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Records of Normanellidae Lang, 1944 (Copepoda, Harpacticoida) from Madeira island support the hypothetical role of seamounts and oceanic islands as "stepping stones" in the dispersal of marine meiofauna

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Abstract Many meiofauna species show a wide and even amphioceanic distribution with populations separated by thousands of kilometres of oceanic deep sea despite their apparently limited dispersal potential (the "meiofauna paradox"). Several studies have attempted to explain this contradiction. One hypothesis is that seamounts act as "stepping stones" in the dispersal of meiofauna, supporting the colonisation of remote habitats by chance dispersal. This would be confirmed if meiofauna species were found on oceanic elevations located between apparently fragmented populations. To test this hypothesis we studied the littoral Normanellidae (Copepoda, Harpacticoida) of the Portuguese islands Madeira and Porto Santo and reviewed their known geographical distribution. All three species of Normanellidae recorded on Madeira were already described from other inshore shallow-water habitats. Furthermore, we also recovered one of these species, *Normanella pallaresae*, formerly only known from the Argentinian coast, on the summit of Seine Seamount, in the adjacent deep sea of Sedlo Seamount and in a Mediterranean cave. The presence of this species on the Atlantic elevations provides a link in its amphiatlantic distribution and faunistic evidence for the "stepping stone" hypothesis. A re-description of *Normanella pallaresae* is also provided.

Keywords Deep sea · Eurybathy · Meiofauna dispersal · Meiofauna paradox · *Normanella pallaresae* · Stepping stones

Introduction

Meiofaunal organisms such as Harpacticoida (Crustacea, Copepoda) are generally characterised by a limited dispersal potential due to their holobenthic life-cycle and associated morphological adaptations (Giere 2009). Nonetheless, many meiofaunal taxa show a wide and often even amphioceanic distribution, a phenomenon known as the "meiofauna paradox" (Giere 2009). Particularly paradoxical is the disjunct distribution of shallow-water species that have populations separated by thousands of kilometres of oceanic deep sea, which presumably constitutes an ecological barrier for shallow-water organisms. However, the topography of the world's oceans floor has been intensively investigated over the last decades (Smith and Sandwell 1997; Kitchingman et al. 2007; Pitcher et al. 2007; Wessel 2007; Yesson et al. 2011) and has found a quite heterogeneous and topographically diverse environment. The ocean floor is in fact traversed by several oceanic ridges and studded with thousands of individual seamounts (up to 100,000 seamounts > 1000 m and up to a million <1000 m, Pitcher et al. 2007) mostly of volcanic origin and often forming long chains (e.g., "Hot Spot Tracks"). Even most oceanic islands, for example, those in the Madeiran Archipelago, are of volcanic origin and actually represent the seamount-stage that breaches the water surface. Therefore, littoral and sublittoral zones of these islands combined with submerged seamounts may offer a network of suitable habitats for shallow-water meiofaunal organisms.

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Individuals of shallow-water meiofauna, which drift away from inshore habitats, would usually sink to the (bathyal or even abyssal) seafloor due to their specific morphology. Some of these individuals may randomly reach an elevated seafloor area and, if providing similar environmental conditions to their coastal origin, survive potentially to establish new populations (George 2013; Packmor et al. 2015). Such populations might then also originate further dispersal events (George 2013; Packmor et al. 2015). Thus, seamounts and oceanic islands, may act as so-called stepping stones, supporting chance dispersal of meiofauna organisms, and thus the colonisation of remote habitats (Rosen 1983, 1984; Cecca 2002).

To assess the hypothetical role of seamounts and islands in the dispersal of meiofauna organisms, a comprehensive knowledge of their respective faunal compositions is necessary. However, little is known about seamount meiofauna (George 2013). Among meiofaunal taxa harpacticoid copepods are one of the most intensely studied at the species level, but detailed faunistic and taxonomic information is only available from three Atlantic seamounts, Seine, Sedlo, and Great Meteor, and their surrounding deep sea (George and Schminke 2002; George 2004a, b, 2013; George and Plum 2009; Plum and George 2009; Büntzow 2011; Koller and George 2011).

Seine Seamount is part of the "Madeira Hot Spot Track", an island and seamount chain running northeast towards the coast of Portugal (Geldmacher et al. 2005, 2006, 2011; the following ages of the seamounts were taken from Geldmacher et al. 2011, except for Madeira and Porto Santo). The youngest elevations on this Hot Spot Track are the Portuguese islands of Madeira and Porto Santo (7 and 19 Ma; Ramalho et al. 2015 and Mata et al. 2013), followed by the seamounts Seine (24 Ma), Unicorn (27 Ma), Ampère/Coral Patch (31/32 Ma), and Ormonde (67 Ma). The geographical nature of the "Madeira Hot Spot Track", as a chain of elevations at increasing distance from the continental coast, make it an ideal model for an investigation of the "meiofauna paradox". In terms of the harpacticoid fauna, the Seine Seamount and surrounding deep sea was investigated during Cruise M60/1 (2003) of RV METEOR. Also, several locations along the coastlines of Madeira and Porto Santo were sampled in 2011 and 2012, providing a first, comprehensive inventory of the Harpacticoida from both islands (Packmor 2013; Packmor et al. 2015). This combined data set afforded a unique opportunity to compare the copepod faunas of successive elevations along the "Madeira Hot Spot Track", with the potential to inform our understanding of any role seamounts play in the dispersal of meiofauna organisms.

The present contribution focused on the Normanellidae Lang, 1944 (Harpacticoida) from Madeira and Porto Santo, with further comparison with species from Seine Seamount and the adjacent deep sea around Sedlo Seamount. Additionally, we update the known distribution of the species of Normanellidae recorded from the Madeiran Archipelago and re-describe *Normanella pallaresae* Lee and Huys, 1999.

Materials and methods

Sediment cores for the quantitative investigation of the harpacticoid copepod communities of Madeira and Porto Santo were taken during April and May 2011 and May 2012. In total, 11 sampling locations were studied, nine along the Madeiran coastline and two on the south coast of Porto Santo (Fig. 1). The sampling locations on Madeira were Seixal, Ponta Delgada, and Porto da Cruz on the north coast, Prainha in the northeast, and Calheta, Ribeira Brava, Funchal (only qualitative samples, which will not be considered in this publication), Reis Magos, and Machico on the south coast (Table 1). The two sampling locations on the south coast of Porto Santo were Porto Santo East and Porto Santo West. Further information on the sampling procedure, sample treatment, and sorting of the Harpacticoida is provided in Packmor (2013). For the present publication all Normanellidae were determined to species level. Drawings were made from whole and dissected specimens mounted in glycerin using a camera lucida on a Leica DMR compound microscope equipped with differential interference contrast. The Normanellidae of Madeira were further compared with material collected from the summits of the seamounts Seine and Sedlo as well as from the adjacent deep sea during expedition M60/1 OASIS of the German RV "METEOR" in 2003 (Christiansen and Wolff 2009). This latter material was processed by Büntzow (2011) and detailed information on sampling locations and sample treatment can be found therein. Furthermore, we also had the opportunity to compare the Normanellidae from Madeira, Seine, and Sedlo with material from a marine cave on the French Mediterranean Coast (near Marseille) at a water depth of about 15 m (Janssen et al. 2013). Geographical maps (Figs. 1 and 2) were created using the program PanMap (Diepenbroek et al. 2000; NGDC/NOAA 1993).

A1 antennule, *A2* antenna, *aes* aesthetasc, *benp/benps* baseoendopod/baseoendopods, *Cphth* cephalothorax, *enp/enps* endopod/endopods, *exp/exps* exopod/exopods, *FR* furcal ramus/furcal rami, *GF* genital field, *Md* mandible, *Mx* maxilla, *Mxl* maxillule, *Mxp* maxilliped, *P1–P6* legs 1–6.

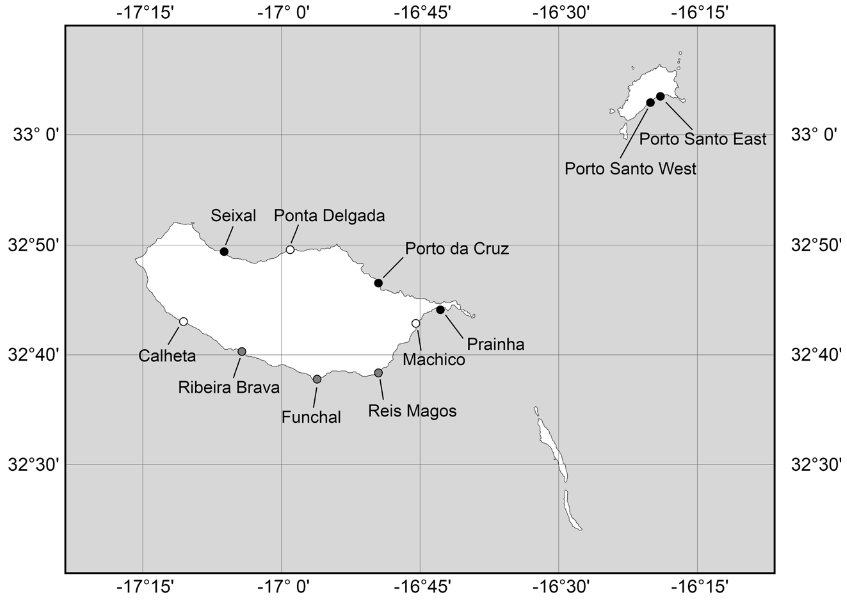

Fig. 1 Geographical position of the sampling locations. Grey dots sampled in 2011, white dots sampled in 2012, black dots sampled in 2011 and 2012 (Map-Source: Pangaea, PanMap)

Results

Species of Normanellidae investigated and their distribution

On Madeira, Normanellidae Lang, 1944 were exclusively found on the south coast at Ribeira Brava, Machico (2 to 3 m depth), and Reis Magos (13 m depth) (Fig. 1). Only the genus *Normanella* Brady, 1880 was recorded, represented by three species, *Normanella dubia* Brady, 1880, *Normanella minuta* (Boeck, 1873), and *Normanella pallaresae* Lee and Huys, 1999. *Normanella dubia* was found at Machico and Reis Magos and showed the highest abundances (up to 18 individuals per sample). *Normanella minuta* was found only at Ribeira Brava (one female) and Reis Magos (one male) and *N. pallaresae* was only found at Ribeira Brava (one female). The investigated material of Porto Santo revealed no Normanellidae.

Table 1 Coordinates of the Madeiran sampling locations and date of sampling

Sampling location	Longitude	Latitude	Date
Calheta	32°43’09.59”N	17°10’32.09”W	08.05.2012
Ribeira Brava	32°40’15.30”N	17°04’03.24”W	29.04.2011
Reis Magos	32°38’49.10”N	16°49’23.16”W	23.05.2011
Machico	32°43’06.00”N	16°45’42.13”W	05.05.2012
Seixal	32°49’18.79”N	17°06’09.18”W	08.04.2011
Ponta Delgada	32°49’41.69”N	16°59’04.04”W	03.05.2012
Porto da Cruz	32°46’30.51”N	16°49’44.27”W	18.05.2011
Prainha	32°44’33.29”N	16°42’57.22”W	05.04.2011
Porto Santo East	33°03’40.81”N	16°19’11.23”W	15.05.2011
Porto Santo West	33°03’07.59”N	16°20’22.07”W	15.05.2011

The re-examination of the Normanellidae from the OASIS material (Büntzow 2011) revealed that all investigated specimens of *Normanella* sp. 1 from Seine Seamount (178–235 m depth, 148 individuals) were *N. pallaresae*, as was the single individual of *Normanella* sp. 2 (Büntzow 2011) recorded in the deep sea southeast of Sedlo Seamount (2875 m depth). Also, the six specimens from 15 m depth in a Mediterranean marine cave (Janssen et al. 2013) determined as *N. minuta* were in fact *N. pallaresae*. The body size of the investigated species are documented and compared with published data in Table 2.

The known geographical distribution of the three investigated Normanellidae (Fig. 2) were adopted and updated (records with Citation) from Lee and Huys (1999):

Known localities of *N. minuta*. Norway: south and west coast, Oslofjorden, Trondheimsfjorden, Bergen; Sweden: Gullmar Fjord, Mitskären; Germany: Helgoland; Ireland: Dublin Bay, Lough Ine; Scotland: Aberdeenshire, Loch Creran (Ólafsson and Moore 1992), Loch Torridon, Borders; England: Norfolk, Southern Celtic Sea, Durham, Northumberland, North Yorkshire; Wales: Pembrokeshire, Menai Strait; Isle of Man; France: Roscoff; Black Sea: Bulgaria, Ukrainian Coast; Portugal: Madeira Island (present study); USA: Gulf of Maine, North Carolina continental shelf.

Known localities of *N. dubia*. England: Isles of Scilly, Northumberland, mouth of the River Tyne, River Tamar, Durham, Devon, Cornwall; Isle of Man; Ireland: Clew Bay; Scotland: northeast of Shetland Islands, east of Orkney Islands, Firth of Forth, Loch Fyne; Portugal: Madeira Island (present study).

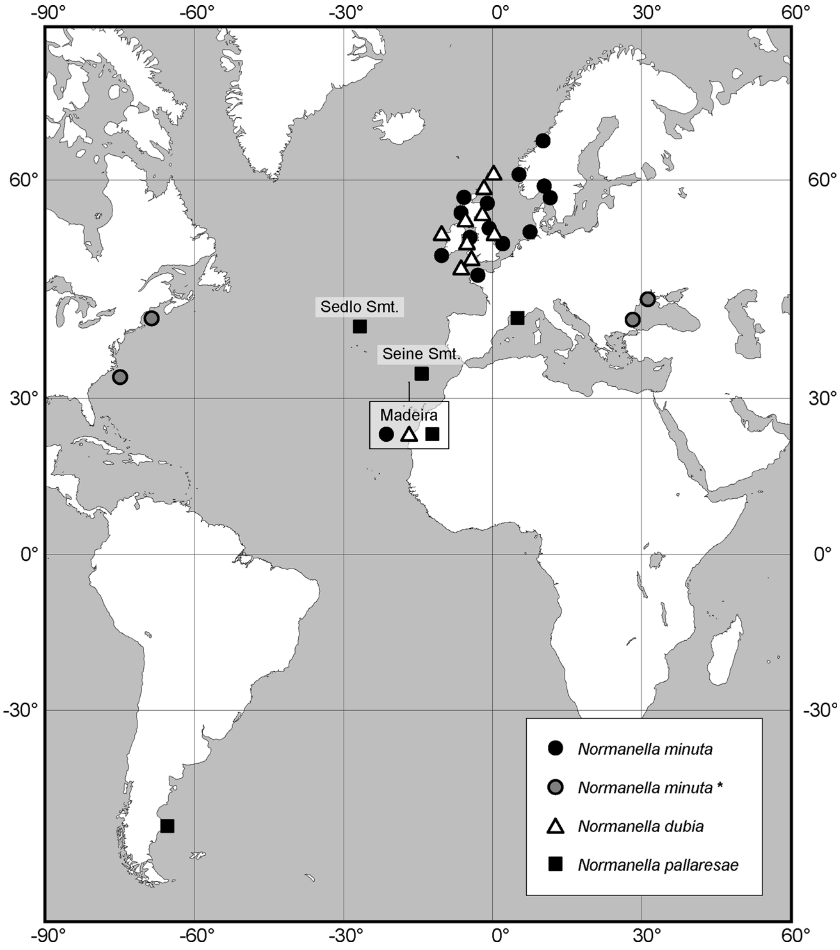

Fig. 2 Overview of the known worldwide distribution of the three species of Normanellidae, recorded on Madeira Island (Portugal) (Map-Source: Pangaea, PanMap). * records of *Normanella minuta* doubted by Lee and Huys (1999)

Known localities of *N. pallaresae*. Argentina: mouth of the Rio Deseado; Portugal: Madeira Island (present study); Atlantic Ocean: Seine Seamount (178–235 m depth; present study, re-examined material from Büntzow 2011), deep sea southeast of Sedlo Seamount (2875 m depth; present study, re-examined material from Büntzow 2011); France:

Table 2 Comparison of the overall body size of *Normanella minuta, Normanella pallaresae*, and *Normanella dubia* at different localities

Species	Location	Reference	♀ body size (μm)	♂ body size (μm)
N. minuta	Madeira Island	present contribution	463	unknown
	British Isles	Lee and Huys 1999	495–550 ($n = 6$, $\bar{x} = 533$)	437–460 ($n = 12$, $\bar{x} = 446$)
N. pallaresae	Madeira Island	present contribution	420	unknown
	Seine Seamount	present contribution (material: Büntzow 2011)	459–525 ($n = 4$, $\bar{x} = 494$)	375–391 ($n = 4$, $\bar{x} = 379$)
	Sedlo Seamount	present contribution (material: Büntzow 2011)	450	unknown
	France, Mediterranean Coast	present contribution (material: Janssen et al. 2013)	525–559 ($n = 2$, $\bar{x} = 542$)	419–447 ($n = 4$, $\bar{x} = 432$)
	Argentina	Pallares 1975	650–710 (n unknown)	430–501 (n unknow)
N. dubia	Madeira Island	present contribution	500–603 ($n = 5$, $\bar{x} = 561$)	394–416 ($n = 4$, $\bar{x} = 404$)
	British Isles	Lee and Huys 1999	626–696 ($n = 11$, $\bar{x} = 669$)	507–563 ($n = 7$, $\bar{x} = 533$)

Mediterranean Coast, marine caves near Marseille (15 m depth; present study, re-examined material from Janssen et al. 2013).

Taxonomy

Harpacticoida Sars, 1903

Normanellidae Lang, 1944

Supplement to the family diagnosis of Kihara and Huys (2009):

Maxilliped with 0–3 setae on syncoxa (see Remarks).

Normanella Brady, 1880

Type species: *Normanella dubia* Brady, 1880

Additional species: *Normanella minuta* (Boeck, 1873), *Normanella mucronata* Sars, 1909, *Normanella tenuifurca* Sars, 1909, *Normanella incerta* Lang, 1935, *Normanella similis* Lang, 1936, *Normanella reducta* Noodt, 1955, *Normanella porosa* Noodt, 1964, *Normanella bolini* Lang, 1965, *Normanella confluens* Lang, 1965, *Normanella bifida* Lee and Huys, 1999, *Normanella obscura* Lee and Huys, 1999, *Normanella pallaresae* Lee and Huys, 1999, *Normanella paratenuifurca* Lee and Huys, 1999, *Normanella sarsi* Lee and Huys, 1999, *Normanella brevispina* Lee, Montagna and Han, 2003, *Normanella chanhoi* Lee, Montagna and Han, 2003, *Normanella texana* Lee, Montagna and Han, 2003, *Normanella spinosa* Kim, Cho and Lee, 2014

Normanella pallaresae Lee and Huys, 1999

Type locality: Argentina, Mouth of the Rio Deseado.

Sampling locations of examined material: Seine Seamount, Northeast Atlantic Ocean; station #754 (33°49.1’N, 14°21.9’W), 210 m depth; station #755 (33°48.0’N, 14°22.0’W), 235 m depth; station #756 (33°46.0’N, 14°22.0’W), 178 m depth. All stations were sampled during expedition M60/1 OASIS of the German RV “METEOR” in 2003 (Christiansen and Wolff 2009) between 11/11/2003 and 05/12/2003 (re-examined material from Büntzow 2011).

Additional known localities: Station #742a (39°50.0’N, 26°17.9’W), 2875 m depth in the Northeast Atlantic Ocean, southeast of Sedlo Seamount (expedition M60/1 OASIS of the German RV “METEOR” (Christiansen and Wolff 2009) sampled between 11/11/2003 and 05/12/2003), one individual re-examined from Büntzow (2011); Ribeira Brava (32°40’15.30”N, 17°04’03.24”W), southwest coast of Madeira, Portugal, sampling date 29/04/2011, 2–3 m depth below sea level at low tide, medium to fine grained sand, mostly of volcanic origin, 1 individual; 3PP Cave (43°09.47’N, 05°36.01’W), 30 km east of Marseille, French Mediterranean coast, sampling dates 07/03/2007 and 11/03/2007, 15 m depth, six individuals (re-examined material from Janssen et al. 2013).

The examined material is deposited at the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt am Main (SMF), Germany; Specimen 1 was sampled at station #755, specimens 2, 4, and 5 at station #756, specimens 3, 6, and 7 at station # 754.

Specimen 1: male, not dissected, 1 slide, collection number SMF 37077/1.

Specimen 2: male, not dissected, 1 slide, collection number SMF 37078/1.

Specimen 3: female, dissected and mounted on 6 slides, collection numbers SMF 37079/1–6.

Specimen 4: female, dissected and mounted on 7 slides, collection numbers SMF 37080/1–7.

Specimen 5: female, dissected and mounted on 9 slides, collection numbers SMF 37081 /1–9.

Specimen 6: female, dissected and mounted on 10 slides, collection numbers SMF 37082/1–10.

Specimen 7: male, dissected and mounted on 4 slides, collection numbers SMF 37083/1–4.

Description of female:

Habitus (Fig. 3a, b). Length from anterior margin of Cphth to posterior margin of FR 459–525 μm ($n=4$, $\bar{x}$ = 494 μm; see discussion on intraspecific morphological variability below). Body slightly tapering, prosome wider than urosome. Rostrum completely defined at base, triangular with straight lateral and slightly pointed anterior margin, and with pair of sensilla, without surface areolations. Cphth strongly areolated, with pair of longitudinal ridges. Cphth and all free body somites with serrate posterior margins, several pairs of sensilla, and single tube pores as shown in Figs. 3a and b. Free body somites densely covered with minute denticles. Last thoracic and first abdominal somites forming genital double-somite. Original segmentation of genital double-somite visible dorsally and laterally, completely fused ventrally. Telson as long as preceding somite. Margin of anal operculum strongly serrated.

FR (Fig. 3d) cylindrical, twice as long as broad, with several broad spinules, 1 tube pore on dorsal surface. Each ramus with 7 setae; seta I bare, relatively short, positioned close to seta II; seta II bare; seta III bare, inserted ventro-laterally; setae IV, V and VI terminal; IV and V pinnate, fused basally; seta VI bare, slender; seta VII pinnate, with double articulation, positioned dorsolaterally at inner margin.

A1 (Fig. 4) 5-segmented, segment 3 longest. First segment with several spinules and 1 articulated, bipinnate seta at distal margin. Second segment with 9 setae (one missing in Fig. 4); 7 bare, 2 pinnate. Third segment with aes and 10 setae (one missing in Fig. 4); 5 setae bare (one articulated, one fused with aes), 5 bipinnate. Fourth segment with 1 bipinnate and 2 bare setae. Fifth segment with acrothek (1 bare and 1 bipinnate seta fused with aes) and 7 setae; 6 setae bare (three articulated), 1 bipinnate. Setal formula: 1/1; 2/9; 3/9 + (1 + aes); 4/3; 5/7 + (2 + aes).

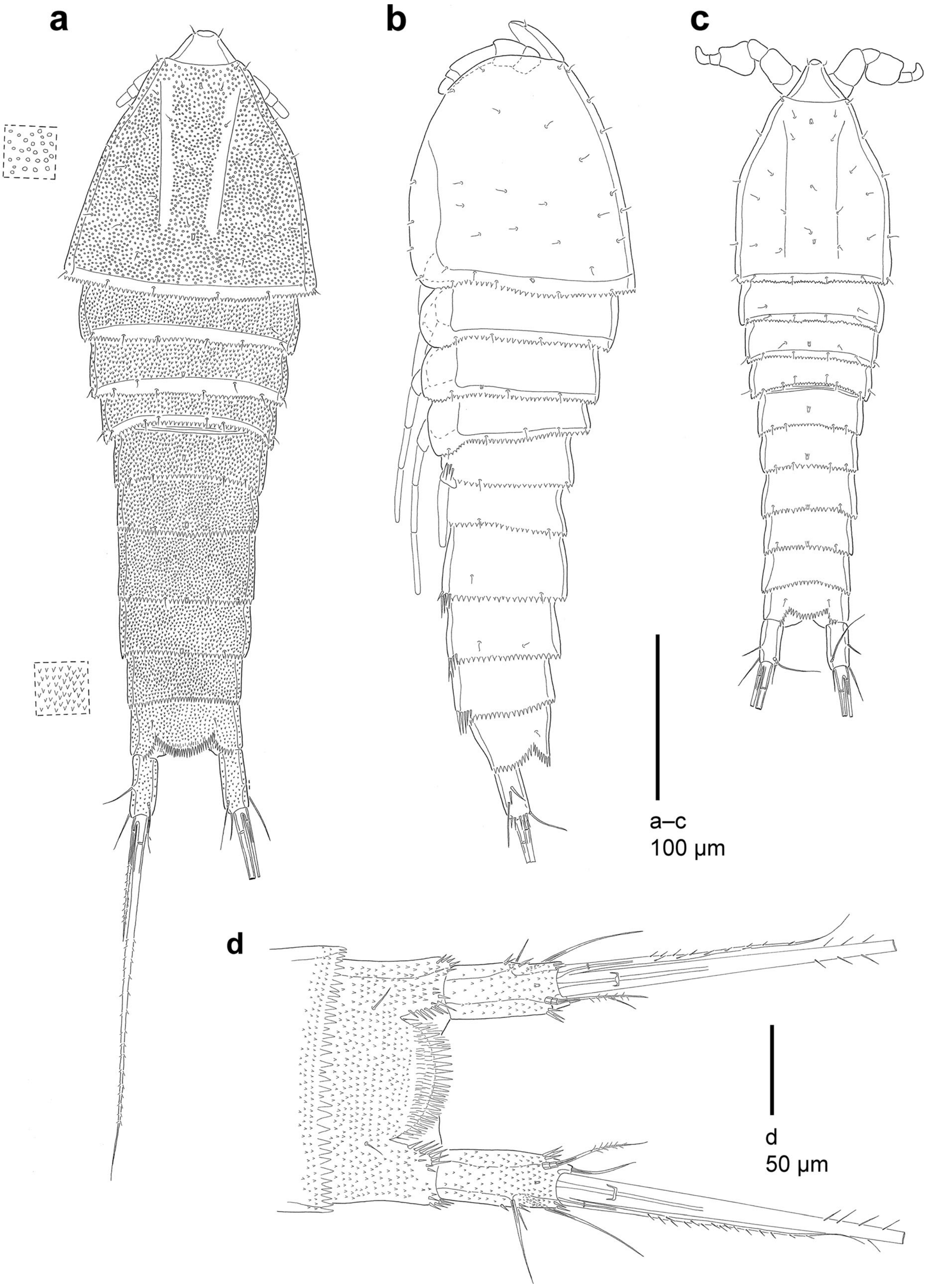

Fig. 3 *Normanella pallaresae*. **a** Female. Habitus dorsal view, examples of the areolations on the cephalothorax and denticles on the body somites shown in boxes; **b** Female. Habitus lateral view; **c** Male. Habitus dorsal view; **d** Female. FR, dorsal view. a, b and d drawn from specimen 3, c from specimen 1

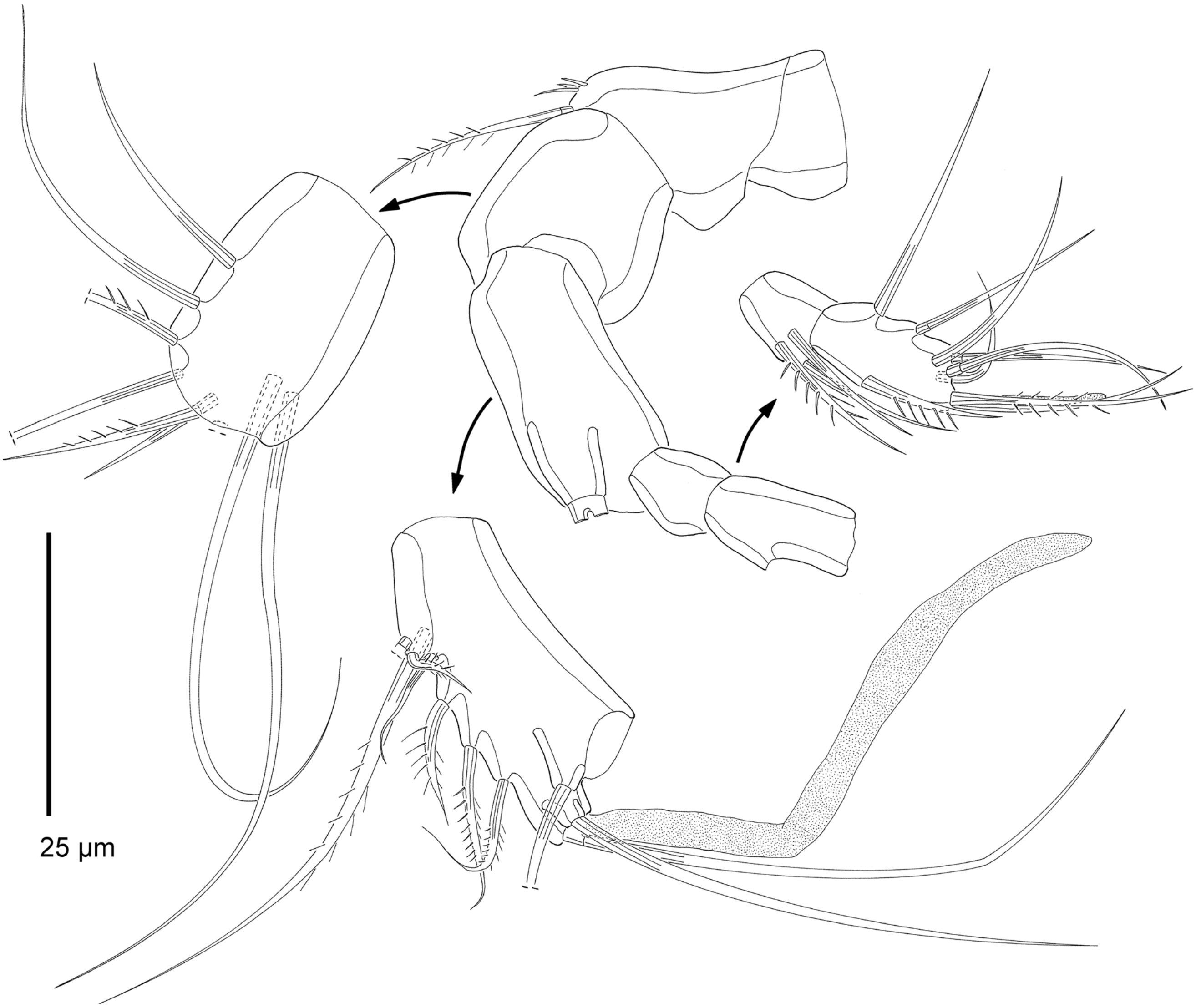

Fig. 4 *Normanella pallaresae*, female A1; shape of A1 (specimen 4), detailed drawings of the segments (specimen 6)

A2 (Fig. 5b, b*). Coxa small. Basis and proximal endopodal segment fused, forming allobasis with clear transverse suture. Abexopodal seta pinnate. Exp 1-segmented with 4 biplumose setae; two setae lateral, two apical. Enp with several rows of spinules, 2 pinnate spines subapically and 2 apically, 3 geniculated setae apically, one of which equipped with strong pinnae.

Md (Fig. 5c). Gnathobase well developed with row of spinules, several cuspidate and multicuspidate teeth on distal margin and pinnate seta. Mandibular palp biramous; basis with 2 multiplumose setae; exp 1-segmented, smaller than enp, with several long spinules and 1 biplumose seta; enp with 4 setae, 1 biplumose seta subapically, 2 biplumose and 1 bare seta apically.

Mxl (Fig. 5d). Praecoxa with few spinules at outer distal margin. Arthrite well developed with 4 setae and 7 spines; 2 bare setae on anterior surface, 7 spines and 1 plumose seta apically and 1 short seta at inner margin. Coxa with cylindrical endite bearing 1 bare and 1 pinnate seta. Basis with 1 biplumose and 1 bare seta subapically and 2 biplumose setae apically. Exp 1-segmented with 2 biplumose setae. Enp incorporated represented by 3 biplumose setae.

Mx (Fig. 5e). Syncoxa with two rows of spinules and 3 endites; proximal endite small with 1 biplumose seta; middle endite with 1 strong, pinnate spine fused to endite, 1 spine and 1 seta; distal endite bearing 2 pinnate and 1 bare setae. Allobasis forming pinnate claw, 1 accessory spine on anterior surface, 1 bare seta each posteriorly and along outer margin; enp with 3 setae (1 plumose, 2 bare).

Mxp (Fig. 5a) with 3 biplumose setae on syncoxa. Basis with 2 rows of spinules. Enp small, drawn out into pinnate claw with 2 accessory setae (both bare and slender, one short, one long).

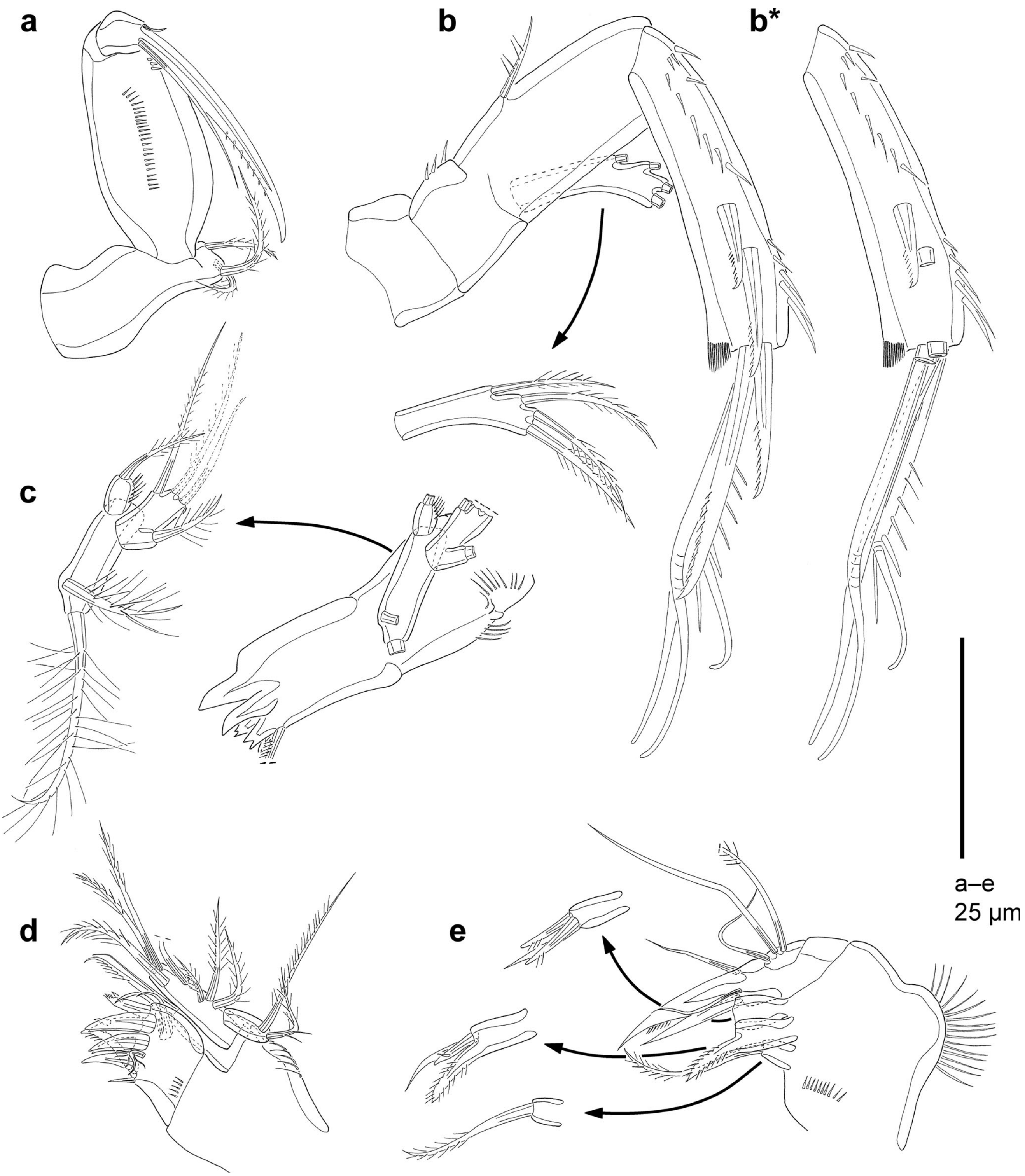

Fig. 5 *Normanella pallaresae*, female. **a** Mxp; **b** and **b*** A2 (arrow indicates detailed drawing of exp); **c** Md (arrow indicates detailed drawing of mandibular palp), dotted setae are drawn from specimen 4; **d** Mxl; **e** Mx, (arrows indicate detailed drawings of endites). a, c and e drawn from specimen 5, b and b* from specimen 4, d from specimen 6

P1 (Fig. 6a, a*). Coxa broad with several rows of spinules (as drawn from P3 in Fig. 6c). Basis with several rows of spinules and strong, bipinnate inner and outer spine. Exp 3-segmented; all segments with rows of spinules; outer spines of exp-1 and exp-2 strongly developed and bipinnate, exp-2 additionally with

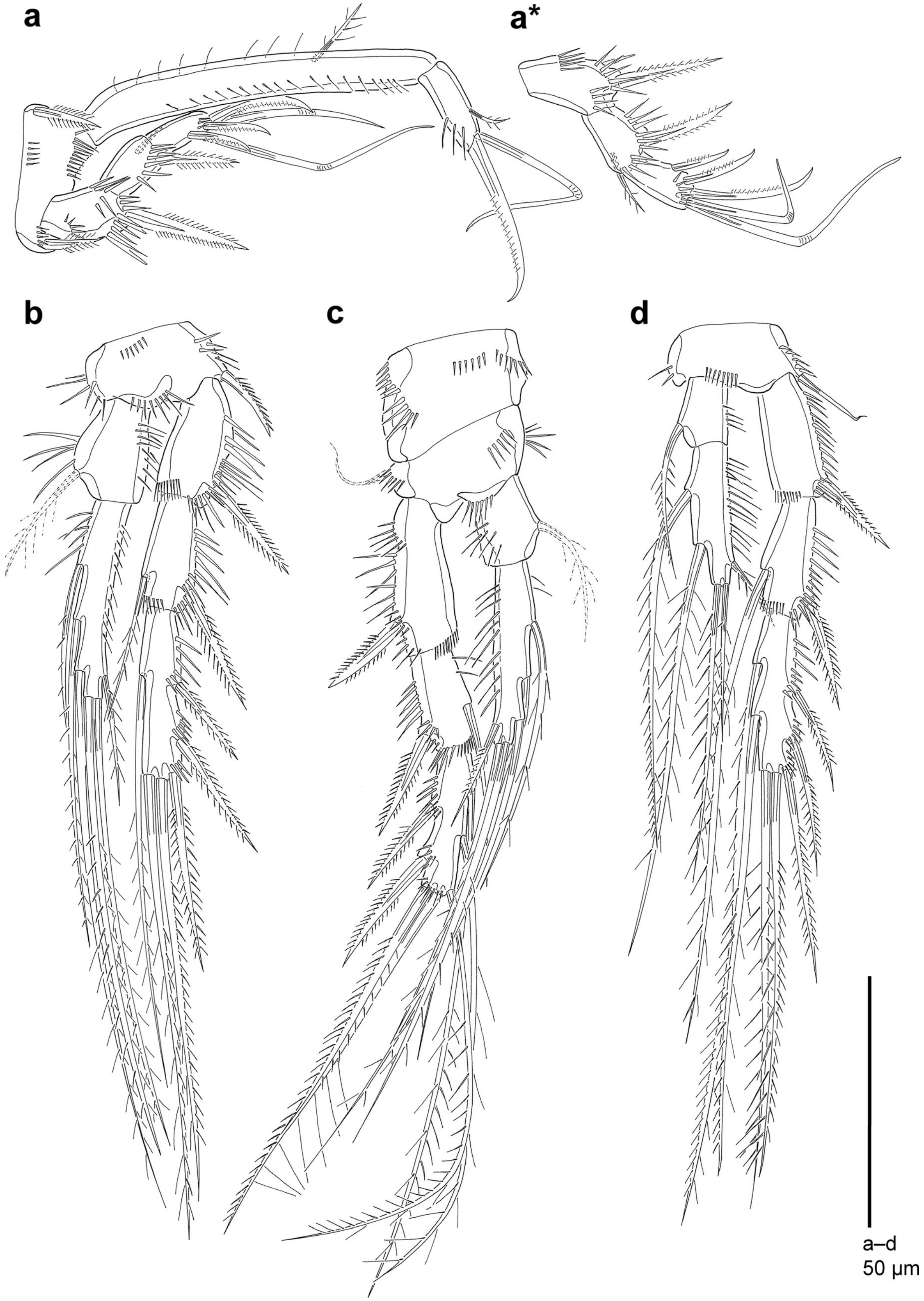

Fig. 6 *Normanella pallaresae*, female. **a** P1; **a*** P1 exp from counterpart; **b** P2, dotted seta drawn from counterpart; **c** P3, dotted setae are drawn from counterpart; **d** P4. a, a* and c–d drawn from specimen 4, b from specimen 3

biplumose inner seta; exp-3 with 3 unipinnate spines at outer margin and 2 geniculate, bare setae terminally. Enp about twice as long as exp, 2-segmented; enp-1 with 2 rows of spinules and short biplumose inner seta; enp-2 with few spinules, 1 plumose, slender, short seta subapically and 2 setae apically (one claw-shaped and pinnate, one bare and geniculated).

P2–P4 (Fig. 6b–d). Coxa broad (Fig. 6c) with several rows of spinules. Basis with several rows of spinules and outer seta, strong and pinnate in P2, slender and bare in P3 and P4. Exp 3-segmented, all segments with rows of spinules at outer and distal margins; outer spines of exp-1 and exp-2 strong and bipinnate, exp-2 additionally with biplumose inner seta (not exceeding exp-3 in P2 and P3; exceeding exp-3 markedly in P4); exp-3 with 3 bipinnate outer spines, 2 biplumose apical setae and 1 (P2) or 2 (P3–P4) biplumose inner setae. Enp 2-segmented, second segment longest, reaching middle of exp-3 (P2) or distal margin of exp-2 (P3–P4); enp-1 with several slender spinules and biplumose inner seta; enp-2 with row of slender spinules and with 3 biplumose inner setae (only 2 in P4), 2 biplumose apical setae and 1 short, biplumose outer seta. Setation of P1–P4 is summarised in Table 3.

P5 (Fig. 7a). Benps of both legs not fused, 3 tube pores at inner margin of endopodal lobe and 1 tube pore near base of exp. Basal seta bare, positioned on short setophore, each setophore and inner and outer margin of endopodal lobe with rows of spinules. Endopodal lobe with 2 pinnate and 3 biplumose setae. Exp not fused to benp, exceeding endopodal lobe, with rows of spinules and 2 pinnate and 4 biplumose setae.

GF (Fig. 7c). Copulatory pore partially covered by anterior, concave, sclerotised structure. P6 represented by small protuberance bearing 1 long, biplumose outer seta and 1 minute, bare inner seta.

Description of male:

Sexual dimorphism expressed by smaller overall body size of 375–391 μm ($n=4$, $\bar{x}$ = 379 μm; Habitus see Fig. 3c), distinct last thoracic and first abdominal somites, and shape, segmentation and/or setation of A1, P2–P4 enps, P5 and P6.

A1 (Fig. 8). 7-segmented; subchirocer with geniculation between segments 5 and 6. First segment with several spinules and 1 articulated, biplumose seta at distal margin. Second segment with 11 setae; 10 bare (two articulated) and 1 biplumose. Third segment with 7 setae; 3 bare, 3 pinnate and 1 undetermined due to damage (Fig. 8). Fourth segment very small with 1 bare and 1 pinnate seta. Fifth segment with 3 spinous processes (not visible in Fig. 8), 1 aes and 12 setae; 4 pinnate and 8 bare setae (1 fused to aes). Sixth segment with 3 spinous processes and 1 bare seta. Seventh segment with acrothek (2 bare setae fused to aes) and 6 bare setae (two with articulation). Setal formula: 1/1, 2/11, 3/7, 4/2, 5/11 + (1 + aes), 6/1, 7/6 + (2 + aes).

P2 enp (Fig. 9a). As in females except, both apical setae of enp-2 distinctly shorter than homologous female setae (compare Fig. 6b).

P3 enp (Fig. 9b, b*). Modified, enp-2 with subapical, mucroniform process, thought to be homologous with outer spine of female enp-2, both apical setae distinctly shorter than in female P3 enp-2 (compare Fig. 6c).

P4 enp (Fig. 9c). As in females except, outer apical seta of enp-2 shorter than homologous female seta (compare Fig. 6d).

P5 (Fig. 7b, b*). Benps of both legs fused, forming single, bilobed plate. Basal seta bare, positioned on short setophore covered with row of spinules. Endopodal lobe with row of spinules at inner and outer margin, 2 biplumose setae apically and 2 tube pores (1 at inner margin, 1 near exp). Exp exceeds endopodal lobe considerably, with several patches of spinules and bearing 4 biplumose setae. Intraspecific variability (3 instead of 2 setae on endopodal lobe) documented in Fig. 7b* (for discussion see section on intraspecific morphological variability).

P6 (Fig. 7b). Small protuberance bearing 3 biplumose setae.

Table 3 *Normanella pallaresae*, setation of P1–P4. In sequence, the numbers indicate outer setae, distal setae, and inner setae

	Exopod			Endopod	
	1	2	3	1	2
P1	1;0	1;1	3;2;0	0;1	0;2;1
P2	1;0	1;1	3;2;1	0;1	1;2;3
P3	1;0	1;1	3;2;2	0;1	1;2;3
P4	1;0	1;1	3;2;2	0;1	1;2;2

Remarks

All the specimens which in this study were determined as *Normanella pallaresae* differ from the diagnosis of the family Normanellidae delivered by Kihara and Huys (2009) in that they have 3 setae on the syncoxa of the maxilliped instead of 2 or less. However, as all remaining characteristics unambiguously designate these specimens as Normanellidae, we decided to amend the diagnosis of the family (see above).

All investigated individuals can be easily assigned to the genus *Normanella* as their morphology coincides with the generic diagnosis of Lee and Huys (1999). The (combined) characters which differentiate all species of *Normanella* from the remaining three genera (*Pseudocletodes* T. and A. Scott, 1893, *Sagamiella* Lee and Huys, 1999, *Paranaiara* Kihara and Huys, 2009) are: a) A2 with 1 abexopodal seta on the allobasis and 4 setae on the exp; b) Md with discrete enp and basis with 2 setae; c) Mx allobasis accompanied by 2 setae and 1 spine. Additionally, the investigated specimens we determined as *N. pallaresae* exhibited the following specific

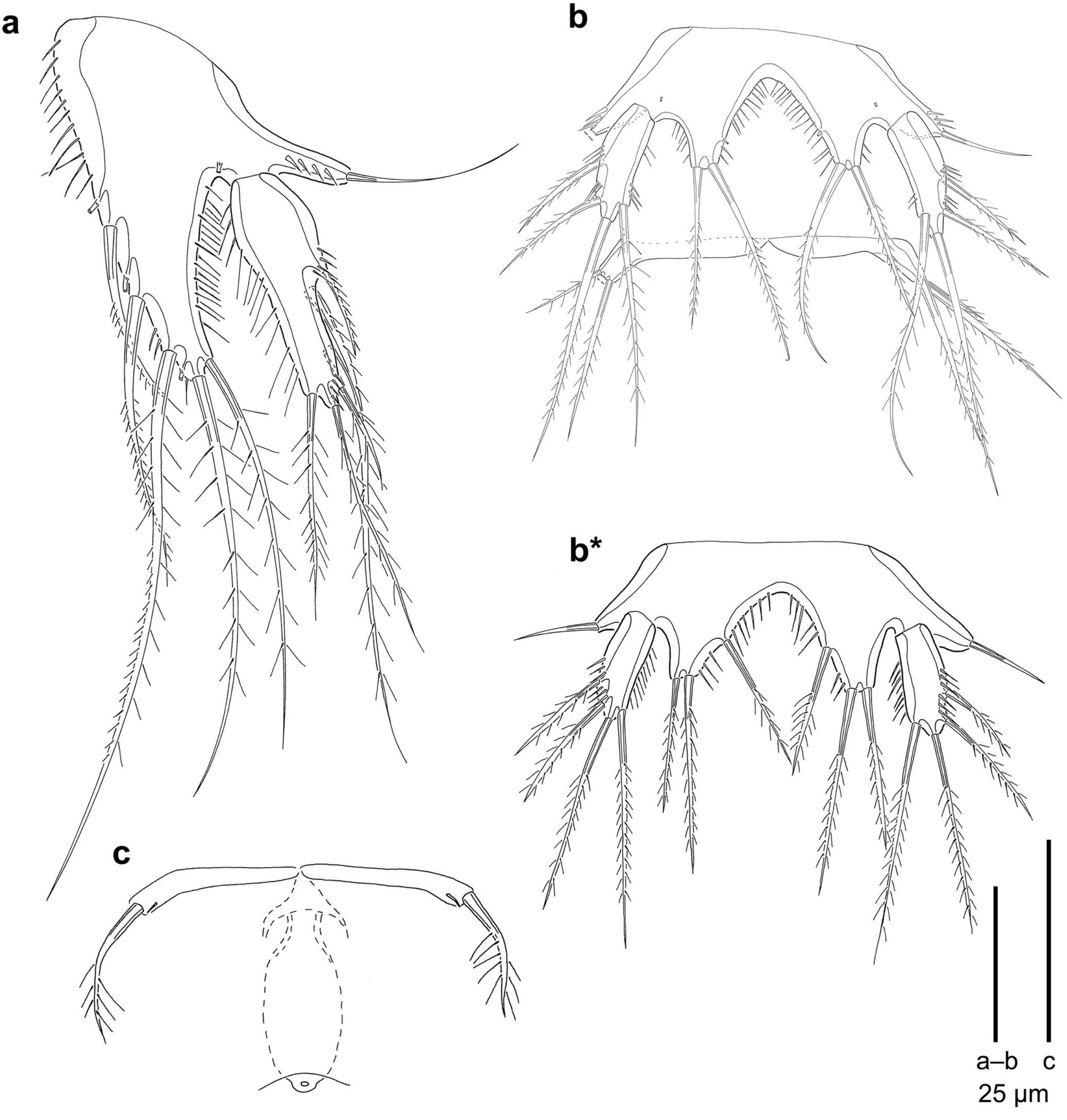

Fig. 7 *Normanella pallaresae*. **a** female, P5; **b** male, P5 and P6; **b*** variability of male P5 (benp with 3 setae at each side); **c** female, GF. a drawn from specimen 4, b from specimen 7, b* from specimen 2, c from specimen 3

combination of characters, which, among all formally described species of the genus *Normanella*, are only found in *N. pallaresae*: a) Rostrum without areolations; b) Cphth with areolations; c) ♀ antennule 5-segmented; d) plesiomorphic armature formula of swimming legs P1–P4 (Tab. 3); e) ♀ P5 baseoendopod shorter than exopod; f) furcal rami at most 2.5 times as long as maximum width; g) all setae of furcal rami with fracture plane. Finally, the investigated specimens coincide with the description of Pallares (1975),[1] only the baseoendopod of the female P5 differs, appearing to be slightly longer. However, according to our experience a certain

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[1] Pallares (1975) described individuals from the mouth of the Rio Deseado (Argentina), which she assumed to be representatives of *N. minuta*. Because of several clear differences between the documented specimens of Pallares (1975) and the original description of *N. minuta*, Lee and Huys (1999) renamed the Argentinian species in *N. pallaresae*.

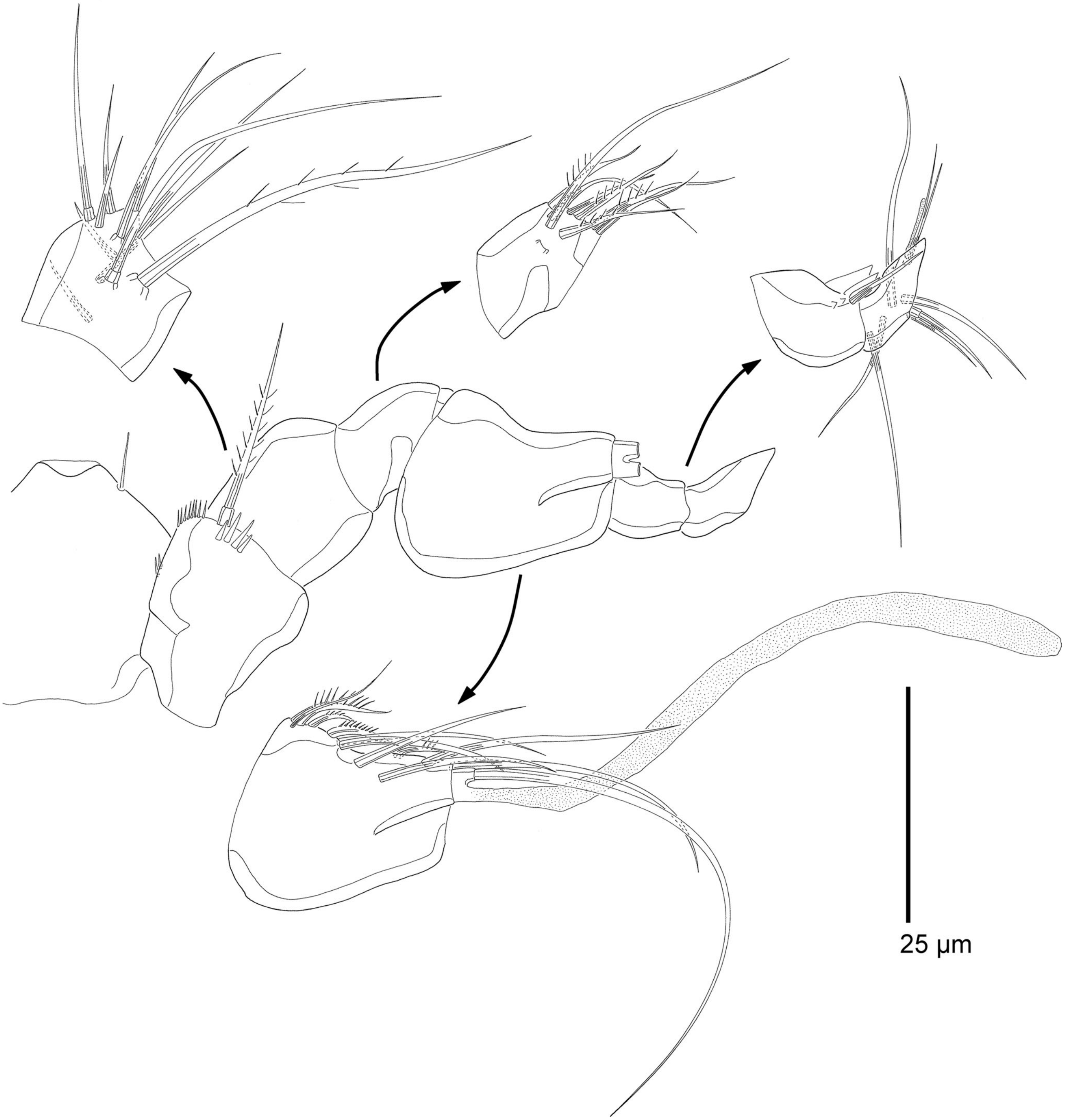

Fig. 8 *Normanella pallaresae*, male A1. Drawn from specimen 1

degree of variation may be recorded in this character due to measurement error arising from their orientation. Unfortunately, the description of *N. pallaresae* is incomplete, especially with regard to the appendages of the cephalothorax (maxillipedal syncoxa!), and the examined material of Pallares (1975) is not available. Therefore, we decided to provide the above re-description of the species based on the material studied in the present contribution.

Discussion

Do seamounts and oceanic islands act as "stepping stones" for Harpacticoida?

Many meiofauna species show a very wide, but disjunct distribution with populations separated by thousands of kilometres of deep-sea habitats. This disjunct

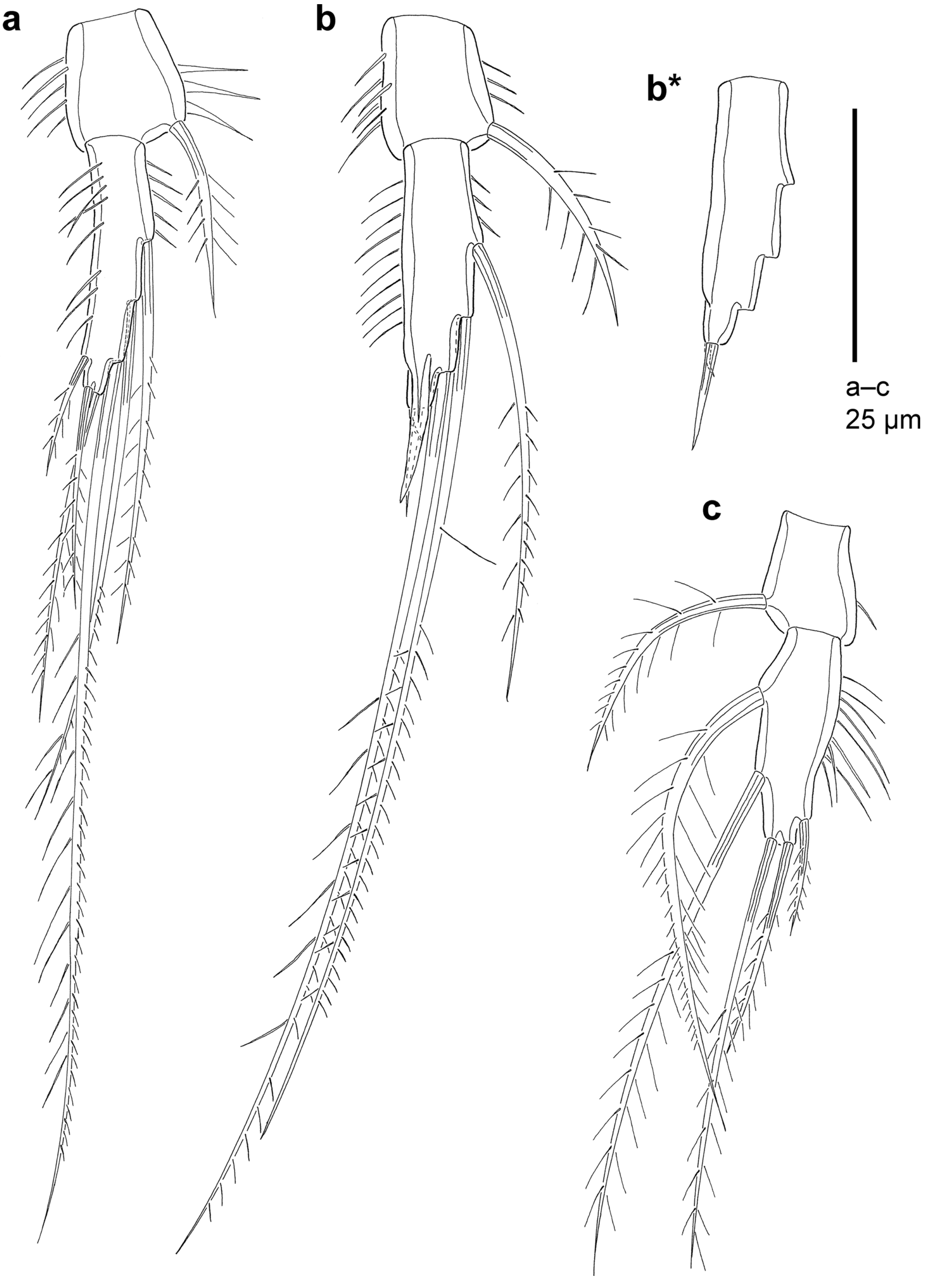

Fig. 9 *Normanella pallaresae*, male. **a** P2 enp; **b** P3 enp; **b*** detailed drawing of apical setae of P3 enp-2; **c** P4 enp. a–c drawn from specimen 7

distribution is enigmatic due to the seemingly limited dispersal potential of meiofauna organisms ("meiofauna paradox", Giere 2009) and the supposedly strong ecological barrier the deep sea represents especially for benthic species adapted to shallow-water habitats. Several mechanisms have been proposed to explain how meiobenthic organisms disperse over long distances, for example, attached to floating material, in ship ballast sands or water, in the plumage of waterfowls and drifting in the water column (Yeatman 1962; Gerlach 1977; Hagerman and Rieger 1981; Palmer 1988; Palmer and Gust 1985; Boeckner et al. 2009). Most of these hypotheses usually refer to single events and are not easily testable on a broader scale. Several studies have provided evidence that drifting appears to be a highly important dispersal mechanism for meiofaunal organisms (Hagerman and Rieger 1981; Palmer and Gust 1985; Armonies 1994; Giere 2009), but it is unlikely that suspension could be maintained over the large distances needed to cross an ocean (Giere 2009; George 2013).

Since Hubbs (1959) proposed the hypothesis that seamounts may act as "stepping stones" in the dispersal of benthic organisms, several studies have discussed this possibility for meiofauna organisms as well (George and Schminke 2002; Gad and Schminke 2004; Plum and George 2009; Büntzow 2011; George 2013; Packmor et al. 2015). A first step to test this hypothesis would be a comparison of the faunal composition of several seamounts located in a relatively small geographical area. The presence of specimens of the same species on more than one seamount would indicate potential dispersal between these seamounts. Furthermore, the hypothetical role of seamounts as "stepping stones" could be supported if meiofauna species showing a disjunct distribution were found on seamounts or oceanic islands between the known disconnected populations. In the case of Harpacticoida, initial evidence for a faunal link between different seamounts (Great Meteor, Seine, and Sedlo Seamounts) was recorded by Plum and George (2009) and Büntzow (2011). These authors recorded previously undescribed species on Great Meteor and Sedlo Seamounts (Plum and George 2009; Büntzow 2011) and on Seine and Sedlo Seamounts (Büntzow 2011).

The results of the present contribution support the "stepping stones" hypothesis as well: All three species of Normanellidae we found at the coast of Madeira (*Normanella minuta*, *N. dubia*, and *N. pallaresae*) were already described and exclusively reported from shallow-water habitats. The detection of these three species on the coast of Madeira extends their known geographical distribution remarkably. Previously, *N. dubia* was only known from the British Isles (Lee and Huys 1999). *Normanella minuta* is widely distributed in Northwest Europe, and was also detected in the Black Sea and on the east coast of North America (see the updated review of the known geographical distribution above). Records from the latter locations are suspected of being neither reliable, nor probable (Lee and Huys 1999; p. 231), but all data were included in the updated list of known localities for *N. minuta* because the original material has not been re-examined.

Normanella pallaresae was formerly only known from the mouth of the Rio Deseado on the Argentinian coast (Pallares 1975). This study considerably extends its distribution, *N. pallaresae* is now also recorded in shallow-water on Madeira (2–3 m depth; 1 individual), on the summit of Seine Seamount (178–235 m depth; frequently recorded), in a shallow marine cave in the Mediterranean (10 m depth; several individuals) and in bathyal sediments southeast of Sedlo Seamount (2875 m depth; 1 individual).

The amphiatlantic distribution of *N. pallaresae* and *N. minuta* is confirmed by the current study. The detection of *N. pallaresae* on Seine Seamount and on Madeira links the amphiatlantic populations of this species on the Argentinian coast and in the Mediterranean. The record of *N. minuta* on Madeira would link its potentially disjunct known amphiatlantic distribution (although the North American record needs to be validated). These findings together with the detection of the typical shallow-water species *N. dubia* on Madeira provide evidence to support the hypothesis that elevations of oceanic seafloor might provide "stepping stones" in the dispersal of at least some shallow-water meiofauna species.

A recent investigation of the Paramesochridae (Harpacticoida) recorded on Madeira, Porto Santo and the adjacent seamounts (Packmor et al. 2015), supports the findings of this study. Several species of Paramesochridae which were formerly known exclusively from inshore shallow-water habitats were recorded on Madeira Island and on one or more of the Atlantic Seamounts. Furthermore, for two of the investigated species these new records linked their formerly disjunct, amphioceanic distribution (Packmor et al. 2015).

To help complete our understanding of meiofaunal biogeography future investigations to study gene flow between meiofauna populations from different oceanic elevations and shallow-water habitats are needed.

Eurybathic distribution of *N. pallaresae*

The Normanellidae currently comprises four genera and 23 valid species (22 summarised in Kihara and Huys 2009, one additional species described by Kim et al. 2014). The genera

Normanella Brady, 1880 and *Sagamiella* Lee and Huys, 1999 comprise 19 and two species, respectively, while the genera *Paranaiara* Kihara and Huys, 2009 and *Pseudocletodes* T. and A. Scott, 1893 are monotypic. All but three species of the Normanellidae are exclusively known from shallow-water habitats (Lee and Huys 1999; Lee et al. 2003; Kim et al. 2014). The only exceptions are *Normanella bifida* Lee and Huys, 1999, which was found in 626 m depth in samples from the Sagami Bay, Japan (Lee and Huys 1999) and both species of *Sagamiella* (*S. aberrans* (Bodin, 1968), Gulf of Biscay, 1200 m depth; *S. latirostrata* Lee and Huys, 1999, Sagami Bay, Japan, 831 m depth), which were found in the middle and deep bathyal. Where deep-sea studies of Harpacticoida have recorded Normanellidae usually only single specimens of unknown species are found (George and Schminke 2002; Shimanaga et al. 2004; Gheerardyn et al. 2009; George et al. 2014). Thus, we conclude that for most of the described shallow-water species of Normanellidae, the deep sea constitutes an ecological barrier. Conversely, as yet none of the described deep-sea species of Normanellidae have been recorded in shallow-water habitats.

Normanella pallaresae is the first species of the family Normanellidae which exhibits an extreme eurybathic distribution.[2] It is recorded over a depth range of almost 2900 m and survives the associated strong differences in biotic and abiotic variables such as light availability, food supply, temperature, sediment composition and pressure (a range of almost 290 bar). Little is known about eurybathy in harpacticoid copepods, and only very few extreme eurybathic species are known so far (Lang 1948; Koller and George 2011; Pointner et al. 2013). One example of an extreme eurybathic harpacticoid copepod is *Emertonia clausi* Pointner and Veit-Köhler, 2013 (in Pointner et al. 2013), a species of the family Paramesochridae. This species has been recorded over a depth range of 235–5415 m, known localities are the Angola and Guinea Basins (Atlantic; 5389–5415 m depth and 5060–5167 m depth, respectively), the Pacific Nodule Province (4980 m depth), the base, slope, and summit of Great Meteor Seamount (292–4005 m depth; Pointner et al. 2013) and the summits of Seine and Sedlo Seamounts (235 m depth and 773–886 m depth, respectively; Packmor et al. 2015). Although both *N. pallaresae* and *E. clausi* are extreme eurybathic species, their distribution differ markedly. Like for several Argestidae Por, 1986 (Menzel et al. 2011), the deep sea does not appear to constitute a barrier for the dispersal of *E. clausi*, which is found in several deep-sea basins and shows an amphioceanic distribution. Conversely, despite a number of deep-sea studies in the Atlantic Ocean, not a single specimen of *N. pallaresae* has been recorded from abyssal depths (Gheerardyn et al. 2009; Büntzow 2011; George et al. 2014). This suggests that abyssal depth may well constitute a barrier for the dispersal of *N. pallaresae*.

Intraspecific morphological variability of the investigated species of Normanellidae

All studied specimens of *Normanella dubia*, *N. minuta* and *N. pallaresae* from Madeira as well as the specimens of *N. pallaresae* from Seine Seamount, the adjacent deep sea of Sedlo Seamount (both material from Büntzow (2011)) and from a marine cave on the Mediterranean Coast of France (material from Janssen et al. 2013) show a smaller overall body size than their conspecifics from European or South American inshore records (Table 2). While the female individual of *N. minuta* found on Madeira was only slightly smaller than its reported conspecifics from other locations, the body size of all investigated specimens of *N. pallaresae* differs remarkably from individuals described in former publications (18–23 % smaller in the Mediterranean than in the original description, 23–34 % smaller on Seine and Sedlo Seamount and 38 % smaller on Madeira; Table 2). The same applies for the investigated specimens of *N. dubia*. The Madeiran individuals are 10–25 % smaller than the mean body size given in the species re-description (Lee and Huys 1999; Table 2). As opposed to this, Lee and Huys (1999) recorded in their review of the genus *Normanella*, that there was a clear consistency in the body size of *N. dubia* between the original description and their own study. However all individuals considered in that publication originate from the same geographical region (United Kingdom and Ireland; Lee and Huys 1999). Because of different climates and specific geographical peculiarities, there are distinct differences in the environmental conditions of the study areas of the present contribution and the additional known locations of this species, thus morphological variability can be expected. Morphological variability, especially of body size, had been reported for other species of Harpacticoida (Seifried et al. 2007; George 2008; Seifried and Martínez Arbizu 2008; Gheerardyn and Veit-Köhler 2009; Packmor et al. 2015). We assume, therefore, that the body size of Harpacticoida is likely to be strongly influenced by biotic and abiotic variables (such as nutrient and food availability, sediment composition, predation pressure, and temperature), as has been indicated by several field and laboratory studies of other copepod taxa (Carter et al. 1983; Klein Breteler and Gonzalez 1988; Klein Breteler et al. 1990; Escribano and McLaren 1992; Tsuda et al. 2001; Kobari et al. 2003; Garzke et al. 2015). Therefore, we consider the reported differences in size as an intraspecific variability of the investigated species.

One additional character with intraspecific variability in *N. pallaresae* was the number of setae on the benp of the male P5. One of the 19 male specimens of *N. pallaresae* examined

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[2] the term "extreme eurybathic" is used here to express a depth distribution range of more than 1000 m

from Seine Seamount showed three instead of two setae on the benps of P5 (Fig. 7b*). This kind of variability is not unusual in Normanellidae and has been documented for other species of the family. In their re-description of *Normanella tenuifurca* Sars, 1909 Lee and Huys (1999) documented the P5 of a male with aberrant setation; this male showed three and five setae on the benps of the P5 instead of two setae each. Moreover the only male paratype of the type material of *Normanella sarsi* Lee and Huys, 1999 shows two setae at the left and three setae at the right benp of the P5.

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