eds) Synopses of the British Fauna (new series, 51). Field Studies Council, Shrewsbury
- Jakubisiak S (1938) Les harpacticoides de la Mer Noire (côtes Roumaines). *Ann Sci Univ Jassy* 24:387–402
- Karanovic T, Lee S, Lee W (2018) Instant taxonomy: choosing adequate characters for species delimitation and description through congruence between molecular data and quantitative shape analysis. *Invertebr Syst* 32:551–580. <https://doi.org/10.1071/IS17002>
- Karaytuğ S, Sak S, Alper A, Sönmez S (2021) Resolving the *Lourinia armata* (Claus, 1866) complex with remarks on the monophyletic status of Louriniidae, Monard 1927 (Copepoda: Harpacticoida). *Zootaxa* 5051:346–386. <https://doi.org/10.11646/zootaxa.5051.1.15>
- Kaymak NB, Karaytuğ S (2014) Systematics of the genus *Heterolaophonte* (Crustacea, Copepoda, Harpacticoida), with redescription of *H. uncinata* and *H. curvata*. *Zootaxa* 3780:503–533. <https://doi.org/10.11646/zootaxa.3780.3.4>
- Lang K (1936) Die Familie der Cletodidae Sars, 1909. *Zool Jahrb Abt Syst* 68:445–480
- Lang K (1948) Monographie der Harpacticiden. H. Ohlsson, Lund
- Marcus A, Por FD (1961) Die Copepoden der polyhalinen Lagunen Sinoe Schwarzes Meer-Rumänische Küsten. *Acta Mus Maced Sci Nat* 7:105–126
- Monard A (1927) Synopsis universalis generum harpacticoidarum. *Zool. Jahrb., Abt. Syst. Geogr Biol Tiere* 54:139–176.
- Monard A (1935a) Les Harpacticoides marins de la région de Salammbo. *Bull Stn Oceanogr Salammbo* 34:1–94
- Monard A (1935b) Étude sur la faune des Harpacticoides marins de Roscoff. *Trav Stn Biol Roscoff* 13:5–89

- Monard A (1937) Les Harpacticoïdes marins de la région d'Alger et de Castiglione. Bulletin de la Station d'Aquiculture et de Pêche de Castiglione 1935:9–93
- Noodt W (1953) Bemerkenswerte Copepoda Harpacticoidea aus dem Eulitoral der deutschen Meeresküste. Zool Anz 151:6–20
- Noodt W (1955a) Copepoda Harpacticoidea von Teneriffa (Kanarische Inseln). Zool Anz 154:200–222
- Noodt W (1955b) Marine Harpacticoiden (Crust. Cop.) aus dem Marmara Meer. Rev Fac Sci Univ Istanbul 20:49–94
- Petkovski T, Apostolov A (1974) Zweite *Nannomesochra*-Art (Copepoda, Harpacticoidea) aus der Adria, *N. zavodniki* n. sp. Fragm Balc 10:1–8
- Por FD (1986) New deep-sea Harpacticoida (Copepoda) of cletodid type, collected in the Indian Ocean by R/V 'Anton Bruun' in 1964. Crustaceana 50:78–98
- Roe K (1960) Some harpacticids from Lough Ine, with descriptions of two new species. Proc R Ir Acad, Sect B 60:277–289
- Sarmento VC, Santos PJP (2012) Species of Harpacticoida (Crustacea, Copepoda) from the phytal of Porto de Galinhas coral reefs, north-eastern Brazil. CheckList 8:936–939. <https://doi.org/10.15560/8.5.936>
- Sars GO (1903) Copepoda Harpacticoida. Parts I & II, Misophriidae, Longipediidae, Cerviniidae, Ectinosomidae (part). An Account of the Crustacea of Norway, with short descriptions and figures of all the species. Bergen Museum 5:1–28
- Scott T (1894) Additions to the fauna of the Firth of Forth. Part VI. Annu Rep Fish Board Scotl 12:231–271
- Scott T (1902) Notes on gatherings of Crustacea collected by the Fishery Steamer 'Garland' and the steam trawlers 'Star of Peace' and 'Star of Hope', of Aberdeen, during the year 1901. Annu Rep Fish Board Scotl 20:447–484
- Thistle D (1982) Aspects of the natural history of the harpacticoid copepods of San Diego Trough. Biol Oceanogr 1:225–238
- Ventham D (2011) Harpacticoid copepods from the Sussex coast (eastern English Channel): records 1992–1997. The Booth Museum of Natural History, Brighton
- Vervoort W (1964) Free-living Copepoda from Ifaluk Atoll in the Caroline Islands with notes on related species. Bull US Natl Mus 236:1–431
- Walter T, Boxshall G (2022) *Nannomesochra* Gurney, 1932. World of Copepods Database. <http://www.marinespecies.org/aphia.php?p=taxdetails&id=115243>. Accessed 04 Jul 2022
- Wells JBJ (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). Zootaxa 1568:1–872. <https://doi.org/10.11646/zootaxa.1568.1.1>
- Wells JBJ, McKenzie K (1973) Report on a small collection of benthic copepods from marine and brackish waters of Aldabra. Indian Ocean Crustaceana:133–146. <https://doi.org/10.1163/156854073X00786>
- Willey A (1930) XI.—Harpacticoid Copepoda from Bermuda.—Part I. (Contributions from the Bermuda Biological Station for Research, No. 160.). Ann Mag Nat Hist 6:81–114. <https://doi.org/10.1080/00222933008673192>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.