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ORIGINAL PAPER

Description of a new species of *Neoargestes* Drzycimski, 1967 (Copepoda, Harpacticoida, Argestidae) from the Clarion Clipperton Fracture Zone (Pacific Ocean), with remarks on the systematics of the genus

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Abstract

Neoargestes laevis sp. nov. (Copepoda, Harpacticoida, Argestidae), the third species of the genus, is described from the Clarion Clipperton Fracture Zone (Pacific Ocean), and a re-description of the holotype of *Neoargestes incertus* Becker, 1979 is provided. The generic diagnosis of *Neoargestes* Drzycimski, 1967 is amended and its allocation to Argestidae is confirmed. The monophyly of *Neoargestes* is recognized by six autapomorphies: transformation of the mandibular gnathobase into a strong masticating apparatus with a broad front, reduction in size of the first endopodal segment in P2–P4, and reduction in size of the P5 baseoendopod and exopod. The presence of 3-segmented endopods in P2–P4 in *Neoargestes* points to a rather basal position of the genus within Argestidae. Its affinities to Argestinae, *Bodinia* George, 2004 and *Odiliacletodes* Soyer, 1964 as well as its intrageneric systematics are briefly discussed.

Keywords Biodiversity · Deep Sea · Meiofauna · Taxonomy · Deep-sea mining

Introduction

Representatives of the family Argestidae Por, 1986 show a world-wide distribution (George 2004) and form one of the dominant groups of meiobenthic deep-sea Harpacticoida (George et al. 2014; Rose et al. 2005). To date, neither a clear family diagnosis nor an unambiguous phylogenetic characterization of Argestidae has been available (Boxshall and Halsey 2004). This has resulted in the exclusion and subsequent re-allocation of genera (e.g., *Argestigens* Willey, 1935 was excluded from Argestidae by Huys et al. (1996), re-allocated to Argestidae by Wells (2007), and excluded again by Huys et al. (2009)), and in rather tentative allocations of genera to Argestidae (e.g. *Austrocletodes* Pallares, 1979 by Fiers (1987); *Argestoides* Huys and Conroy-Dalton, 1997 by Huys and Conroy-Dalton (1997); *Bodinia* George, 2004 by George (2004)). Huys and Conroy-Dalton (1997) and Huys et al. (2009) noted that family boundaries of Ameiridae and Argestidae are not well defined, and molecular analyses indicate that Argestidae may be paraphyletic, encompassing a monophyletic Ameiridae as the terminal clade (Huys et al. 2009). Nonetheless, George (2004, 2008, 2011) as well as Corgosinho and Martínez Arbizu (2010) listed a series of putative morphological apomorphies indicating the monophyly of Argestidae, and George (2011) characterized the monophyletic subfamily Argestinae Por, 1986.

To further elucidate the phylogeny of Argestidae, the description of new species may provide valuable phylogenetic information. During a study of the harpacticoid copepods from an area within the Clarion Clipperton Fracture Zone

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(Pacific Ocean) licensed for the exploration of polymetallic nodules, a single female was found of a new representative of the genus *Neoargestes* Drzycimski, 1967. This genus was established by Drzycimski (1967) to include *Neoargestes variabilis* Drzycimski, 1967 found in muddy sediments in Husnesfjorden, western Norway at a depth of 520 m. Becker (1979) added a second species, *Neoargestes incertus* Becker, 1979, described from a single female collected in the Iberian deep sea at a depth of 3820 m. Since then, *Neoargestes* has been reported in a number of deep-sea ecological studies: the Slope of Sergipe, northeast of Brazil, Atlantic Ocean (Vasconcelos 2008); the Pacific Nodule Province, northeast Pacific Ocean (Mahatma 2009); the Kuril and Ryukyu regions, western Pacific Ocean (Kitahashi et al. 2014); and the Porcupine Abyssal Plain, northeast Atlantic Ocean (V. Kalogeropoulou, personal communication). While these findings confirm a wide distribution of the genus, they provide no additional species level information.

Drzycimski (1967) included the genus *Neoargestes* into Cletodidae T. Scott, 1905. Por (1986) subsequently revised the Cletodidae and established the family Argestidae to encompass *Neoargestes* and 13 other genera. The primitive setation and segmentation of the swimming legs of *Neoargestes* suggests that this genus occupies a rather basal position within Argestidae (cf. Drzycimski 1967; Becker 1979). A revision of *Neoargestes* will help to clarify the phylogeny of the genera within the Argestidae and to define the monophyletic status of *Neoargestes*. A description of the new species, as well as the re-description of *N. incertus* and remarks on the systematic position of *Neoargestes* are presented herein.

Material and methods

The holotype of the new species of *Neoargestes* was collected with a multicorer during expedition GSRNOD15A to the Global Sea mineral Resources (GSR) exploration area in the Clarion-Clipperton Fracture Zone (CCFZ, Pacific Ocean) in September–October 2015. It has been deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium; labeled COP). More details on sample processing and environmental data can be found in Pape et al. (2017).

Additional material of the new species and of *Neoargestes incertus* was collected from the Porcupine Abyssal Plain (NE Atlantic Ocean) during cruises RRS Challenger 135, and RRS Discovery 226 and 229. For detailed sampling and sample treatment information, see Kalogeropoulou et al. (2010). This material has been deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany.

Specimens were dissected under a dissecting microscope, mounted in glycerine, and preparations were sealed with transparent nail varnish. All drawings were made using a drawing tube on a Leica DMLB microscope equipped with differential interference contrast (max. magnification × 1000). The descriptive terminology used in the text is adopted from Huys et al. (1996). Abbreviations are A1, antennule; A2, antenna; aes, aesthetasc; benp, baseoendopod; cphth, cephalothorax; exp, exopod; enp, endopod; exp(enp)-1(2,3) for the proximal (middle, distal) segment of the respective ramus; FR, furcal rami; GF, genital field; P1–P6, first to sixth legs; md, mandible; mxl, maxillule; mx, maxilla; and mxp, maxilliped.

Results

Systematics

Family Argestidae Por, 1986

Genus *Neoargestes* Drzycimski, 1967

Type species: *Neoargestes variabilis* Drzycimski, 1967

Other species: *Neoargestes incertus* Becker, 1979; *Neoargestes laevis* sp. nov.

Generic diagnosis (females only; males unknown)

Body cylindrical, ~400–1000 μm long, distinction between prosome and urosome inconspicuous. Cphth and body somites smooth. Rostrum small, fused to cphth; the latter approximately one-fourth of total body length. Genital double-somite, subdivided by (dorso-)lateral sutures. Telson squarish, as long as or slightly longer than preceding somite; anal operculum smooth. FR squarish to almost three times longer than wide, set wide apart, with seven setae. A1 6–7-segmented, with bare and pinnate setae/spines, aesthetascs on 4th and last segments. A2 with allobasis, or basis and enp-1 not completely fused; exp small, 1-segmented, with 1–2 setae. Mandibular gnathobase short, with broad masticating front; palpus 2-segmented, basis elongated, with 1 strong pinnate seta and at most 1 accompanying small seta; enp 1-segmented, with 5 setae; exp absent. Mxl with small basis; enp and exp absent or each represented by up to two setae. Mx with two endites (both Drzycimski (1967) and Becker (1979) erroneously interpreted the basis as third endite), distal endite with one very strong spine, basis with claw and one additional spine or seta; enp small, carrying or being represented by 1–2 setae. Mxp prehensile; syncoxa with several spinules, and 1–2 pinnate setae; basis with spinules; enp small, with long claw and 1–2 bare setae. Coxae of swimming legs larger than bases; endopodal and exopodal rami displaced towards outer margin of basis. P1 not prehensile, with 3-segmented exp and 2–3-segmented enp; exp-1 without inner seta, exp-2 with inner

seta, exp-3 with 3 outer spines and 2 apical setae. P2–P4 with 3-segmented rami; endopods shorter than exopods; enp-1 smallest; exp-3 with 3 outer spines. P5 small, with reduced benp bearing 1–3 setae; exp small, distinct or fused to benp, with 3–4 setae. GF represented by single gonopore; P6 represented by one seta and two tube pores, or two setae.

Neoargestes incertus Becker, 1979

Material examined. Holotype female, Cop. No. 1077; deposited in the Zoologisches Museum der Christian-Albrechts-Universität in Kiel, Germany. The material was collected on 19 March 1970 by K.-H. Becker during cruise M19 of German RV METEOR to the Iberian deep sea (Becker 1979). Additional material from the Porcupine Abyssal Plain (NE Atlantic Ocean): one female (body length including FR: 1094 μm) from station 13077#24, coordinates 48° 49.97′ N/16° 30.39′ W, 4844 m depth, collected in March 1997 during cruise RRS Discovery 226, slide reference 13077#24#4-5(6); one female (body length including FR: 1009 μm) dissected on three slides, from station 13200#1, coordinates 48° 49.98′ N/16° 30.00′ W, 4843 m depth, collected in July 1997 during cruise RRS Discovery 229, slide reference 13200#1#2-3(1) (Kalogeropoulou 2014). This material is deposited in Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany.

Type locality. Iberian deep sea, station #263, 37° 44′ N/10° 31′ W; depth 3820 m.

Re-description of female. Habitus (Fig. 1a, b) cylindrical. Cphth about one-fourth of total body length. Whole body with smooth, weakly sclerotized integument, with pattern of sensilla and pores as figured. No clear distinction between prosome and urosome, the latter slightly tapering posteriorly. Second and third urosomites fused to form genital double somite, original segmentation indicated by a weak dorsolateral chitinous bar. Rostrum small, triangular, fused to cphth. Posterior margin of cphth and all somites with broad, smooth hyaline frill, margin not denticulate. Genital double-somite, and fourth and fifth urosomites with row of spinules ventrally near posterior margin.

Telson (Figs. 1a, b and 2d) slightly broader than long, with row of ventral spinules and few spinules near posterior margin. Anal operculum with smooth margin, weakly developed, flanked by pair of sensilla.

FR (Fig. 2a–c) about 1.5 times as long as wide, smooth, with seven setae. Seta I very small, inserted next to seta II; seta III with two spinules at base; seta I, II, III, and VII inserted subapically; seta III and VI subequal in length; seta IV and V longest (seta V, 746 μm long), inserted apically, not fused; seta VI inserted apically; dorsal seta VII close to inner margin, triarticulated at base. Hyaline tube pore near middle of ventral surface and pore at one-third of outer margin.

A1 (Fig. 2f–h) seven-segmented. Third segment longest, with one bi-articulated seta. Second segment slightly shorter than third. Fourth segment with aes (length not discernible). Fifth segment smallest. Seventh segment with slight suture; six setae bi-articulated at their bases, and aes, fused to one seta. Setal formula: 1/1; 2/8; 3/8; 4/4 + aes; 5/2; 6/3; 7/9 + (1 + aes).

A2 (Fig. 3a). Coxa short, with some fine spinules. Basis and enp-1 partially fused, both with some fine spinules along abexopodal margin, abexopodal seta absent. Enp-2 with strong inner spinules and slender subapical outer spinules, two bipinnate lateral spines, and six apical elements: two bipinnate inner spines, two geniculate setae, and one geniculate outer seta bearing long pinnules near geniculation and fused basally to small outermost slender seta. Exp one-segmented, bearing two setae.

Md (Fig. 3b). Short gnathobase, with broad masticating front and tooth-like projection. Basis of mandibular palp with one strong pinnate seta and one slender, small and bare seta. Enp 1-segmented, with five bare setae. Exp absent.

Mxl (Fig. 3c–g). Praecoxal arthrite (Fig. 3c, d) with seven apical spines, three of which strongly unipinnate, and two bare surface setae. Coxa (Fig. 3e, f) drawn out into strong and blunt claw, with six setae and a row of short spinules at its base. Basis (Fig. 3g) with three apical setae. Enp and exp each represented by two setae.

Mx (Figs. 4a and 5a). Syncoxa with two endites. Proximal endite small and bulbous proximally, with two fused setae. Distal endite with one strong unipinnate spine fused to endite, and two slender setae. Basis with unipinnate claw (fused to basis) and one additional seta. Enp 1-segmented, small, bearing two bare setae.

Mxp (Fig. 4b) prehensile. Syncoxa with sparse short inner spinules and two apical setae, one of which plumose, thick and very long. Basis with long, slender outer spinules, and shorter medial inner spinules. Enp produced into long claw with two strong pinnules, and two bare setae at base of claw, one of which approximately same length as claw.

P1 (Fig. 4c). Coxa rectangular in shape, slightly broader and larger than more triangularly-shaped basis. Basis with inner and outer bipinnate spines subequal in length. Coxa and basis with several rows of spinules. Exp and enp 3-segmented, subequal in length. Exp-1 without inner seta. Exp-2 with short, inner seta. Exp-3 with three bipinnate outer spines, one outer terminal spine and one inner terminal seta. Enp-1 with inner seta, bearing short row of pinnae near tip. Enp-2 with one bipinnate inner seta. Enp-3 with two bipinnate terminal setae, and one bipinnate outer spine.

P2–P4 (Figs. 5b, c and 6a). Exp and enp 3-segmented. Intercoxal sclerites with three strong spinules on each side. Coxa rectangular, distinctly larger than basis. Basis

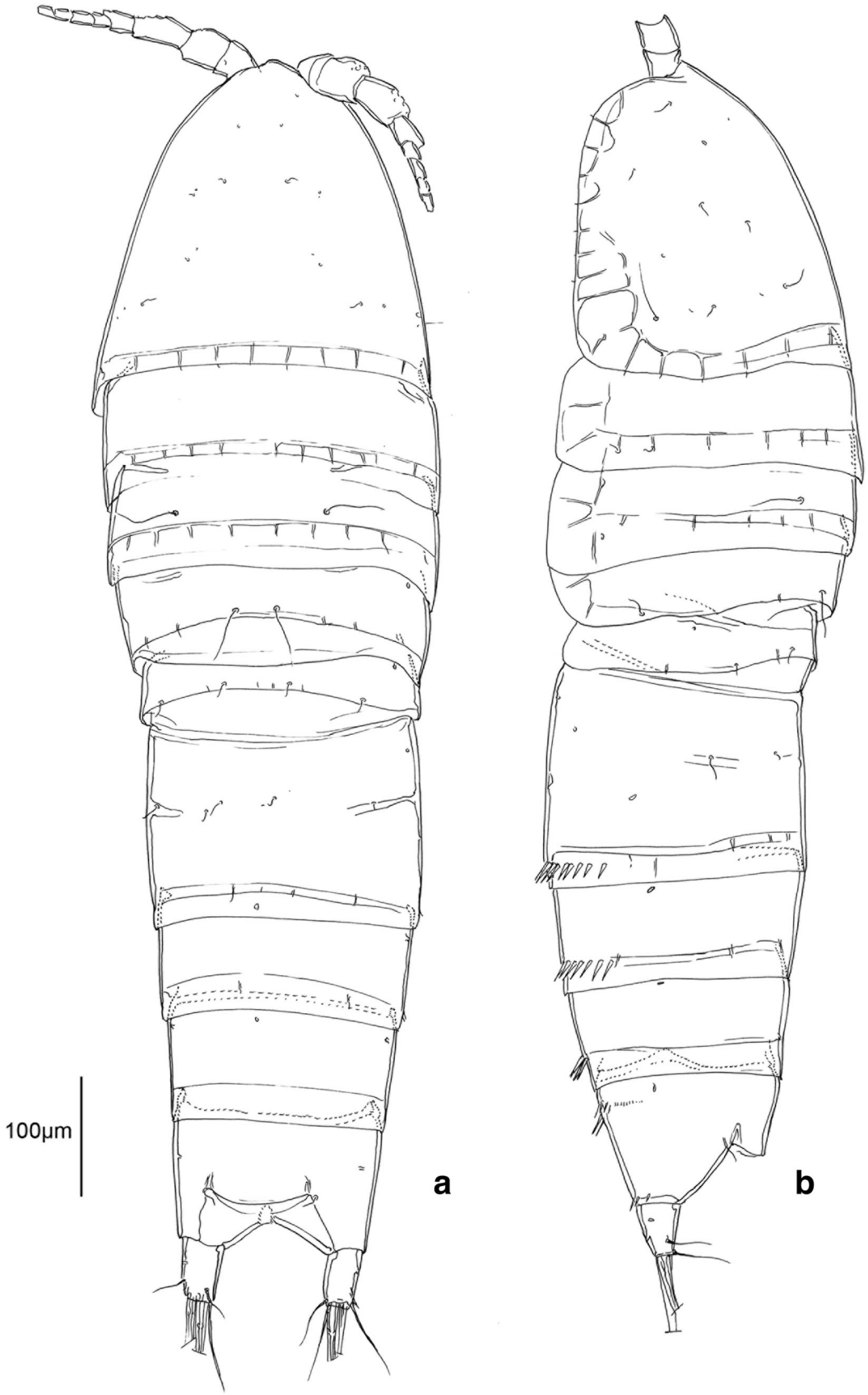

Fig. 1 *Neoargestes incertus.* Female from Porcupine Abyssal Plain. **a** Habitus, dorsal; **b** Habitus, lateral

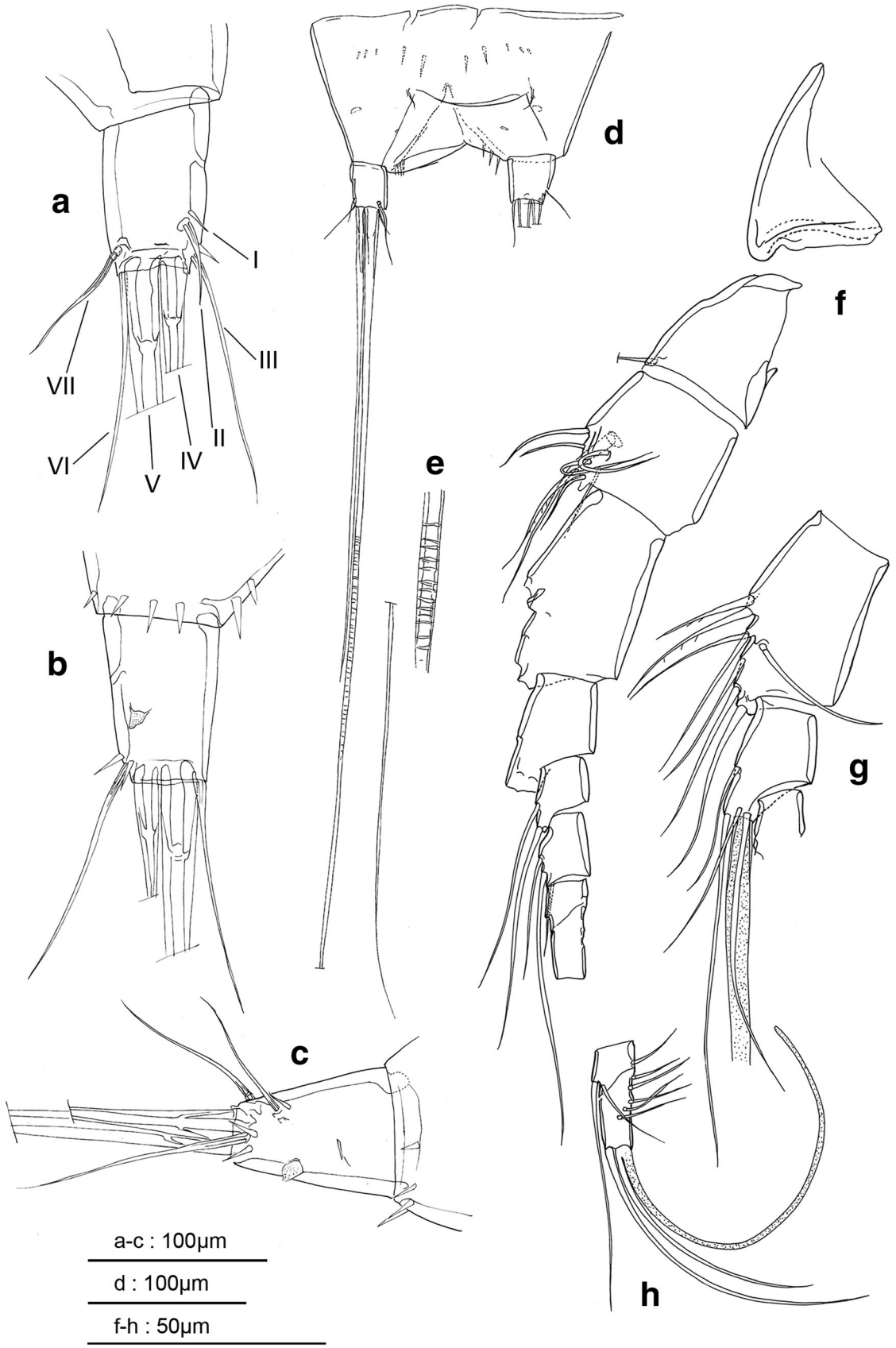

Fig. 2 *Neoargestes incertus*. Female from Porcupine Abyssal Plain. **a** Right furcal ramus, dorsal (furcal setae numbered I–VII); **b** Right furcal ramus, ventral; **c** Right furcal ramus, lateral. Female holotype; **d** Telson and furcal rami; **e** Detail of middle part of furcal seta V; **f** Rostrum and left antennule, dorsal (setation of segments 3, 4, and 7 omitted); **g** Left antennule, segments 3 and 4; **h** Left antennule, segment 7

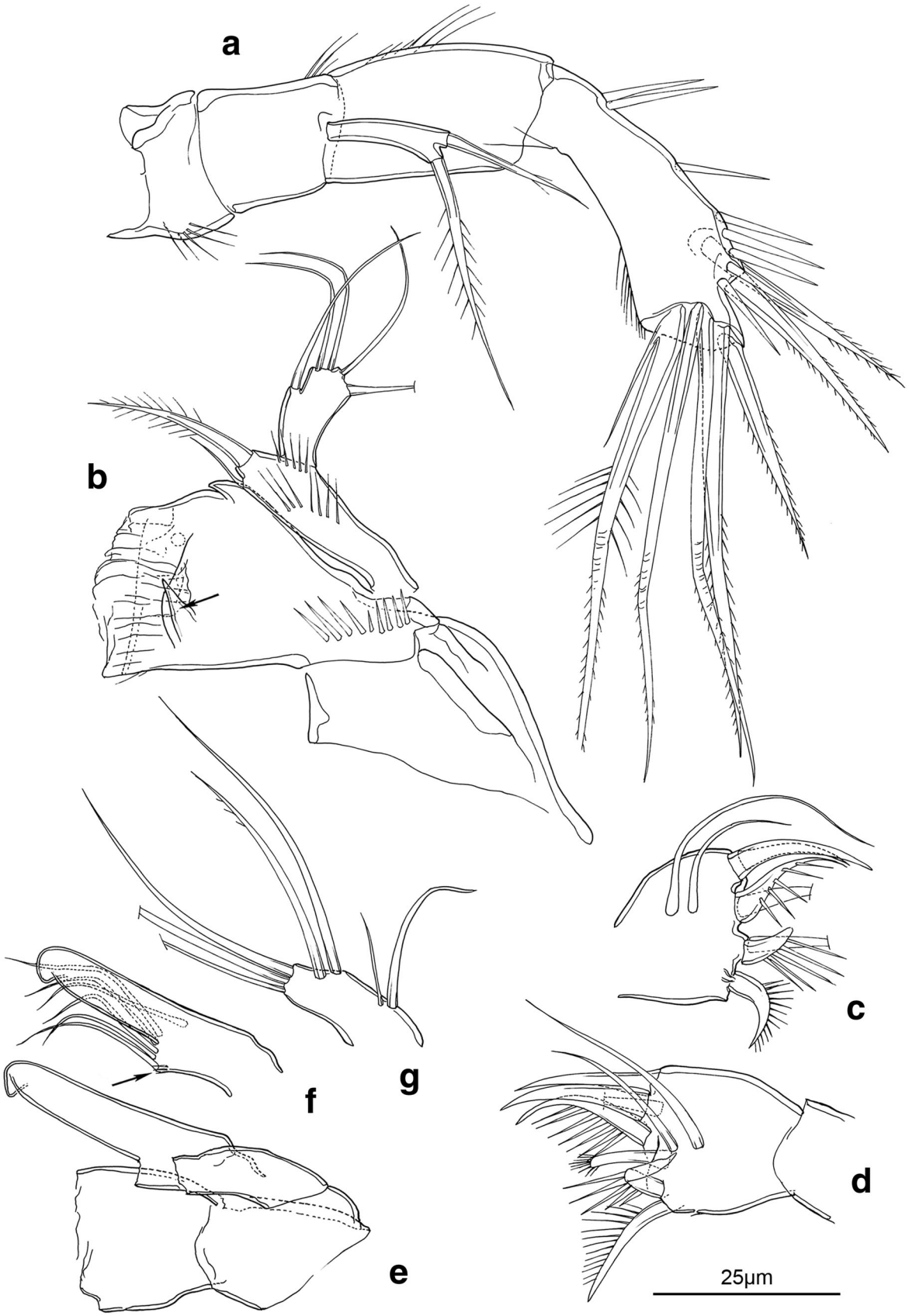

Fig. 3 *Neoargestes incertus.* Female holotype. **a** Antenna; **b** Mandible (tooth-like projection on gnathobase arrowed); **c**–**g** Maxillule (short spinule row indicated by arrow)

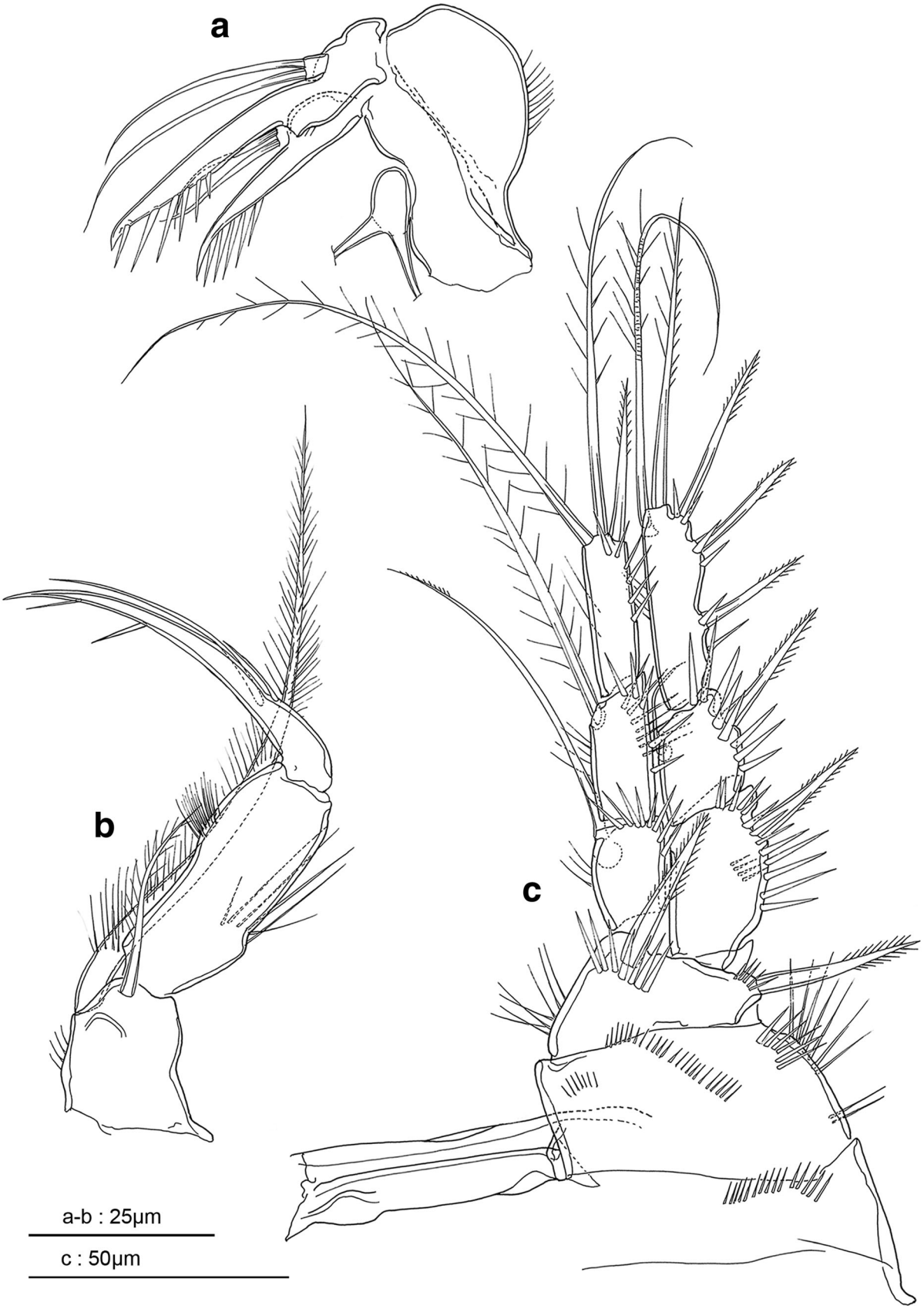

Fig. 4 *Neoargestes incertus*. Female holotype. **a** Maxilla; **b** Maxilliped; **c** P1, anterior

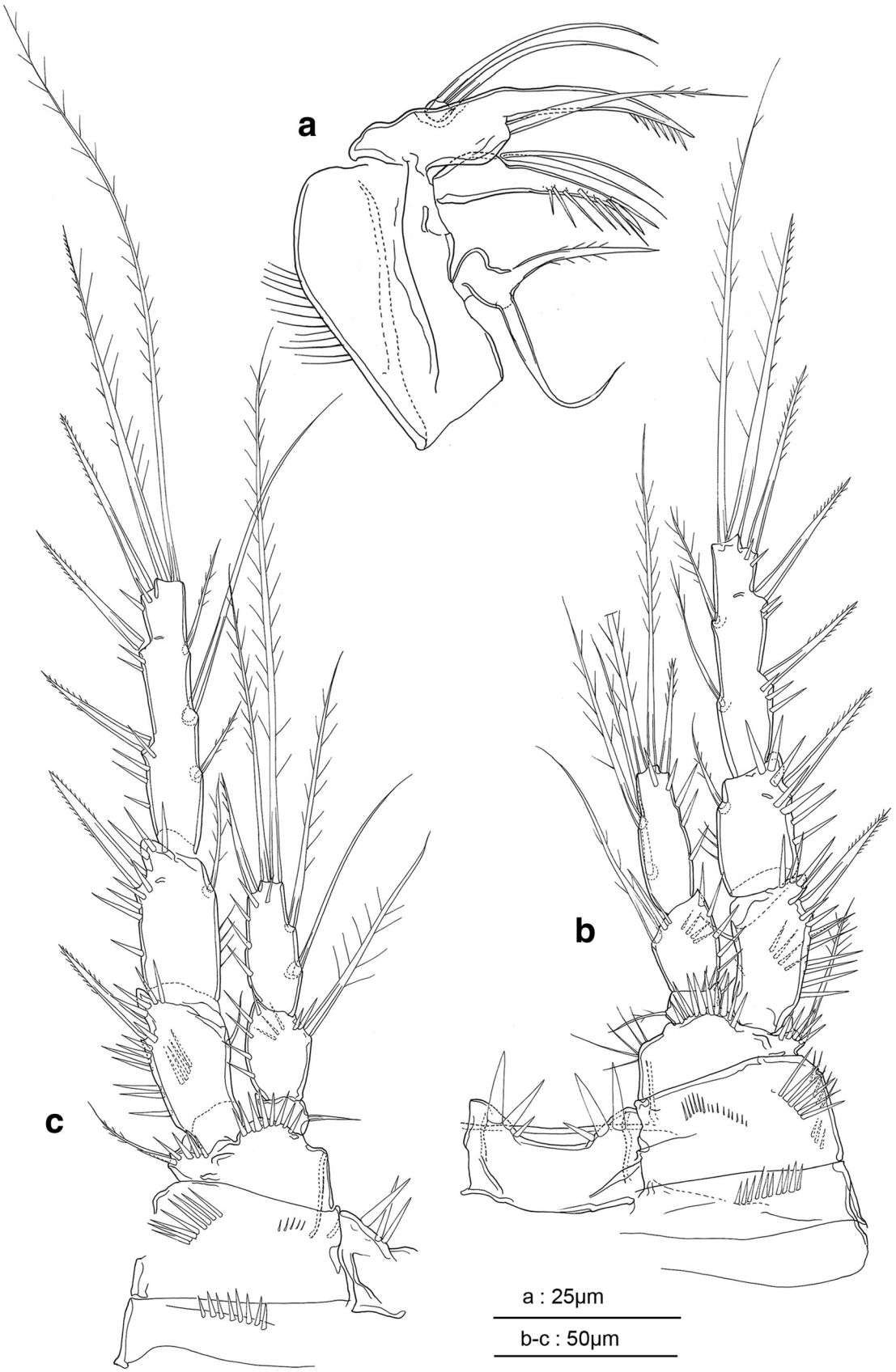

Fig. 5 *Neoargestes incertus*. Female holotype. **a** Maxilla; **b** P2, anterior; **c** P3, anterior

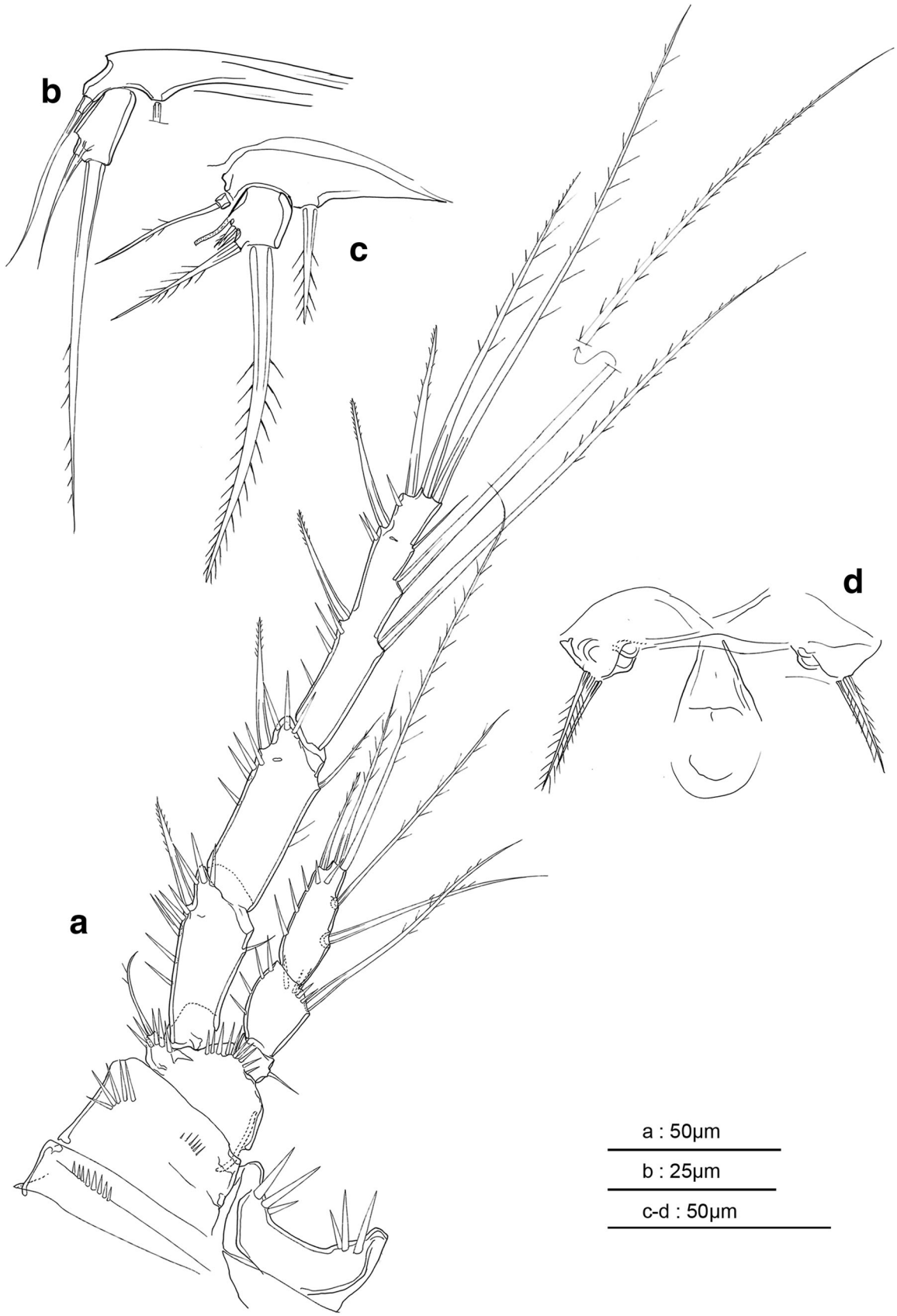

Fig. 6 *Neoargestes incertus*. Female holotype. **a** P4, anterior; **b** P5, posterior. Female from Porcupine Abyssal Plain; **c** P5, anterior; **d** P6 and GF, anterior

approximately triangular, about twice as broad as long, with outer basal seta. Praecoxa, coxa and basis with spinule rows. Exp-1 and exp-2 subequal in length, each with short inner seta and bipinnate outer spine. Exp-3 almost as long as exp-1 and exp-2 combined, with three bipinnate outer spines, one outer spine and one inner seta apically, and two short inner setae (P2; Fig. 5b), three inner setae (P3; Fig. 5c) of which proximal and distal short and subequal in length, middle one long, or with three inner setae (P4; Fig. 6a) of which distal one short, slender and bare, proximal and middle ones long, bipinnate and almost equal in length. Endopod of P2 reaching barely beyond tip of exp-2 (Fig. 5b); enp of P3 not reaching tip of exp-2 (Fig. 5c), enp of P4 reaching the middle of exp-2 (Fig. 6a). Enp-3 slightly longer than enp-1 and enp-2 combined. Enp-1 short, with one inner, short, and slender seta (bipinnate in P2, bare in P3 and P4). Enp-2 with one inner, pinnate seta. Enp-3 with two inner and two apical bipinnate setae, and one pinnate outer spine. Setal formulae of P1–P4 as in Table 1.

P5 (Fig. 6b, c). Endopodal lobe poorly developed, with one bipinnate seta. Exp distinct, bearing two long, bipinnate apical setae and two short outer elements, and with one long tube pore.

P6 (Fig. 6d) represented by two short setae. Genital field near middle of second urosomite, with single gonopore.

Male unknown.

Neoargestes laevis sp. nov.

Material examined. Holotype female, dissected onto 12 slides (COP 10500/1-12; I.G. 33763), deposited in the Invertebrate Collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium). The material was collected on 7 October 2015 with a multiple corer from station B4N01 (MUC deployment MUC009) (see Pape et al. 2017). Additional material from the Porcupine Abyssal Plain (NE Atlantic Ocean): one female (body length including FR: 376 μm) from station 54301#9, coordinates 48° 50.50′ N/16° 31.3′ W, depth 4843 m, collected on 22 October 1997 during RRS Challenger 135, slide reference 54301#9#0-1(5) (Kalogeropoulou 2014). This specimen is deposited in Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt, Germany.

Type locality. GSR exploration area in the Clarion-Clipperton Fracture Zone (Pacific Ocean), coordinates 14° 42′ 23.36″ N/125° 26′ 31.34″ W, depth 4501 m.

Etymology. The Latin adjective laevis (meaning smooth) refers to the smooth body surface of this species.

Description of female. Habitus (Fig. 7a, c) moderately slender, body length including FR approximately 443 μm. Cphth about one quarter of total body length. Whole body with smooth, weakly sclerotized integument, with pattern of sensilla and pores as figured. No clear distinction between prosome and urosome, urosome slightly tapering posteriorly. Second and third urosomites fused to form genital double-somite, original segmentation indicated by a weak dorso-lateral chitinous bar. Rostrum small, approximately triangular, fused to cphth. Posterior margin of cphth and all somites with broad, smooth hyaline frill, margin not denticulate. Fourth and fifth urosomites with row of spinules ventrally near posterior margin.

Telson (Figs. 8a and 9a) approximately as long as penultimate somite, with row of short spinules near insertion of furcal rami and row of ventral spinules covered by hyaline frill of penultimate somite. Anal operculum weakly developed, covered entirely by hyaline frill of penultimate somite (margin not entirely visible). Pair of sensilla associated with anal operculum displaced posteriorly.

FR (Fig. 8b, c) almost three times as long as wide, smooth, with few spinules on inner and outer apical margins, with six setae. Seta I absent; seta II, III, and VII inserted subapically: seta II on dorsal surface, with pore near insertion; seta III inserted ventrally, longer than seta II; setae IV and V longest, fused, inserted apically, seta IV pinnate, seta V broken; seta VI shortest, inserted apically; seta VII dorsally, tri-articulated at base. Pore at two thirds of ventral surface.

A1 (Fig. 9b–f) six-segmented. Segment one with few, short spinules along inner margin and one bipinnate seta apically. Second segment with three pinnate and five bare setae, and one strong, long and bipinnate spine, the latter inserted on ventral surface. Third segment about as long as second segment, with three unipinnate and three bare setae. Fourth segment small, with two bare setae and aes. Fifth segment

Table 1 Setation of P1–P4 in *Neoargestes variabilis*, *N. incertus*, and *N. laevis* sp. nov.

	P1		P2		P3		P4	
	exp	enp	exp	enp	exp	enp	exp	enp
N. variabilis	0.1.023	1.121 or 1.1.021	1.1.223	1.1.121	1.1.223	1.1.221	1.1.223	1.1.221
N. incertus	0.1.023	1.1.021	1.1.223	1.1.221	1.1.323	1.1.221	1.1.323	1.1.221
N. laevis sp. nov.	0.1.023	1.121	0.1.223	1.1.221	0.1.223	1.1.221	0.1.223	1.1.221

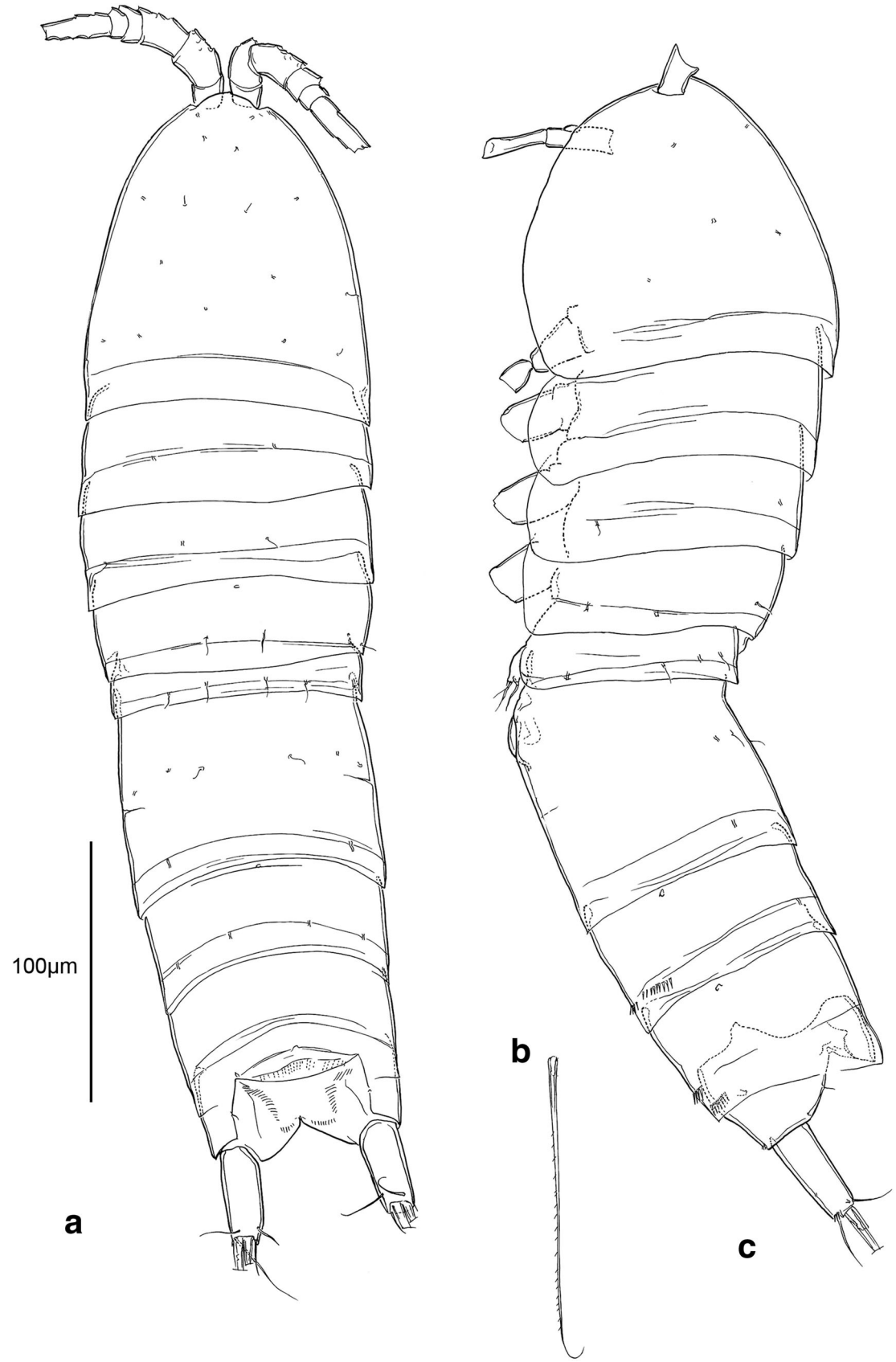

Fig. 7 *Neoargestes laevis* sp. nov. Female holotype. **a** Habitus, dorsal; **b** Furcal seta V; **c** Habitus, lateral

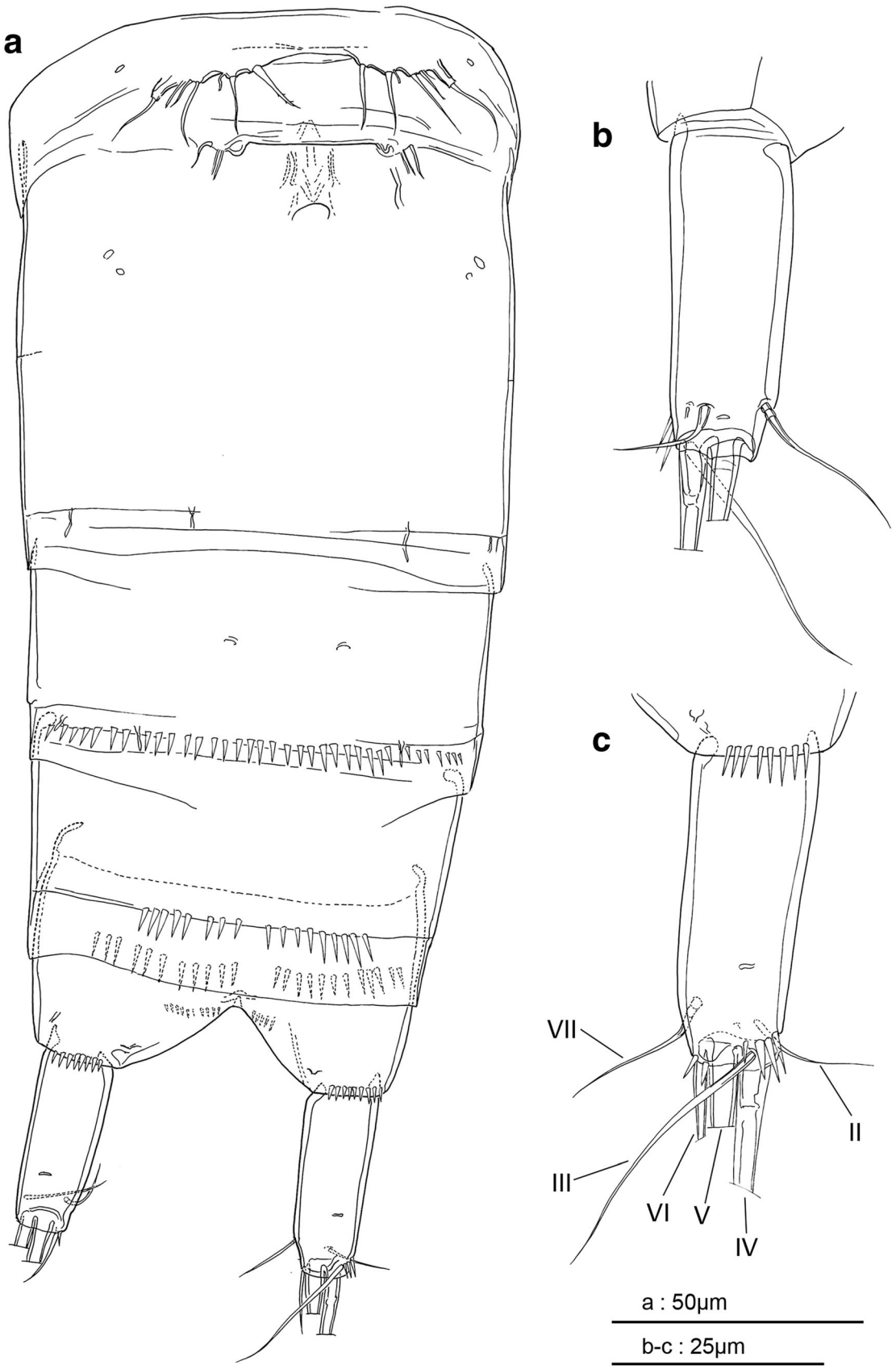

Fig. 8 *Neoargestes laevis* sp. nov. Female holotype. **a** Urosome with P5, P6, and GF, ventral; **b** Left furcal ramus, dorsal; **c** Left furcal ramus, ventral (furcal setae numbered II–VII)

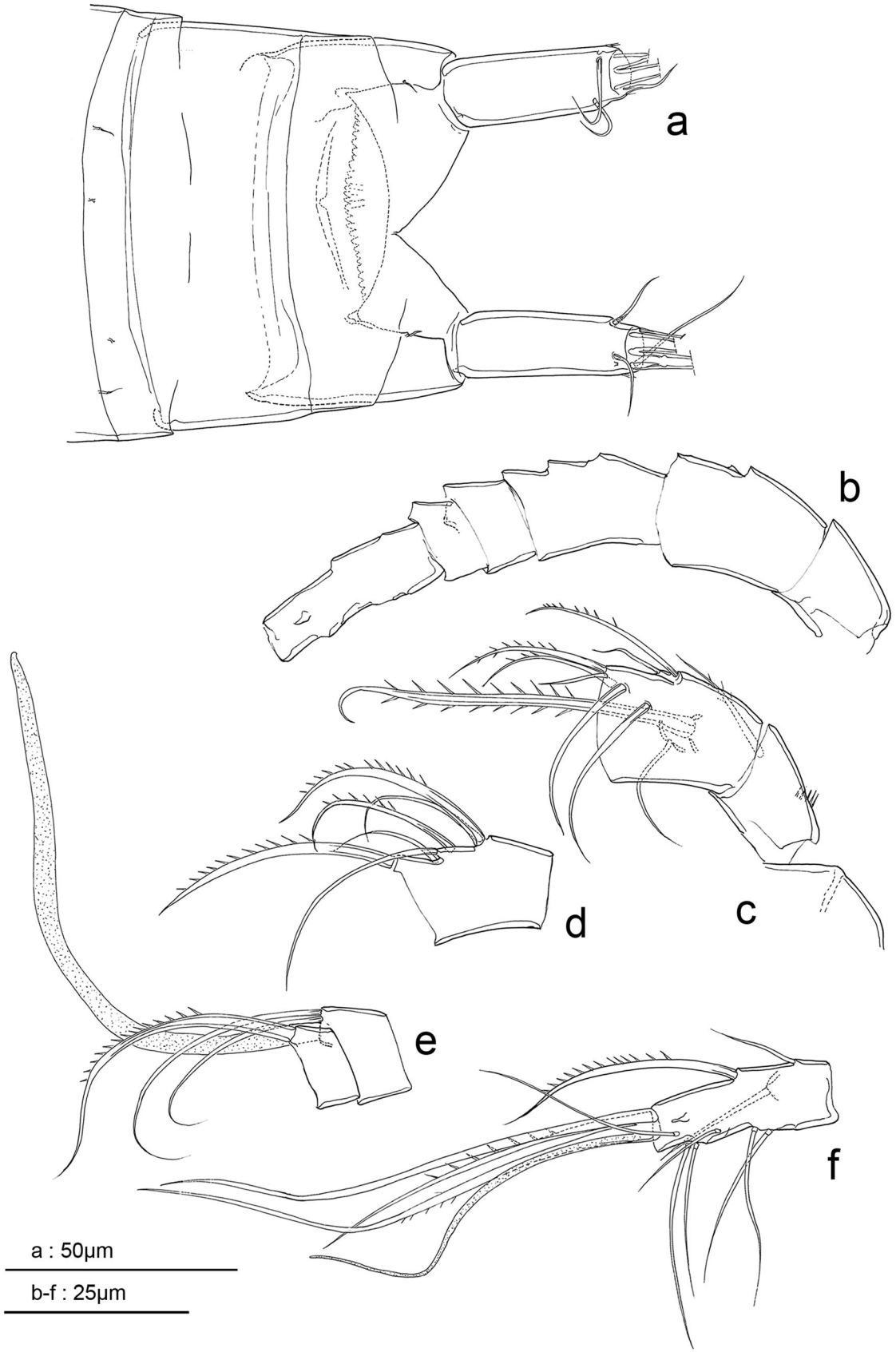

Fig. 9 *Neoargestes laevis* sp. nov. Female holotype. **a** Fourth and fifth urosomites, telson, and furcal rami, dorsal; **b** Left antennule, armature omitted; **c** Rostrum and segments 1 and 2 of antennule; **d** Segment 3 of antennule; **e** Segments 4 and 5 of antennule; **f** Segment 6 of antennule

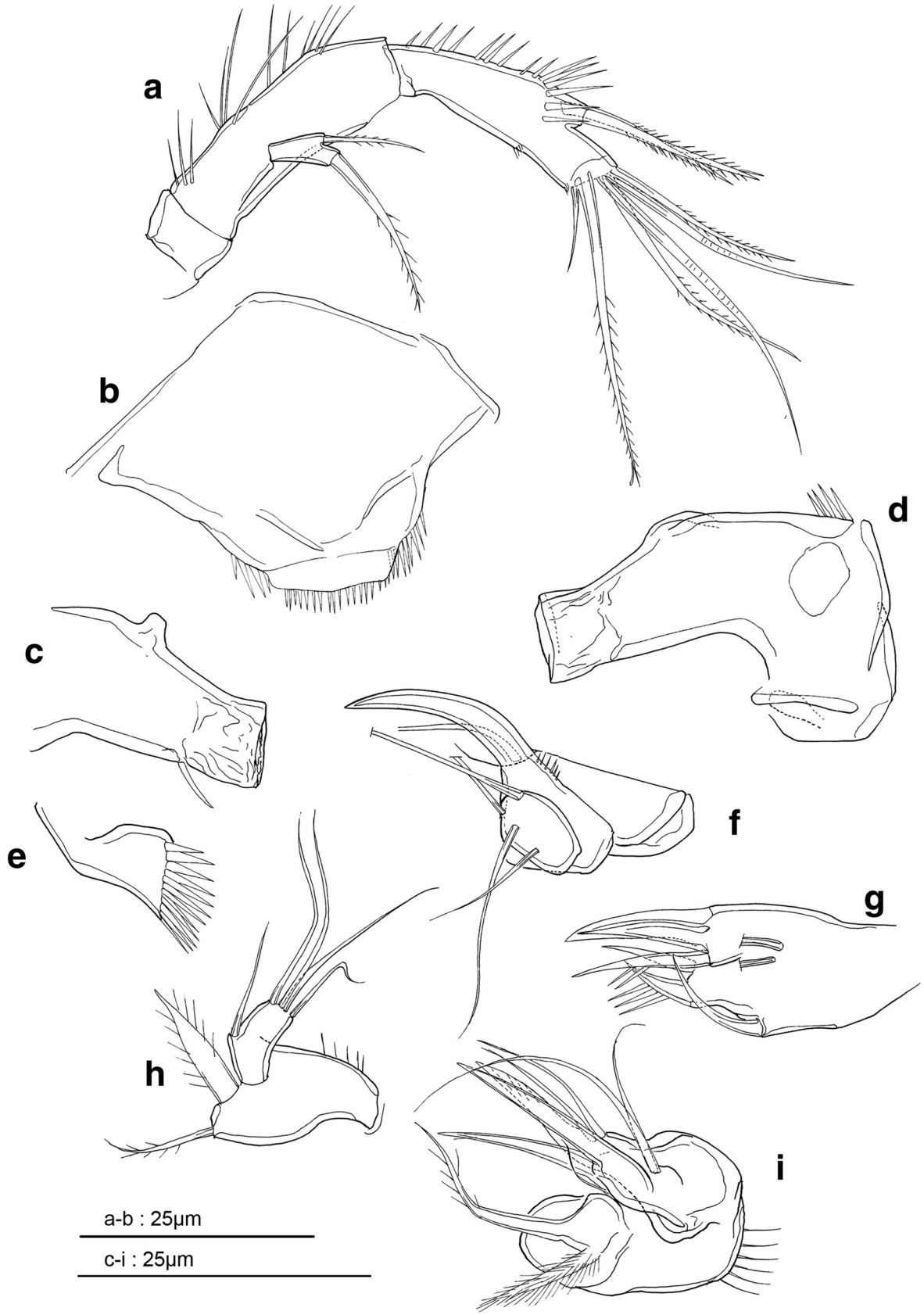

Fig. 10 *Neoargestes laevis* sp. nov. Female holotype. **a** Antenna; **b** Labrum; **c** Right mandibular gnathobase; **d** Left mandibular gnathobase; **e** Right paragnath; **f** Coxa and basis of maxillule; **g** Praecoxal arthrite of maxillule; Female from Porcupine Abyssal Plain; **h** Mandibular palp; **i** Maxilla

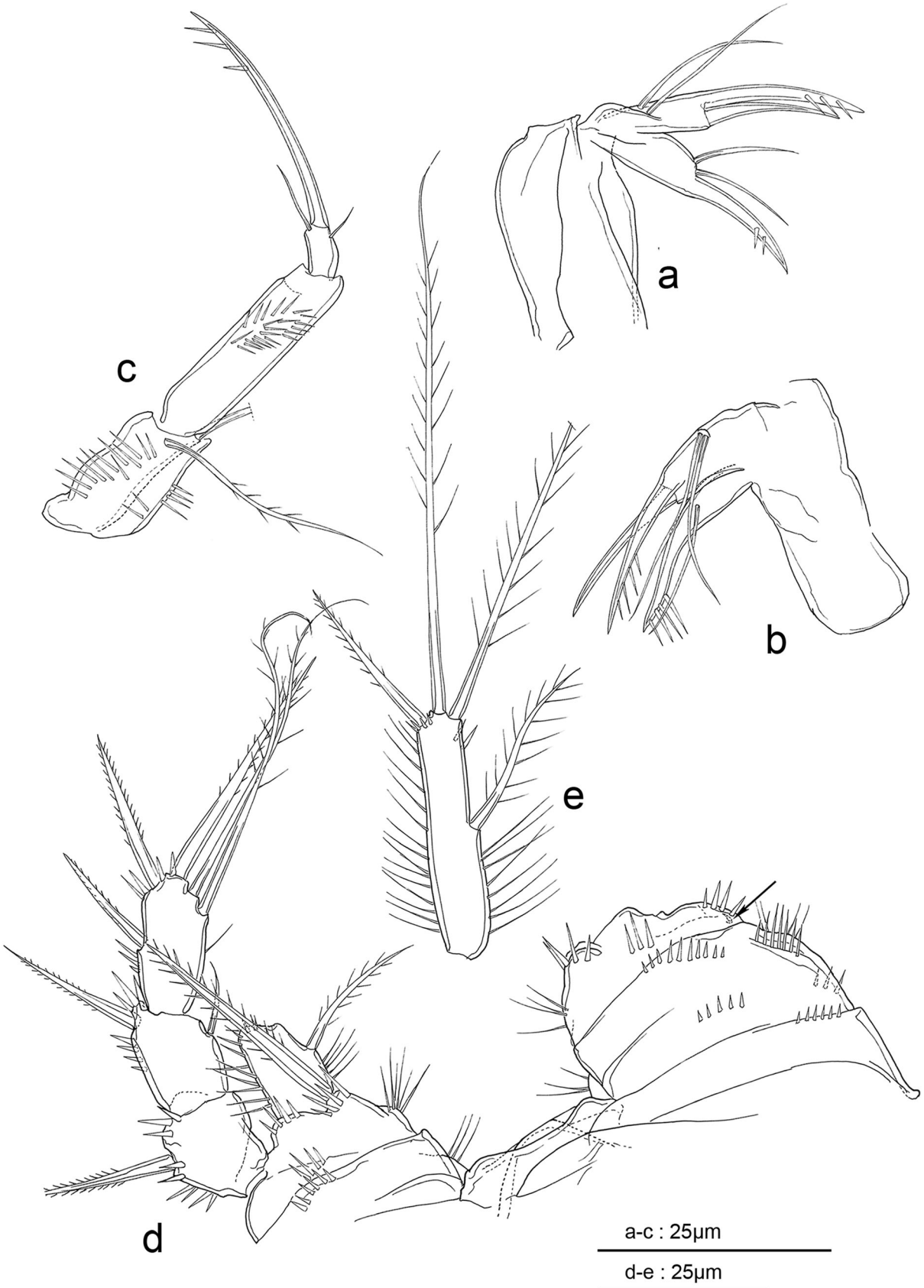

Fig. 11 *Neoargestes laevis* sp. nov. Female holotype. **a** Right maxilla; **b** Left maxilla; **c** Maxilliped; **d** Left P1, anterior (outer basal seta indicated by arrow); **e** P1 enp-2, anterior

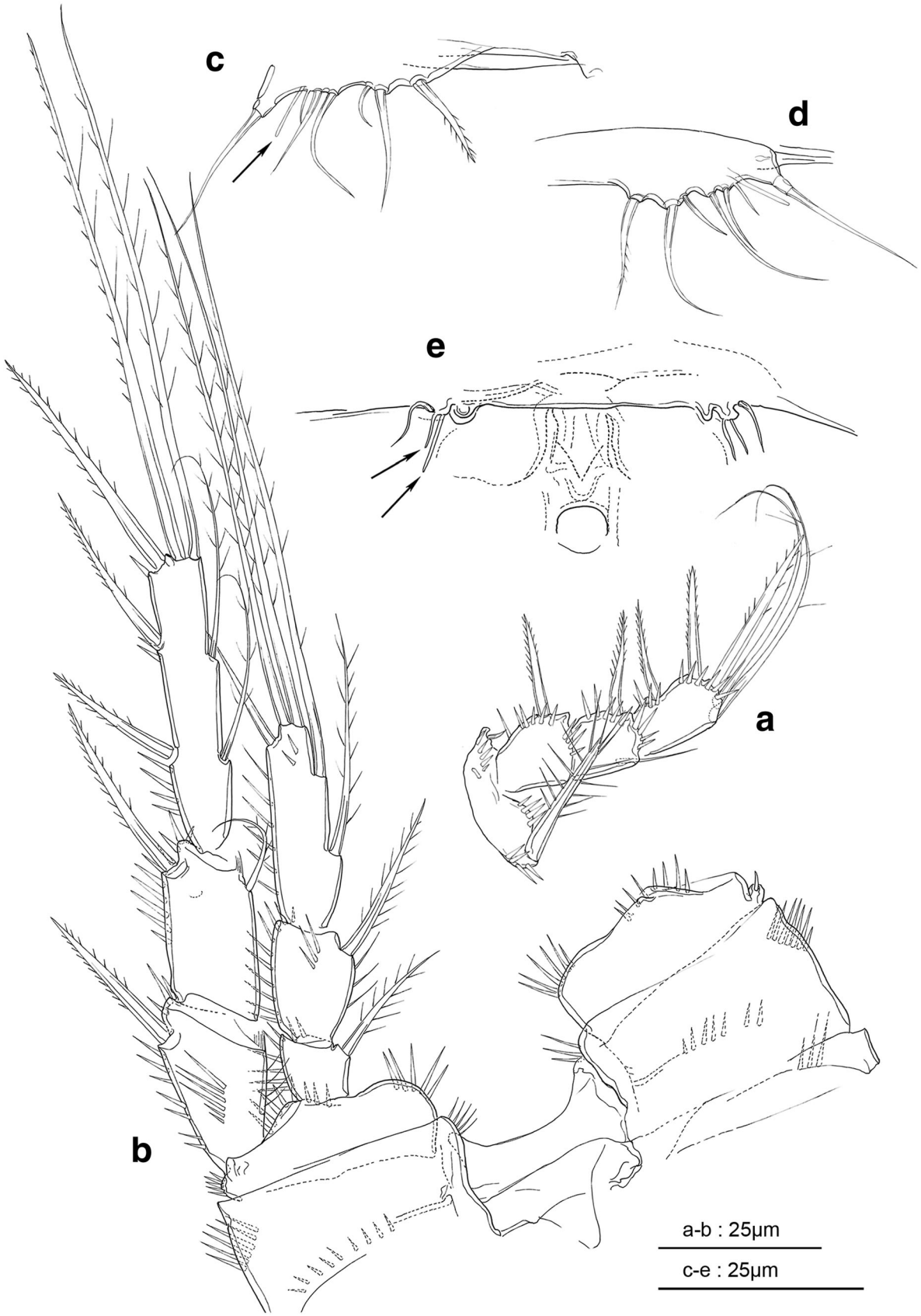

Fig. 12 *Neoargestes laevis* sp. nov. Female from Porcupine Abyssal Plain. **a** P1 basis and exopod, anterior. Female holotype; **b** P2, posterior; **c** Right P5 (tube pore indicated by arrow); **d** left P5; **e** P6 and GF (tube pores indicated by arrows)

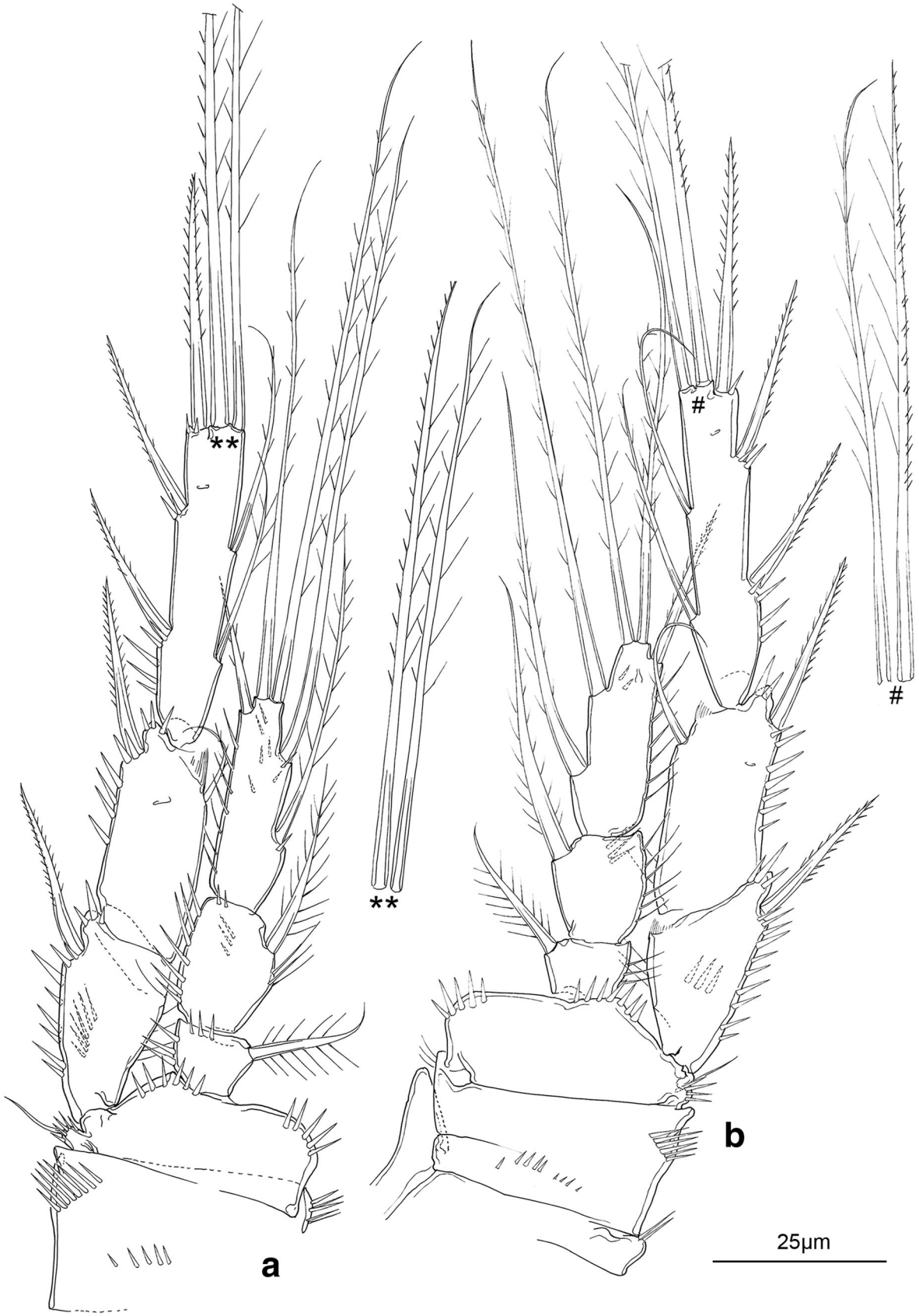

Fig. 13 *Neoargestes laevis* sp. nov. Female holotype. **a** P3, anterior; **b** P4, anterior

smallest, with one unipinnate seta. Sixth segment with ten setae, six of which bi-articulate at base, and acrothek (consisting of aes, one unipinnate seta and one bipinnate seta fused at base). Setal formula: 1/1; 2/9; 3/6; 4/2 + aes; 5/1; 6/10 + acrothek.

A2 (Fig. 10a) with allobasis and one-segmented exp. Exp bearing two bipinnate setae. Allobasis without abexopodal seta, with long spinules along abexopodal margin. Endopod with long spinules along margin, short subapical spinules, two bipinnate lateral spines, five apical setae (three of which bipinnate), and one small, slender seta fused at base to neighboring seta.

Labrum (Fig. 10b) with one medial and two lateral rows of spinules.

Paragnaths (Fig. 10e) on each side of labrum with row of strong spinules.

Md (Fig. 10c, d, h) Gnathobase (Fig. 10c, d) with broad masticating front and dorsal seta. Basis of mandibular palp (Fig. 10h) with two setae, one of which strong and bipinnate. Enp with five bare setae. Exp absent.

Mxl (Fig. 10f, g) in bad condition, description tentative. Praecoxal arthrite with six strong terminal elements, two of which pinnate; with two long, slender surface setae (broken in Fig. 10g). Coxa (Fig. 10f) with strong claw and 1 seta. Basis (Fig. 10f) with at least four setae.

Mx (Figs. 10i and 11a, b) probably damaged. Syncoxa with one endite armed with one strong unipinnate spine fused to endite and two setae. Proximal endite possibly lost. Basis with unipinnate claw (fused to basis) and one additional strong spine. Enp represented by two bare setae.

Mxp (Fig. 11c) prehensile, basis 1.5 times as long as syncoxa. The latter with spinules and with two long apical setae (one broken, one bipinnate). Basis with patch of spinules. Enp 1-segmented, with long distinct claw carrying few, strong pinnules, enp additionally with two bare, short setae subapically.

P1 (Fig. 11d, e) with three-segmented exp and two2-segmented enp, enp slightly longer than exp. Intercoxal sclerite short. Coxa slightly broader than basis, both with several short spinule rows. Basis with strong, bipinnate inner spine reaching middle of enp-2, and minute outer seta inserted on posterior surface, hardly discernible (see arrow in Fig. 11d). Exp-1 without inner seta, exp-2 with short inner seta. Exp-3 with five elements (three bipinnate outer spines and two bipinnate apical setae). Enp-1 with one bipinnate inner seta. Enp-2 with one inner and two apical bipinnate setae, and one bipinnate outer spine.

P2–P4 (Figs. 12b and 13a, b) with three-segmented exp and three-segmented enp. Intercoxal sclerites short. Coxa slightly larger than basis. Basis about twice as broad as long. Praecoxa, coxa and basis with short spinule rows as figured. Outer basal setae short, slender and bare. Exp-3 almost as long as exp-1 and exp-2 combined, exp-1 slight shorter than exp-2. Exp-1 without inner seta, with outer bipinnate spine. Exp-2 with one short, slender, and pinnate inner seta and one bipinnate outer spine. Exp-3 with three bipinnate outer spines, two slender, short inner setae and apically with one bipinnate outer spine and one bipinnate inner seta. Enp of P2 reaching insertion site of proximal inner seta of exp-3 (Fig. 12b); enp of P3 (Fig. 13a) and P4 (Fig. 13b) reaching slightly beyond tip of exp-2. Enp-3 slightly longer than enp-1 and enp-2 combined. Enp-1 short. Enp-1 and enp-2 with one bipinnate inner seta. Enp-3 with two inner and two apical bipinnate setae, and one bipinnate outer spine. Setal formulae of P1–P4 as in Table 1.

P5 (Fig. 12c, d) strongly reduced, endopodal lobe and exopod fused, each forming a weakly protruded lobe. Endopodal lobe with three setae (innermost pinnate), exopodal lobe with three setae and one tube pore. Basal seta on short setophore.

P6 (Fig. 12e) represented by one short seta and two tube pores. Genital field and P6 located near anterior margin of genital double-somite, with single gonopore.

Male unknown.

Variability. The single female of *Neoargestes laevis* sp. nov. (Figs. 10h, i and 12a) from the Porcupine Abyssal Plain differs only slightly from the holotype in the following characters:

Mx (Fig. 10i) carries a proximal endite with two setae (presumably lost in the type material); the inner basal spine on P1 carries fewer and longer spinules (Fig. 12a).

Discussion

Neoargestes is a small genus apparently restricted to the deep sea. So far, only two species have been described, *N. variabilis* and *N. incertus*. *Neoargestes variabilis* has only been found in Husnesfjord (Bergen, Norway; Drzycimski 1967), while *N. incertus* has been collected from two distant localities in the eastern Atlantic Ocean (Iberian Abyssal Plain and Porcupine Abyssal Plain) (Becker 1979; present contribution). Here, we describe a third species, *Neoargestes laevis* sp. nov., from the Clarion Clipperton Fracture Zone (Pacific Ocean) and from the Porcupine Abyssal Plain (Atlantic Ocean). All three *Neoargestes* species fit the generic diagnosis by Drzycimski (1967). However, Drzycimski's (1967) diagnosis does not discriminate between apomorphic and plesiomorphic characters. The placement of *Neoargestes* into Argestidae and its monophyletic status are discussed.

Assignment of *Neoargestes* to Argestidae

George (2011) listed several presumptive apomorphies of the monophylum Argestidae. However, these apomorphies [plesiomorphic conditions in square brackets] have not been proved for all argestid taxa (e.g., *Coralliclectodes* Soyer, 1966, *Hypalocletodes* Por, 1967, *Leptocletodes*

Sars, 1921), and, following George (2004, 2011), are considered here as provisional:

1. Integument weakly sclerotized [cuticle of regular strength]
2. Telson nearly square, large [telson tapering distally, shorter than preceding abdominal somite]
3. Anal operculum displaced anteriorly [anal operculum at posterior margin of telson]
4. FR set wide apart at outer corners of telson [FR apically on telson, not widely apart]
5. A2 exp at most one-segmented [A2 exp at least two-segmented]
6. P2 rami displaced toward outer margin of basis [no displacement]
7. P3 rami displaced toward outer margin of basis [no displacement]
8. P4 rami displaced toward outer margin of basis [no displacement]
9. Mx distal endite armed with strong spine [armed with moderate seta/spine]
10. Mx basis with claw and strong spine [claw accompanied by moderate seta]

Characters 6–8 were pooled by George (2011) into one single apomorphy. However, for detailed phylogenetic comparison, we considered characters 6–8 separately, raising to 10 the number of probable autapomorphies for Argestidae. George (2004) proposed two further derived characters, (i) the presence of, at the most, one seta on A2 exp and (ii) the loss of the accompanying seta on the maxillipedal claw. However, the ancestral states of both characters (i.e., the presence of a second seta on A2 exp and/or at least one accompanying seta on the maxillipedal claw) are present in single argestid taxa (e.g., Argestinae, *Argestigens*, *Mesocletodes* Sars, 1909, *Megistocletodes* Por, 1986, *Neoargestes*) and therefore, characters (i) and (ii) cannot be regarded as apomorphies of Argestidae.

Neoargestes shares all ten presumptive apomorphies listed above, although some are weakly developed. For example, *N. variabilis* (Drzycimski 1967) and *N. incertus* possess a large, squarish telson (character 2), while the telson of *N. laevis* sp. nov. is broader than long and, at most, as long as the preceding somite. Also, the rami of P2–P4 are displaced toward outer basal margin in *N. variabilis* and *N. laevis* sp. nov. (characters 6–8), but *N. incertus* shows only a slight displacement. Further, in *N. incertus*, the claw on Mx basis is accompanied by a moderate seta rather than a claw (character 10). Nevertheless, as *Neoargestes* meets characters 1, 3–5, and 9 (and with certain reservations characters 2, 6–8, and 10), its allocation to Argestidae is confirmed.

Systematic position of *Neoargestes* within Argestidae

These presumptive apomorphies 2, 6, 7, and 8 confirm that *Neoargestes* holds a relatively basal position within Argestidae, as suggested by Drzycimski (1967) and Becker (1979). *Neoargestes* shares the three-segmented endopods of P2–P4 with Argestinae (*Argestes* Sars, 1910 and *Fultonia* T. Scott, 1902; note that George (2011) commented on the possible allocation of *Dizahavia* Por, 1979 to this subfamily), *Bodinia peterrummi* George, 2004, and *Odiliacletodes* Soyer, 1964. However, the three species of *Neoargestes* differ remarkably from the other genera. For example, *Neoargestes* cannot be assigned to Argestinae since it lacks the dense dorsal and lateral spinular ornamentation of cphth and body somites, the development of a strong, long apical seta on the sixth antennular segment, and the strong elongation of the dorsal thoracic sensilla (see George 2011). Furthermore, it lacks the derived apron that is characteristic for *Bodinia*, and it also differs clearly from *Odiliacletodes* in several morphological features, like, e.g., the size and shape of the P5 and P2–P4 endopods. Instead, *Neoargestes* is characterized here by six autapomorphies that are considered indicative of its monophyletic status [plesiomorphic states in square brackets]:

11. Mandibular gnathobase transformed into broad masticating front [gnathobase equipped with cuspidate teeth]
12. P2 enp-1 strongly reduced in size, at most half as long as enp-3 [enp-1 at least half as long as enp-3]
13. P3 enp-1 strongly reduced in size, at most half as long as enp-3 [enp-1 at least half as long as enp-3]
14. P4 enp-1 strongly reduced in size, at most half as long as enp-3 [enp-1 at least half as long as enp-3]
15. P5 benp strongly reduced in size [benp lobate]
16. P5 exp strongly reduced in size, at most 1.5 times as long as broad [exp at least twice as long as broad]

A gnathobase with a broad masticating front (character 11) is also present in *Mesocletodes* and *Fultonia* (Argestinae). However, as discussed above, *Neoargestes* cannot be assigned to *Fultonia* or even Argestinae. Similarly, it differs from *Mesocletodes*, a derived representative of Argestidae, characterized by several apomorphies, including the presence of a robust protrusion bearing a strong, backwardly pointing bipinnate seta on the second antennular segment, a reduced proximal outer spine on P1 exp-3, and further deviations regarding the size and the shape of swimming legs, furcal rami and others (cf. Menzel and George 2009). Thus, it is concluded here that the formation of a mandibular gnathobase with a strong and broad masticating front has occurred several times within

Argestidae and must be regarded as convergent in *Fultonia*, *Mesocletodes*, and *Neoargestes*.

Neoargestes, Argestinae (*Argestes-Fultonia*), *Bodinia peterrummi*, *Dizahavia*, and *Odiliacletodes* also share the primitive three-segmented endopod on P2–P4, while the remaining Argestidae possess a reduced number of segments on the P2–P4 endopod. *Neoargestes*, however, is unique in the drastic reduction of the first endopodal segment of P2–P4 (characters 12–14), and in the strongly reduced female P5 benp (character 15), which are regarded here as derived conditions, and therefore interpreted as autapomorphic for this taxon. Contrary to the apomorphic condition of the strongly reduced P5 endopodal lobe of *Neoargestes*, *Bodinia*, and *Odiliacletodes* possess a well-developed endopodal lobe of P5 and is regarded here as plesiomorphic. As demonstrated above, both Argestinae and *Mesocletodes* present several apomorphies that are not shared by *Neoargestes*, so a closer relation between the latter and Argestinae/*Mesocletodes* can be ruled out. Thus, both Argestinae and *Mesocletodes* are excluded from further comparison. The strongly reduced P5 endopodal lobe observed in *Dizahavia* and *Neoargestes* might suggest a closer relationship between these genera. However, *Dizahavia* lacks apomorphies 11–16, and following Por's (1979) description, *Dizahavia* might be closely related to *Argestes* and *Fultonia*, thus possibly forming part of Argestinae as suggested by George (2011).

Finally, the small P5 exp (character 16), which is distinct or fused to the baseoendopod, is exclusively present in *Neoargestes*. This strong reduction of the P5 exopod is unique within Argestidae, and is interpreted here as apomorphic for the genus.

Systematic relationships within *Neoargestes*

The three species so far attributed to *Neoargestes* share characters 11–16, which are regarded here as synapomorphies supporting the monophyletic status of the genus. Relationships between these species remain vague and the re-description of the type species, *N. variabilis*, is still pending. Type material of *N. variabilis* deposited at Bergen University Zoological Museum and other material deposited at the Marine Biology Station in Blomsterdalen could not be found and is presumed lost. Comparison of all three *Neoargestes* species reveals that *N. variabilis* shares two derived characters with *N. laevis* sp. nov. [plesiomorphic state present in *N. incertus*]:

17. Maxillary endopod lost, represented by 1–2 setae [endopod 1-segmented, with 2 setae]
18. P5 exopod and baseoendopod fused [P5 exopod distinct]

A third tentative apomorphy refers to the segmentation of the P1 enp. In *N. laevis*, it is two-segmented, and also Drzycimski (1967, Table 1, p. 204) lists nine individuals of *N. variabilis* presenting a two-segmented P1 enp. However, that author noticed a remarkable variability in the segmentation of the P1, reaching from a three-segmented enp to a partial and even complete fusion of P1 enp-2 and enp-3. That variability applies even to both P1 legs of single specimens, for which reason it is not considered here.

These mutually derived features might point towards a close relationship between *N. variabilis* and *N. laevis* sp. nov. In addition, both species share the presence of only two inner setae in P3 and P4 exp-3, whereas *N. incertus* bears three inner setae. However, it cannot be confirmed if *N. variabilis* and *N. laevis* sp. nov. lost homologous setae and their exact relationship cannot be determined.

Neoargestes variabilis and *N. incertus* also share one derived character [plesiomorphic state present in *N. laevis* sp. nov.]:

19. Maxillipedal enp fused with apical strong claw [enp and claw still distinct]

A maxillipedal enp carrying a distinct apical claw forms part of the podogennontan groundpattern (Willen 2000; Seifried 2003) and, therefore, is regarded as the ancestral state in those families composing that taxon. Consequently, the fusion of the enp with the apical claw constitutes the derived state. Within Argestidae, the ancestral state is distributed quite randomly over the different genera and appears sporadically, for example, in some *Eurycletodes* Sars, 1909 species (e.g., *Eurycletodes* (*E.*) *laticauda* Sars, 1909, *E.* (*E.*) *serratus* Sars, 1921, *E.* (*Oligocletodes*) *peruanus* Becker, 1979), in *Leptocletodes* sp. (Soyer, 1964), *Mesocletodes duosetosus* Schriever, 1985, *M. kunzi* Schriever, 1985, and *Neoargestes laevis* sp. nov. Regarding *Neoargestes*, the presence of the derived state (maxillipedal endopod and endopodal claw fused) in both *N. incertus* and *N. variabilis* may support their close relationship, while *N. laevis* sp. nov. (maxillipedal endopod and endopodal claw distinct) may represent the ancestral state within *Neoargestes*.

The phylogenetic relationships within *Neoargestes* remain unclear. The re-description of the type species *N. variabilis* would certainly provide valuable data, potentially allowing all species to be characterized by distinct autapomorphies. According to Drzycimski's (1967) description, *N. variabilis* is unique in possessing four autapomorphies [plesiomorphic conditions in square brackets]:

20. A2 exp carrying only 1 seta [with two setae]
21. Maxillary endopod represented by only 1 seta [mx enp with two setae]

22. Maxillipedal syncoxa with only 1 spine [with two spines]
23. P2 third endopodal segment with one inner seta [with two inner setae].

N. laevis sp. nov. also presents at least four autapomorphies [plesiomorphic conditions in square brackets] in comparison to *N. variabilis* and *N. incertus*:

24. A2 with allobasis [A2 with basis]
25. P2 exp-1 without inner seta [with one inner seta]
26. P3 exp-1 without inner seta [with one inner seta]
27. P4 exp-1 without inner seta [with one inner seta]

Autapomorphies 20–27 show fusion of segments or the loss of setae or spines. We have applied the general oligomerization principle (Huys 1996), whereby the retention of segments, setae, or spines is considered to be the plesiomorphic state, and their fusion or loss as the derived state.

Finally, *N. incertus* shows at least three unique autapomorphies [plesiomorphic conditions in square brackets]:

28. Subapical seta of maxillipedal syncoxa multipinnate [corresponding seta uni- to bipinnate]
29. Subapical seta of maxillipedal syncoxa extremely elongated and strengthened, as long as syncoxa and basis combined [seta slender, at most reaching length of syncoxa]
30. Female P5 baseoendopod with 1 endopodal seta [with at least two setae]

In contrast to characters 20–27, apomorphies 28–29 present neither fusions nor reductions but qualitative modifications of the respective elements. The development of multipinnate setae (character 28) is relatively unusual, being bare, uni- or bipinnate elements more common: the maxillipedal seta of the remaining *Neoargestes* species and even other Argestidae is at most bipinnate. Therefore, the development of a multipinnate syncoxal seta on the mxp is interpreted as autapomorphic for *N. incertus*. Similarly, the extreme elongation and strengthening of that seta (character 29) is unique not only within *Neoargestes* but the whole Argestidae. Finally, according to the general oligomerization principle, character 30, the reduction to 1 baseoendopodal seta in the female P5 of *N. incertus,* is regarded as apomorphic.

Briefly, *Neoargestes* constitutes a monophylum composed of three known species, *N. incertus*, *N. laevis* sp. nov., and *N. variabilis*, sharing six apomorphic characters. The allocation of *Neoargestes* to Argestidae is confirmed. Within the genus, each species is characterized by a series of autapomorphies, but the relationships between them remain unclear due to missing morphological data.

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