

Rhizotrichidae Por, 1986 (Copepoda: Harpacticoida) of Madeira and Porto Santo: description of two new species of the genus *Tryphoema* Monard, 1926

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Abstract Two new species of the genus *Tryphoema* Monard, 1926 (Copepoda: Harpacticoida: Rhizotrichidae) are described from sandy sediments in coastal shallow waters of the islands Madeira and Porto Santo. *Tryphoema weneri* sp. nov. occurs on both islands, while *Tryphoema irmgardae* sp. nov. was solely found on Madeira. *Tryphoema weneri* sp. nov. displays one-segmented exopods at the swimming legs 2–4, which are two-segmented in congeners. *Tryphoema irmgardae* sp. nov. retains four setae on the endopods of the swimming legs 2–4 while all other representatives of the genus display at most 3 setae. Both species differ from each other in many morphological characters especially concerning the armature of the swimming legs 1–4 and their exopodal segmentation, the length of the furcal setae and the ornamentation of the maxilliped. By contrast, some synapomorphies between *Tryphoema irmgardae* sp. nov. and *Tryphoema porca* Monard, 1926 (known from shallow waters of the Mediterranean and the English Channel) have been identified and are discussed. Furthermore, a revised key to the species of the genus *Tryphoema* is provided.

Keywords Meiofauna · Shallow water · Morphological taxonomy · *Tryphoema irmgardae* sp. nov. · *Tryphoema weneri* sp. nov.

Introduction

The genus *Tryphoema* Monard, 1926 was established based on the type species *Tryphoema porca* Monard, 1926, which had been found in the Mediterranean Sea (coast of France

(Monard 1926, 1928); coast of Algeria (Monard 1937)), and in coastal waters of the English Channel (coast of France (Monard 1935); estuary of the River Exe (Wells 1963)). Monard (1926) placed *Tryphoema* within the taxon Cletodidae T. Scott, 1905, close to the genus *Rhizothrix* Sars, 1909. Pennak (1942) established the genus *Adelopoda* Pennak, 1942 based on the type species *Tryphoema (Adelopoda) ramabula* (Pennak, 1942) and positioned the genus within the Canthocamptidae Sars, 1906. However, Božić (1953) considered *Adelopoda* as a subgenus of *Rhizothrix* while Wells (1963) considered it to be synonymous with *Tryphoema* and placed *Tryphoema* as a subgenus within *Rhizothrix*. Lang (1965) recognised the genera *Tryphoema* and *Rhizothrix* as distinct. Por (1986) finally established the family Rhizotrichidae Por, 1986 comprising these two genera. Currently, the genus *Tryphoema* includes 6 species (Wells 2007), the type species *Tryphoema porca*, *Tryphoema ramabula* (Pennak, 1942), which was found at the northeast coast of the United States, *Tryphoema bocqueti* (Božić, 1953), which is known from the north and south coast of France (Božić 1953; Bodin 1970a, b), the Estuary of the River Exe (United Kingdom, Wells 1963), the Skagerrak (Por 1964) and from sand flats around the German island Sylt (Mielke 1975), *Tryphoema lusitanica* (Wells and Clark, 1965), which was found at the Atlantic coast of Portugal, *Tryphoema scilloniensis* (Wells, 1968) from the coast of the Isles of Scilly (United Kingdom), and *Tryphoema riedli* Coull, 1971, which was found at the east coast of the United States. In the course of an ongoing project, to inventory the harpacticoid copepods of Madeira and the neighbouring island Porto Santo and to compare the obtained data with summit communities of nearby seamounts (particularly seamounts of the “Madeira Hot Spot Track”), two new species of the Rhizotrichidae were identified, both belonging to the genus *Tryphoema*. The present publication provides the species descriptions of both new species, a discussion of

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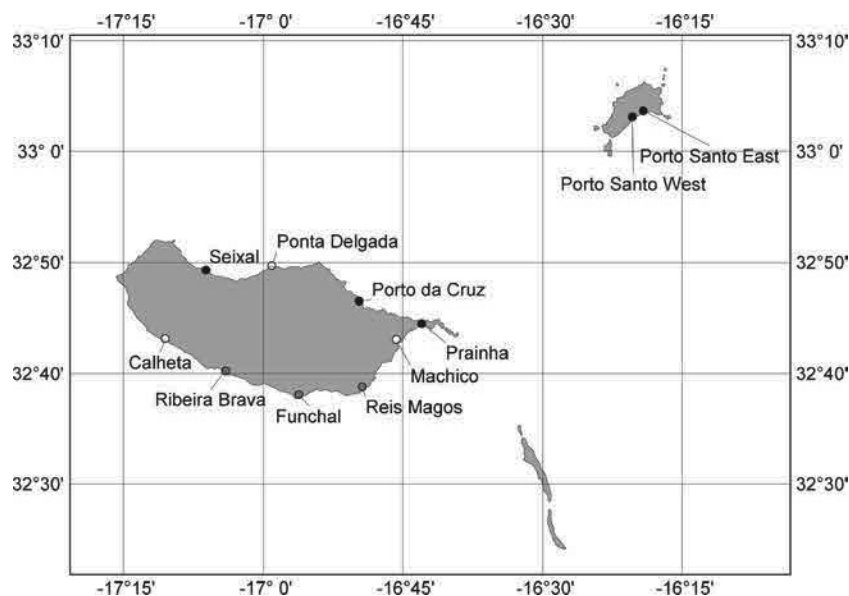
morphological characteristics within the genus and a revised key to the species of *Tryphoema*.

Materials and methods

Sediment cores for quantitative investigations of the harpacticoid copepod community of Madeira and Porto Santo were taken during April and May 2011 and May 2012. In total, 11 sampling locations were chosen of which 9 are situated along the coastline of Madeira and 2 along the south coast of Porto Santo (Fig. 1). All sediment cores were sampled in the uppermost subtidal zone at a water depth of 2–3 m below sea level, and a water depth of 10–13 m in the case of Reis Magos and Funchal. Plastic corers with a sampling surface of 22 cm² were used to sample the uppermost 5 cm of sediment (sediment volume of 110 cm³). The sediment cores were immediately preserved in 4 % formaldehyde solution. In the current publication, only the material collected in 2011 has been considered. Sample treatment follows Rose et al. (2005). The meiofauna samples were sorted using a Leica MZ 125 stereo microscope. All copepods were transferred in a 1:1 water-glycerin solution on hollow-ground slides. 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 geographical maps (Figs. 1, 14) were created using the program PanMap (Diepenbroek et al. 2000; NGDC/NOAA 1993).

Abbreviations used in the text: A1 – antennule, A2 – antenna, aes – aesthetasc, benp/benps – baseopod/baseopods, 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)



Taxonomy

Harpacticoida Sars, 1903

Rhizotrichidae Por, 1986

Tryphoema Monard, 1926

Type species: *Tryphoema porca* Monard, 1926.

Additional species: *Tryphoema ramabula* (Pennak, 1942), *Tryphoema bocqueti* (Božić, 1953), *Tryphoema lusitanica* (Wells and Clark, 1965), *Tryphoema scilloniensis* (Wells, 1968), *Tryphoema riedli* Coull, 1971, *Tryphoema irmgardae* sp. nov., *Tryphoema weneri* sp. nov.

Generic diagnosis: Rhizotrichidae. Body cylindrical, slightly tapering posteriorly, without clear demarcation between prosome and urosome. Entire body surface covered with denticles (unknown in *T. ramabula*). Prosome four-segmented, comprising cephalothorax (bearing first pedigerous somite) and three free pedigerous somites. Rostrum not prominent, rounded or bifid and fused to the cephalic shield. Last thoracic and first abdominal somite fused to form a genital double-somite in female. Telson broader than long. Furcal rami conical; at most slightly longer than broad; apically with scale-shaped process (unknown in *T. porca*). Furcal rami with six setae (ambiguous in *T. ramabula* and *T. riedli*); Setae I and II laterally, setae III absent, setae IV, V and VI apically, seta VII dorsolaterally. Sexual dimorphism in body size, antennule, P5 and genital somites; P1 to P4 without sexual dimorphism. Antennule four- to five-segmented in female, chirocer in male; number of segments ambiguous or unknown in most species, seven-segmented in *T. irmgardae* sp. nov. and *T. weneri* sp. nov.; aesthetasc arising from segment three and distal segment in female, segment four and distal segment in male. Antenna with allobasis, abexopodal margin with seta in *T. porca*, *T. irmgardae* sp.

nov. and *T. wernerii* sp. nov.; antennary exopod one-segmented with three to four setae. Mandibular palp with basis, strongly reduced exopod (bearing one seta) and endopod. Maxillula with strong arthrite; coxal endite cylindrical; endopod and exopod incorporated in basis or exopod distinct. Maxillary syncoxa with two endites; allobasis produced into strong claw with 2 accompanying setae; endopod one-segmented. Maxilliped prehensile; second endopodal segment forming a claw (proximally with two short setae). P1 with two-segmented endopod and three-segmented exopod; distal segment of endopod and exopod apically with two setae with brush-like tip. P2 to P4 endopod one-segmented, exopod one- to two-segmented. Outer margin of coxa and praecoxa laterally widened in P1 to P4 (unknown in *T. porca*, *T. bocqueti* and *T. riedli*). Baseoendopods of both legs of female's P5 fused or separated, exopod distinct. Male's P5 strongly reduced, baseoendopods of both legs fused or separated, exopod incorporated (except in *T. riedli*). P6 unknown in most species, female's P6 strongly reduced in *T. irmgardae* sp. nov. and *T. wernerii* sp. nov. not covering the genital field, male's P6 absent.

Tryphoema irmgardae sp. nov.

Type locality: Reis Magos, south coast of Madeira (32°38' 49.10"N, 16°49'23.16"W); sampling date 15/05/2011; sediment: medium to fine grained sand mostly of volcanic origin; water depth 10–13 m below sea level.

Material examined: Type material is deposited at the Museu Municipal do Funchal (História Natural; Funchal, Madeira, Portugal); Holotype: female, dissected and mounted on 11 slides, collection numbers MMF 42471/1–11. Paratype 1: female, not dissected, 1 slide, collection number MMF 42472/1. Paratype 2: female, dissected on 9 slides, collection numbers MMF 42473/1–9. Paratype 3: female, dissected on 4 slides, collection numbers MMF 42474/1–4. Paratype 4: female, dissected on 7 slides, collection numbers MMF 42475/1–7. Paratype 5: female, dissected on 6 slides, collection numbers MMF 42476/1–6. Paratype 6: male, not dissected, 1 slide, collection number MMF 42477/1. Paratype 7: male, dissected on 2 slides, collection numbers MMF 42478/1–2.

Etymology: The species name *irmgardae* is given in grateful dedication to the author's mother, Mrs Irmgard Packmor (Banteln, Germany).

Description of female:

Habitus (Fig. 2) cylindrical, slightly depressed dorsoventrally. Length from anterior margin of cephalothorax to posterior margin of FR approximately 420 µm. Entire body surface and parts of mxp and swimming legs squamous covered with tiny cuticular denticles. Rostrum small and bifid, fused to cephalic shield, apically with 2 sensilla. Cephalothorax and all body somites (except third abdominal somite) with several pairs of sensilla. Last thoracic and first abdominal somite fused, forming genital double-somite.

Telson (Fig. 3a) only slightly longer than preceding somite. Anal operculum dorsally with denticles, ventrally with fringe of setules (not drawn in Fig. 3a) and 1 pair of sensilla near lateral edge of operculum.

FR (Fig. 3a, a') 1.3 times as long as wide. Six setae present, seta III absent. Seta II inserting dorsolaterally, little longer than seta I. Seta I inserting ventrolaterally. Setae I and II bare, several strong spinules between them (Fig. 3a'). Setae IV, V and VI apically, VI bare, IV and V biplumose, V longest seta but only slightly longer than FR. Seta VII located dorsolaterally at inner distal margin of FR. Seta VII articulated and biplumose, its base inserted in pocket-shaped cuticular invagination. Dorsal and ventral distal margin of FR partly covered by scale-shaped cuticular process (Fig. 3a, arrow). FR completely covered with small denticles, like entire body surface.

A1 (Fig. 3b) 4-segmented, first segment with several spinules at inner and outer margin (not drawn) and with 1 bare seta at anterior distal margin. Second segment with 7 setae and 1 spinulose spine; 4 setae bipinnate (one of which articulated), 3 biplumose (two of which articulated); spinulose spine apically equipped with tube pore, its spinules flat, broad at their base and tapering towards their distal end (shape almost like husks of artichokes but more slender). Third segment with 8 setae, 1 spinulose spine and 1 aes; 4 setae bare (one of which articulated and fused with aes), 3 plumose (two of which articulated) and 1 seta unipinnate; spinulose spine resembles that of segment-2. Fourth segment with 8 setae, 2 spinulose spines and 1 slender aes; 6 bare setae (two of which fused with aes and form acrothek, and 3 articulated), 1 articulated biplumose seta and 1 unipinnate seta; inner spinulose spine resembles those of segments 2 and 3, distal spinulose spine much broader and lacks tube pore. Setal formula: 1/1; 2/8; 3/9 + aes; 4/10 + aes.

A2 (Fig. 3c). Allobasis with several setules and 1 small abexopodal unipinnate seta. Exp 1-segmented, with 2 slender, bare and 2 strong, biplumose setae. Enp with several small spinules and row of broad and flat spinules at anterior margin; two rows of smaller spinules apically and laterally; apically with 2 bare geniculate setae and 2 spinulose spines (outermost spinulose spine very strong, articulated at its tip and displaying heteromorphic spinules, 1 long and slender tube pore, inserting at its base); near anterior margin with 3 spinulose spines and 1 sensillum.

Md (Fig. 4a, a'). Coxa with strong gnathobase with 5 major blunt teeth overlapping each other, innermost articulated; with 2 pinnate accessory setae and row of slender, long setules. Mandibular palp (Fig. 4a') with basis, exp and enp. Basis with 1 strong multiplumose seta distally at inner margin. Exp 1-segmented, strongly reduced, with 1 bare seta. Enp 1-segmented with 1 strong uniplumose seta laterally and 4 bare setae apically, which are fused at their bases. Basis completely, enp patchily covered with slender, long setules.

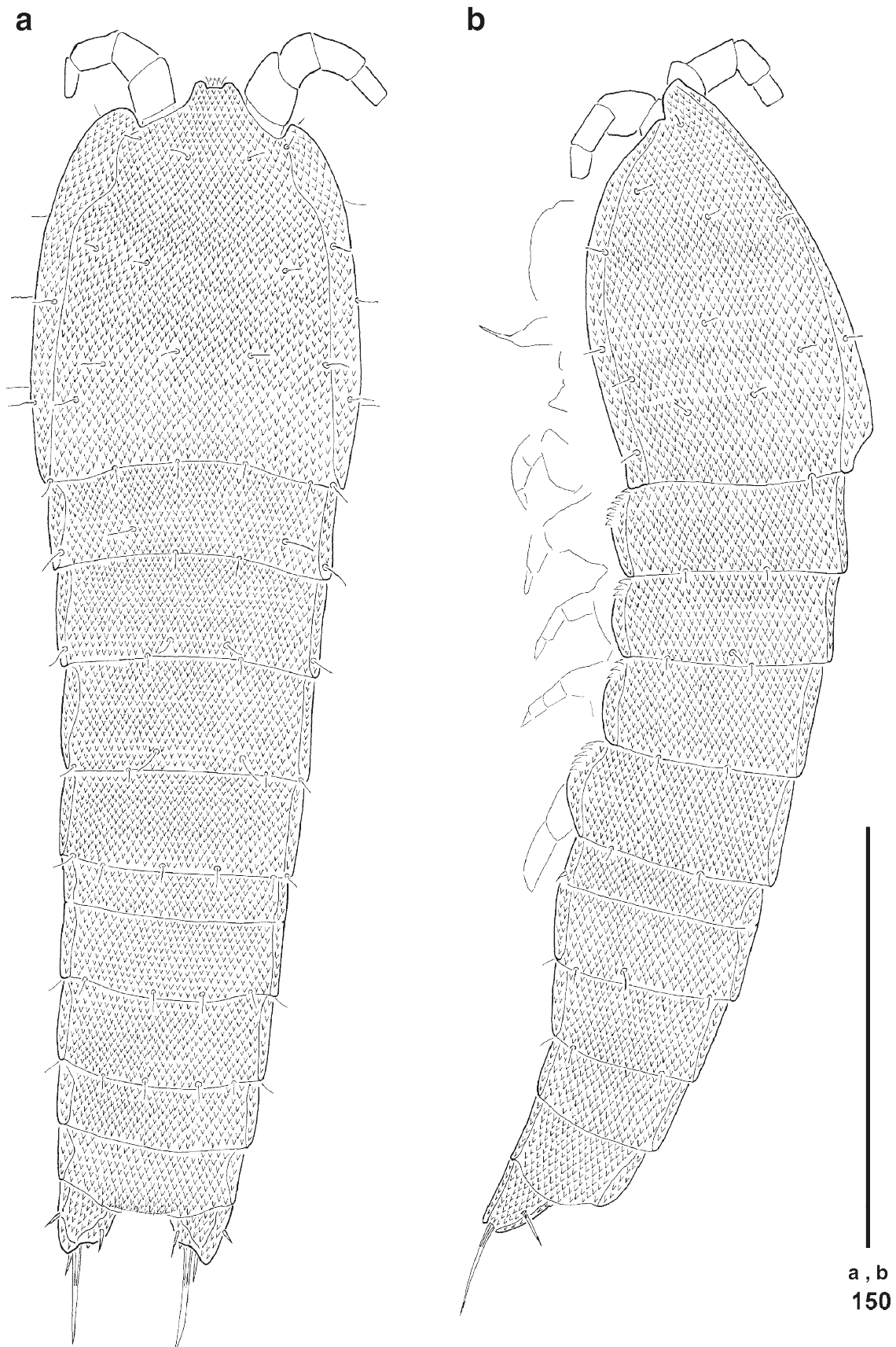


Fig. 2 *Tryphoema irmgardae* sp. nov., female. **a** Habitus dorsal, **b** habitus lateral. Both paratype 1. Scale bar in μm

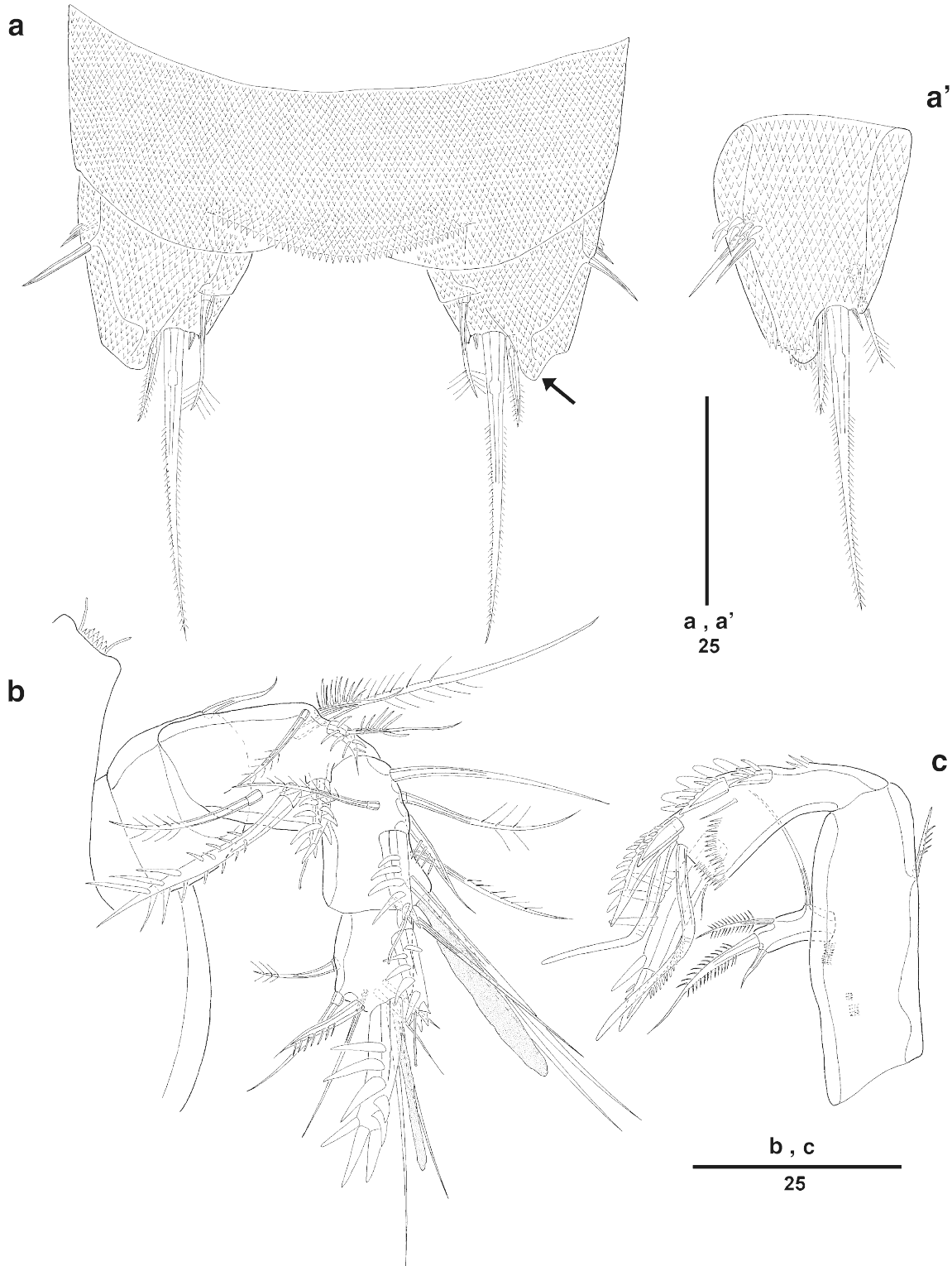


Fig. 3 *Tryphoema irmgardae* sp. nov., female. **a** Telson and FR, dorsal (*arrow* indicates scale-shaped process of FR), **a'** left FR, ventral, **b** A1, **c** A2. **a, b** paratype 1, **c** holotype. *Scale bars* in μm

Mxl (Fig. 4b). Praecoxa with spinules at outer margin; arthrite incorporated, strongly developed, with 2 surface setae and 9 apical setae and spines. Coxa with cylindrical endite bearing 2 setae. Basis with 5 setae, enp and exp

incorporated in basis; enp and exp represented by 3 setae and 2 setae, respectively.

Mx (Fig. 4c, c'). Syncoxa with row of spinules at inner and outer margin, with two endites bearing 3 setae each.

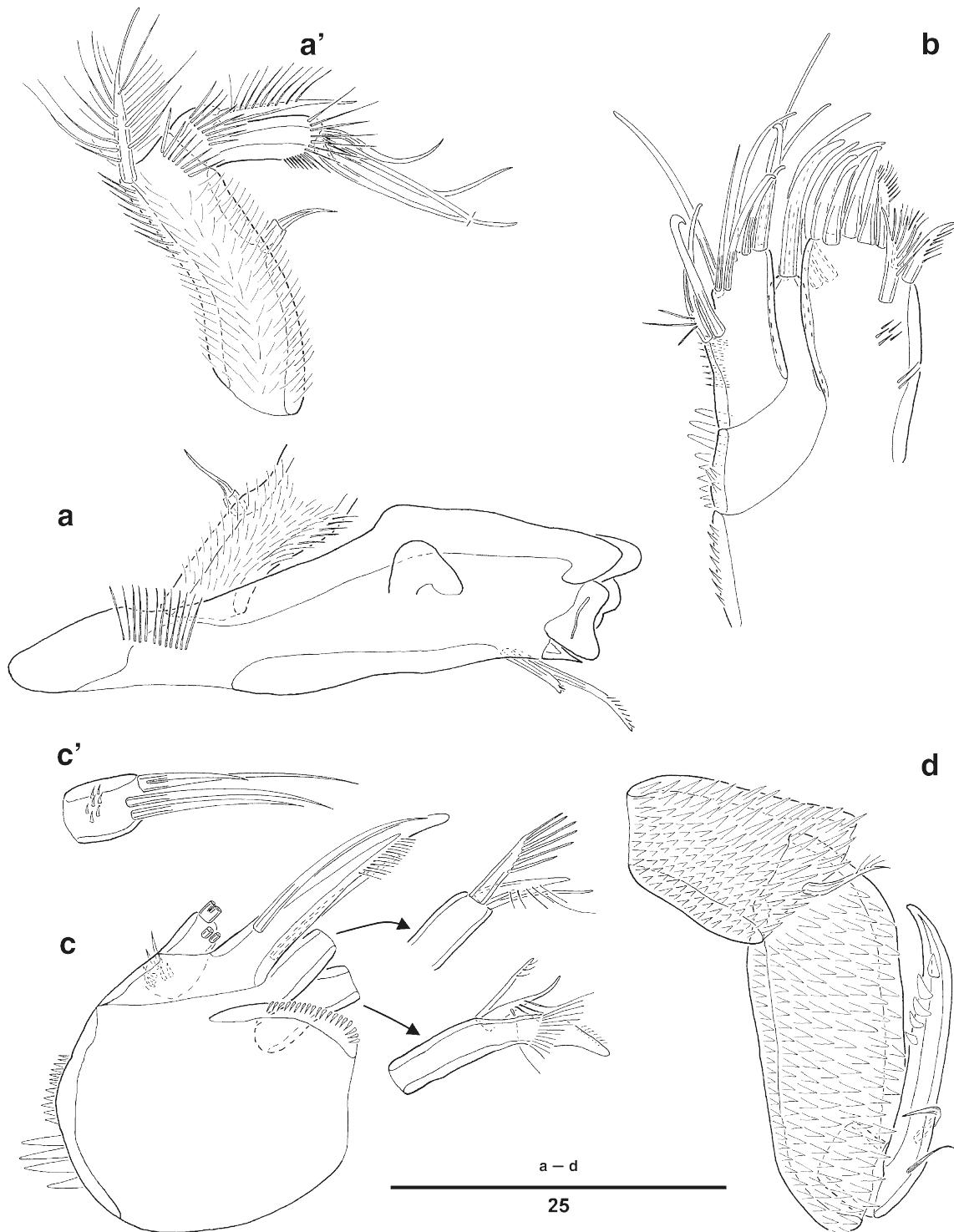


Fig. 4 *Tryphoema irmgardae* sp. nov., female. **a** Md, coxa, **a'** Mandibular palp from counterpart, **b** Mx1, **c** Mx (arrows indicate detailed drawings of endites), **c'** Mx enp from counterpart, **d** Mxp. **a** paratype 3, **b** paratype 2, **a'**, **c**, **c'** paratype 5, **d** paratype 4. Scale bar in μm

Allobasis produced into strong claw with 2 accompanying bare setae, one on anterior side, one on posterior side. Endopod (Fig. 4c') 1-segmented with 4 bare setae (two of which fused at their bases).

Mxp (Fig. 4d) prehensile. Syncoxa with short unipinnate seta at its distal margin. Syncoxa and basis completely

covered with broad denticles. Enp 2-segmented; enp-1 bare and small; enp-2 forming claw with distal row of spinules and proximally with 2 short bare setae (one on anterior, one on posterior side).

P1 (Fig. 5a) not prehensile. Outer margin of coxa and praecoxa laterally widened. Basis with 1 small, bare inner

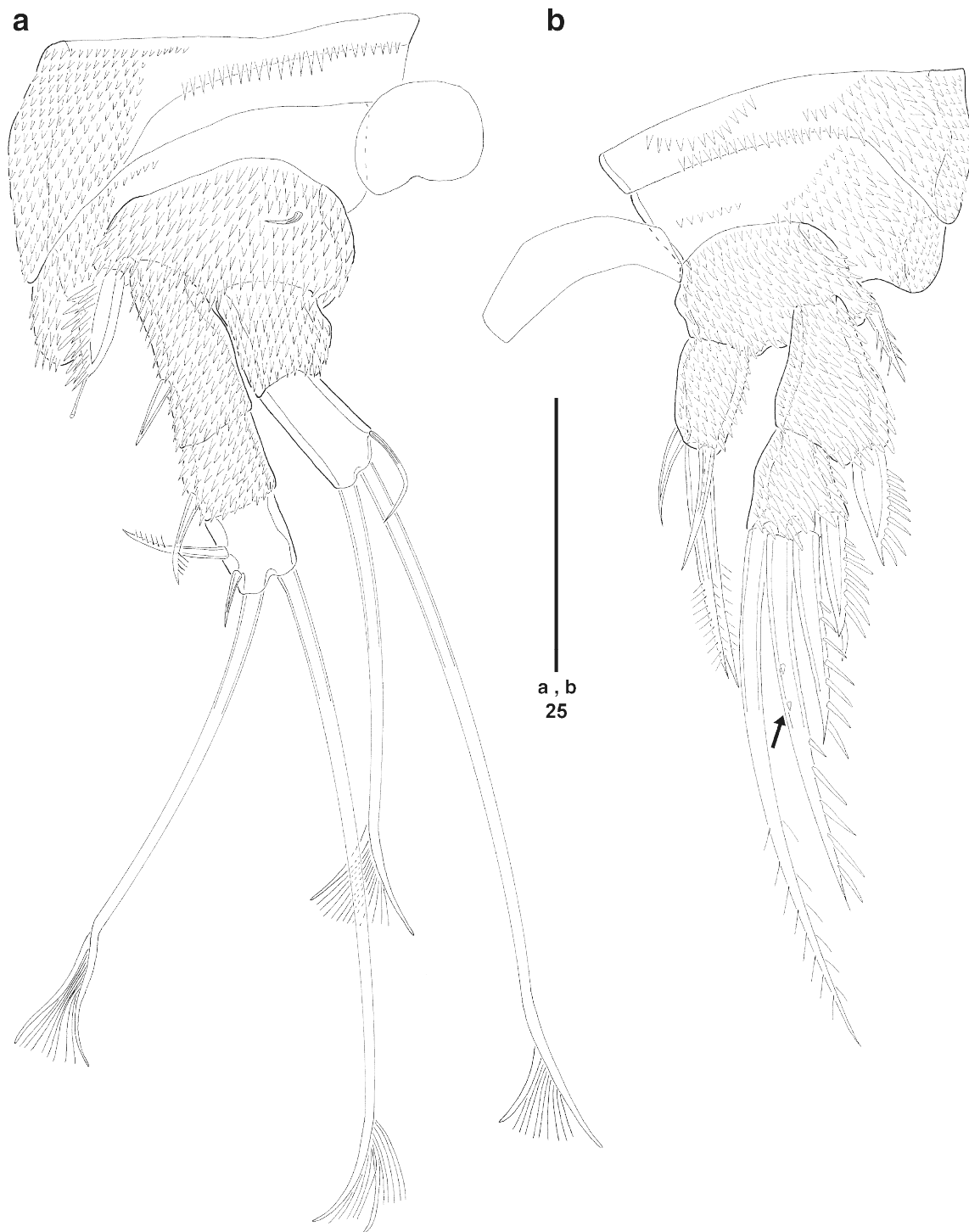


Fig. 5 *Tryphoema irmgardae* sp. nov., female. **a** P1, **b** P2 (arrow indicates ventrally shifted spinules). Both holotype. Scale bar in μm

seta and 1 strong, short und multipinnate outer spine. Enp 2-segmented, enp-1 shorter than enp-2 and without setae. Enp-2 distally with 2 long, apical setae with brush-like tip and 1 subapical, bare inner seta. Exp 3-segmented, exp-1 longest, about as long as exp-2 and -3 together. Exp-1 and exp-2 each with 1 outer spine (bare in exp-1, uniplumose in exp-2). Exp-3 with 2 outer spines (1 bare, 1 uniplumose);

apically with 2 long setae with brush-like tip. Except enp-2, exp-3 and intercoxal sclerite, all segments of P1 largely covered with denticles.

P2–P4 (Figs. 5b, 6a, b) outer margin of coxa and praecoxa laterally widened. Basis with 1 outer seta (short, strong and bipinnate in P2, longer and biplumose in P3 and P4). Basis, coxa and praecoxa mostly covered with

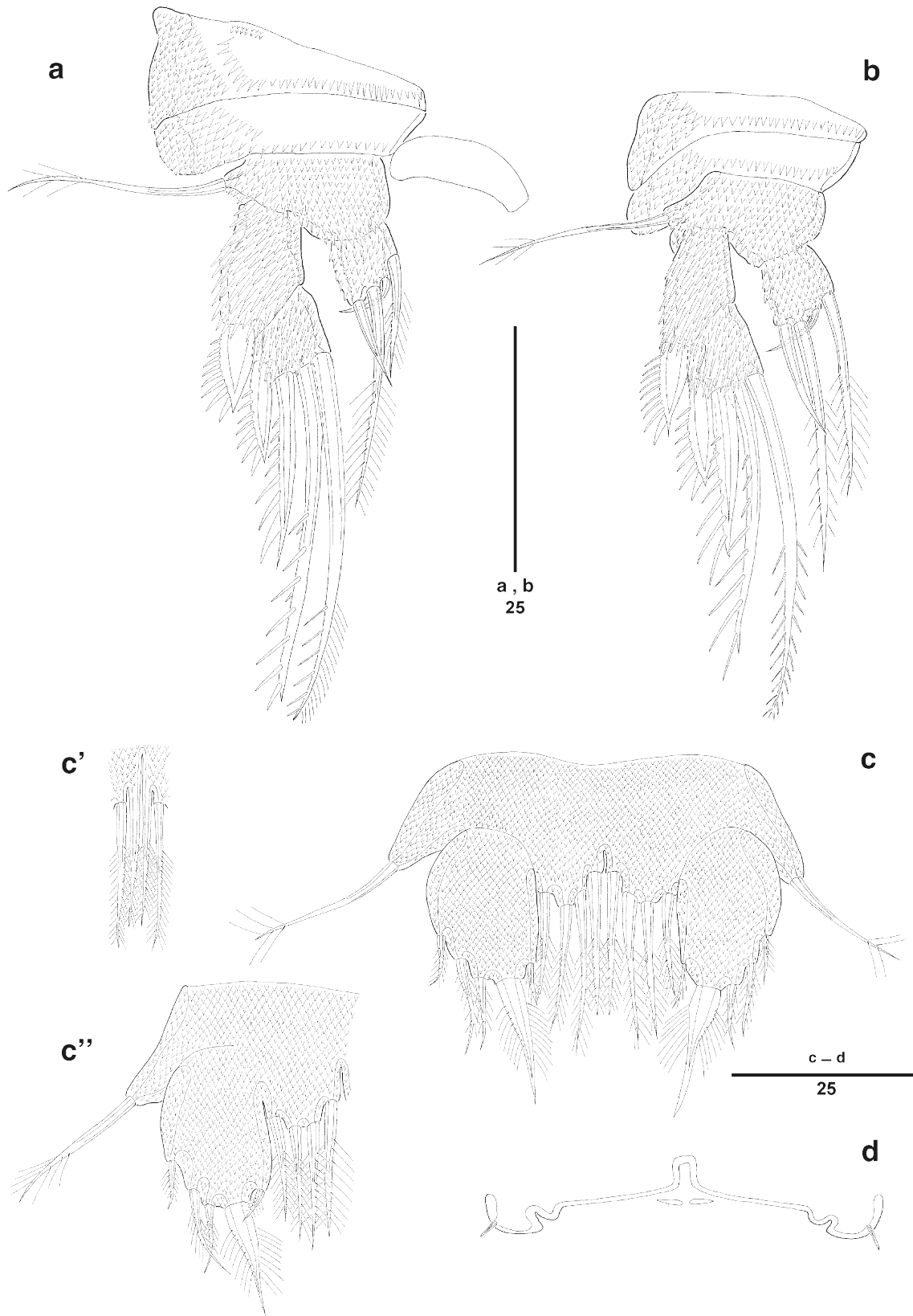


Fig. 6 *Tryphoema irmgardae* sp. nov., female. **a** P3, **b** P4, **c** P5, **c'** variability of P5, innermost setae of benp fused to the segment, **c''** variability of P5, exp partially fused to benp, **d** GF. **a–c** holotype, **c''**, **d** paratype 2, **c'** paratype 1. Scale bars in μm

denticles. Enp 1-segmented, with 4 setae in total; 1 subapical, inner seta (bare in P2, biplumose in P3–P4), 3 setae apically (outermost short and bare, second long and biplumose, third long and biplumose in P2, short, bare and characteristically curved backwards in P3 and P4). Exp 2-segmented. Exp-1 with 1 remarkably strong and short spinulose spine. Exp-2 with 4 spines in total; 1 subapical spinulose outer spine and 3 spines apically (outermost 2 spines spinulose, innermost spine biplumose). Exp and enp completely covered with denticles. Setation of P1–P4 is summarized in Table 1.

P5 (Fig. 6c, c', c''). Exp distinct, longer than broad (ca. 1.5 times); bearing 5 biplumose setae, fourth seta (counted from outer margin) remarkably strong. Left and right benp fused, each with 1 biplumose basal seta and 4 biplumose endopodal setae. Benps and exps completely covered with denticles.

GF (Fig. 6d). P6 strongly reduced, with 1 minute seta, not covering GF.

Description of male:

Sexual dimorphism expressed in following characters: body and appendages comparatively smaller, body length 320 μm (Fig. 7a), last thoracic and first abdominal somite not fused, shape and setation of A1 and P5.

A1 (Fig. 7c) 7-segmented, chirocer with geniculation between segments 6 and 7. First segment partially covered with denticles, with 1 plumose seta. Second segment with 9 setae; 2 biplumose, 2 bipinnate, 3 multipinnate (one of which articulated), 1 unipinnate and 1 bare. Third segment very small, with 9 setae; 8 bare (two of which articulated) and 1 biplumose. Fourth segment swollen, with 10 setae and 1 aes; 9 setae bare (one of which fused with aes), 1 seta biplumose. Fifth segment short and bare. Sixth segment bare. Seventh segment claw-shaped, equipped with 8 setae and 1 aes; 3 setae bare (two of which fused with aes (acrothek), third articulated), 4 setae plumose (three of which articulated), 1 spinulose spine. Setal formula: 1/1, 2/9, 3/9, 4/10 + aes, 5/0, 6/0, 7/8 + aes.

P5 (Fig. 7b) forming one continuous plate, exps incorporated into benps, benps fused. Six setae on each side; 1 bare basal seta, 2 biplumose endopodal setae at benp, 3 biplumose exopodal setae. Entire P5 covered with tiny denticles.

Intraspecific variation

Table 1 *Tryphoema irmgardae* sp. nov., setation of P1–P4

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

Several individuals of *T. irmgardae* sp. nov. show intra-specific variation in some spinulose spines of the distal exopodal segments of P2 to P4. A few spinules of these spines are not positioned in a perfect row, but are shifted laterally or ventrally (e.g. arrow Fig. 5b). Furthermore, the right exopod of the P5 in paratype 2 is partially fused with the baseoendopod (Fig. 6c'') and the innermost baseoendopodal seta of the P5 in paratype 1 is fused with the segment (Fig. 6c').

Tryphoema weneri sp. nov.

Type locality: Prainha, east coast of Madeira (32°44' 32.45"N, 16°42'57.41"W), sampling date 05/04/2011, sediment: medium grained sand mostly of volcanic origin; Reis Magos, south coast of Madeira (32°38'49.10"N, 16°49' 23.16"W), sampling date 23/05/2011, sediment: medium to fine grained sand mostly of volcanic origin; Seixal, north coast of Madeira (32°49'18.79"N, 17° 6'9.18"W), sampling date 08/04/2011, sediment: medium to fine grained sand of volcanic origin; southwest coast of Porto Santo (33° 3'7.59" N, 16°20'22.07"W), sampling date 15/05/2011, sediment: medium grained sand, mostly calcareous coral sands; water depth between 2 and 3 m, except Reis Magos at 13 m below sea level.

Material examined: Type material is deposited at the Museu Municipal do Funchal (História Natural; Funchal, Madeira, Portugal); Holotype: female, not dissected, 1 slide, collection number MMF 42479/1. Paratype 1: female, dissected on 16 slides, collection numbers MMF 42480/1–16. Paratype 2: female, dissected on 14 slides, collection numbers MMF 42481/1–14. Paratype 3: female, dissected on 4 slides, collection numbers MMF 42482/1–4. Paratype 4: male, dissected on 5 slides, collection numbers MMF 42483/1–5. Paratype 5: male, not dissected, 1 slide, collection number MMF 42484/1. Paratype 6: male, dissected on 2 slides, collection numbers MMF 42485/1–2.

Etymology: The species name *weneri* is given in grateful dedication to the author's father, Mr Werner Packmor (Banteln, Germany).

Description of female:

Habitus (Fig. 8) cylindrical, slightly dorsoventrally depressed. Length from anterior margin of cephalothorax to posterior margin of FR approximately 465 μm . Entire body surface and parts of mxp and swimming legs squamous covered with tiny cuticular denticles. Rostrum small and rounded, fused to cephalic shield, apically with 2 sensilla and one straight tube pore (drawn in Fig. 9b). Cephalothorax and all body somites (except third abdominal somite) with several pairs of sensilla. Last thoracic and first abdominal somite fused to genital double-somite. Telson (Fig. 9a) only slightly longer than preceding somite, 1 pair of sensilla near anterior margin of telson. Anal operculum dorsally with denticles, ventrally with fringe of setules and 1 pair of sensilla near lateral edge of operculum.

FR (Fig. 9a, a') 1.3 times as long as wide. Six setae present, seta III absent: I and II bare, closely together, seta II slightly longer than seta I, II inserting dorsolaterally, I inserting ventrolaterally. One tube pore inserting ventrolaterally besides seta II (Fig. 9a'). Setae IV, V and VI apically, IV and VI bare, V uniplumose and longest seta, more than 3 times longer than FR. VII located dorsolaterally at inner distal margin of FR, articulated and biplumose, its base inserted in pocket-shaped cuticular invagination. Dorsal distal margin of FR partly, ventral distal margin completely covered by scale-shaped cuticular process (arrow in Fig. 9a). FR completely covered with small denticles, like entire body surface.

A1 (Fig. 9b) 4-segmented, first and third segment with several spinules at inner and outer margin. First segment with 1 bipinnate seta at anterior distal margin. Second segment with 8 setae; 3 bipinnate (one of which articulated), 3 biplumose (two of which articulated), 2 multipinnate (one of which articulated). Third segment with 8 setae, 1 spinulose spine and 1 aes; 3 setae bare (one of which articulated and fused with aes), 4 biplumose (three of which articulated) and 1 unipinnate; spinulose spine apically with tube pore, its spinules flat, broad at their base and tapering towards their distal end (shape almost like husks of artichokes but more slender). Fourth segment with 8 setae, 2 spinulose spines and 1 slender aes; 4 bare setae (two of which fused with aes (acrothek)) and

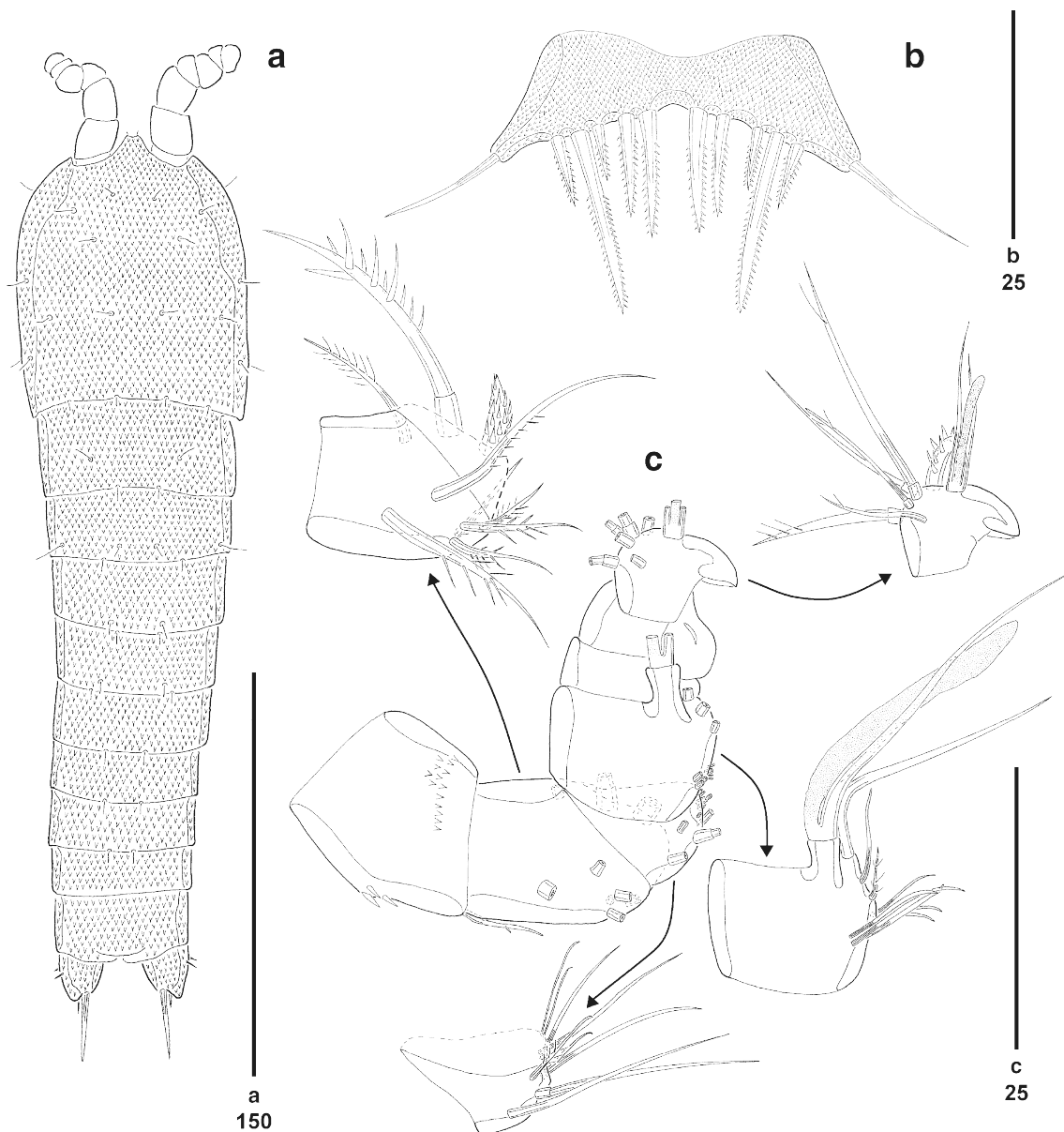


Fig. 7 *Tryphoema irmgardae* sp. nov., male. **a** Habitus dorsal, **b** P5, **c** A1, ventral (arrows indicate detailed drawings of several segments). **a**, **b** paratype 6, **c** paratype 7. Scale bars in μm

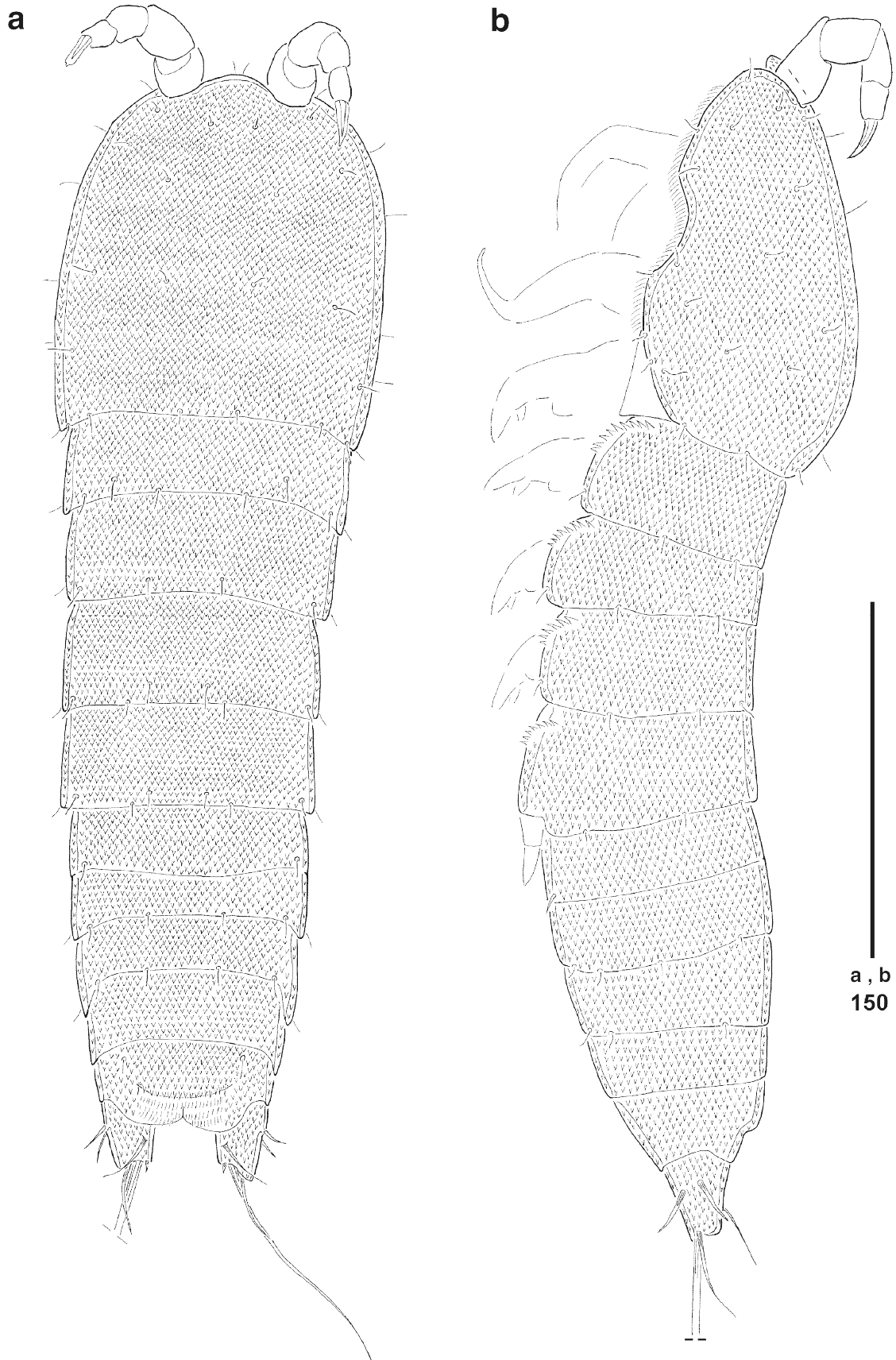


Fig. 8 *Tryphoema wernerii* sp. nov., female. **a** Habitus dorsal, **b** habitus lateral. **a** holotype, **b** paratype 1. Scale bar in μm

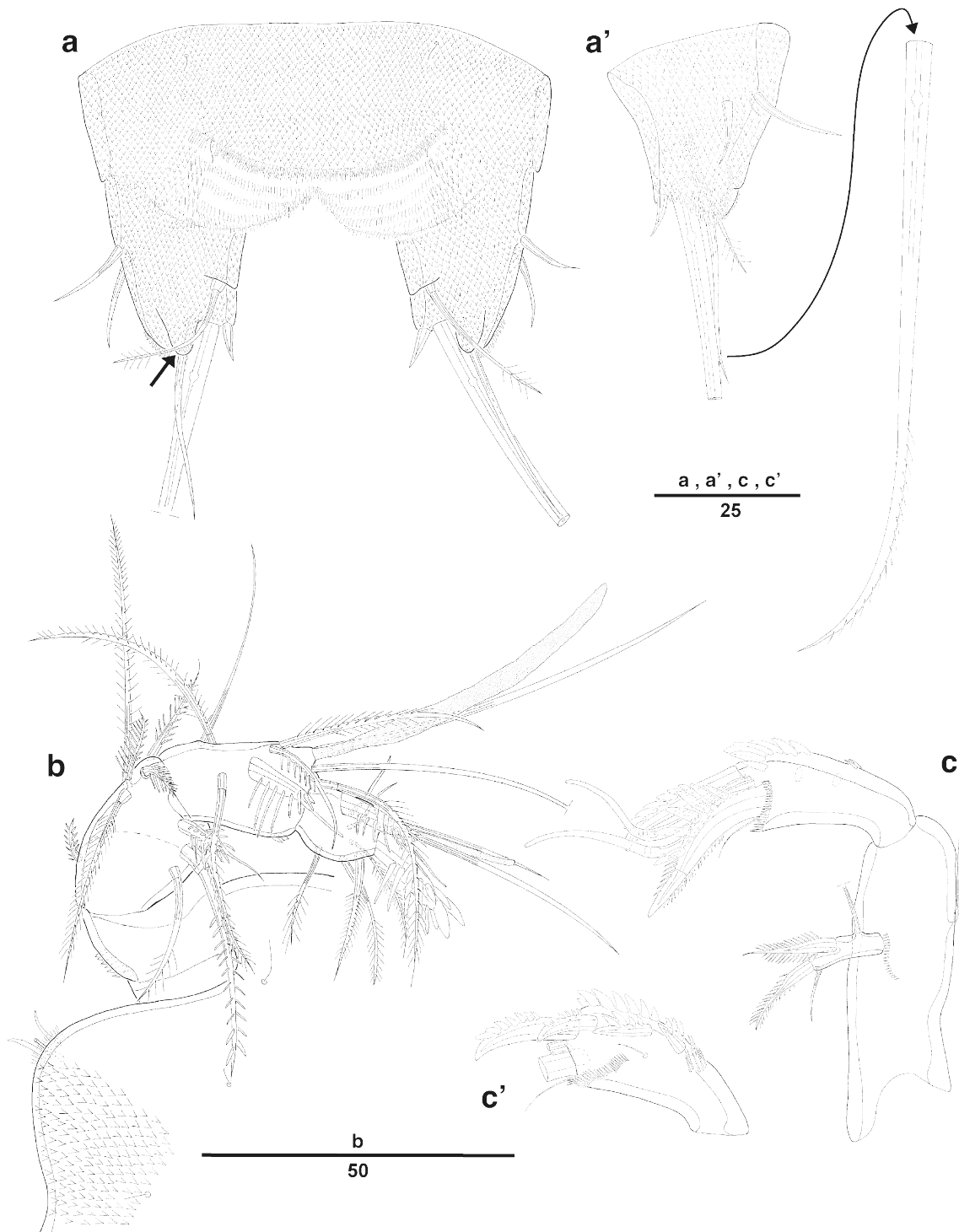


Fig. 9 *Tryphoema weneri* sp. nov., female. **a** Telson and FR, dorsal (arrow indicates scale-shaped process of FR), **a'** left FR, ventral (arrow indicates detailed drawing of seta V), **b** A1, **c** A2, **c'** A2 enp from counterpart. **a**, **b** holotype, **a'**, **c**, **c'** paratype 1. Scale bars in μm

4 biplumose; spinulose spine at inner margin resembles that of segment 3, while distal spinulose spine is much broader and lacks tube pore. Setal formula: 1/1; 2/8; 3/9 + aes; 4/10 + aes.

A2 (Fig. 9c, c') allobasis with row of setules and 1 abexopodal unipinnate seta. Exp 1-segmented, with 2 slender,

bare and 2 strong, biplumose setae. Enp with several slender spinules and row of broad and flat spinules at anterior margin, with row of small spinules each apically (Fig. 9c) and laterally (Fig. 9c'); apically with 2 bare geniculate setae and 2 spinulose spines (outermost spinulose spine very strong, articulated

at its tip and displaying heteromorphic spinules, 1 long and slender tube pore, inserting at its base); near anterior margin with 3 spinulose spines and 1 sensillum (Fig. 9c').

Md (Fig. 10a). Coxa with strong gnathobase with 6 major blunt teeth overlapping each other, innermost articulated; with 1 bare and 1 minute, unipinnate accessory seta and row of slender, long setules. Mandibular palp with basis, exp and enp. Basis with 1 strong multiplumose seta distally at inner margin. Exp 1-segmented, strongly reduced, with 1 bare seta. Enp 1-

segmented with 1 strong biplumose seta laterally and 4 bare setae apically, which are fused at their bases. Basis and enp covered with several rows and patches of slender, long setules.

Mxl (Fig. 10b). Praecoxa with numerous spinules at outer margin; arthrite incorporated, strongly developed, with 2 surface setae and 9 apical setae and spines. Coxa with cylindrical endite bearing 2 setae. Basis with 6 setae, enp and exp incorporated in basis; enp and exp represented by 3 setae and 2 setae, respectively.

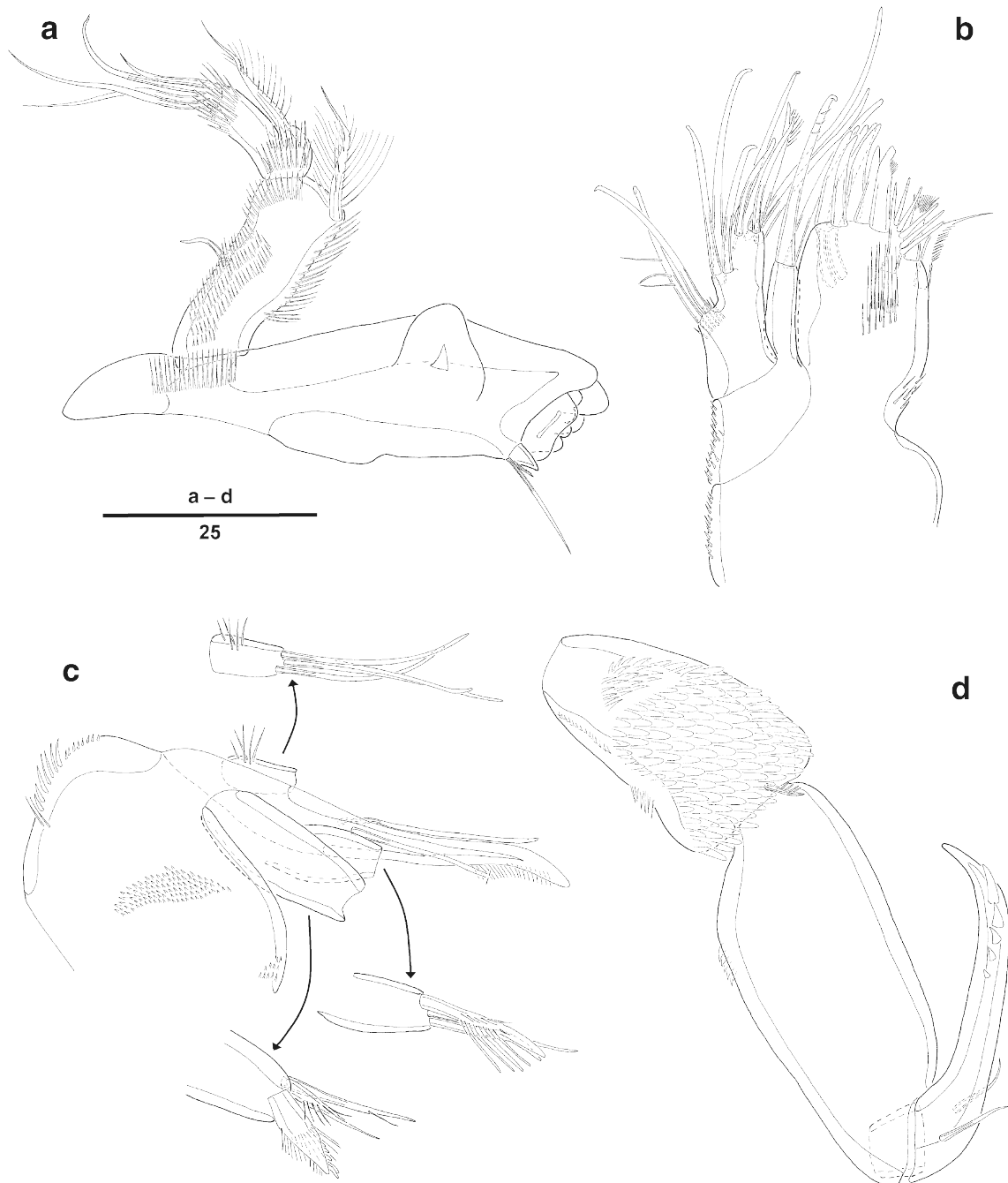


Fig. 10 *Tryphoema wernerii* sp. nov., female. **a** Md, **b** Mxl, **c** Mx (arrows indicate detailed drawings of endites and exp), **d** Mxp. **a–d** paratype 1. Scale bar in μm

Mx (Fig. 10c). Syncoxa with several rows and groups of setules and spinules, with two endites bearing 3 setae each. Allobasis produced into strong claw with 2 accompanying, bare setae (one on anterior side, one on posterior side). Enp

1-segmented with 4 bare setae (two of which fused at their bases).

Mxp (Fig. 10d) prehensile. Syncoxa with 1 minute, unipinnate seta at its distal margin, surface covered with

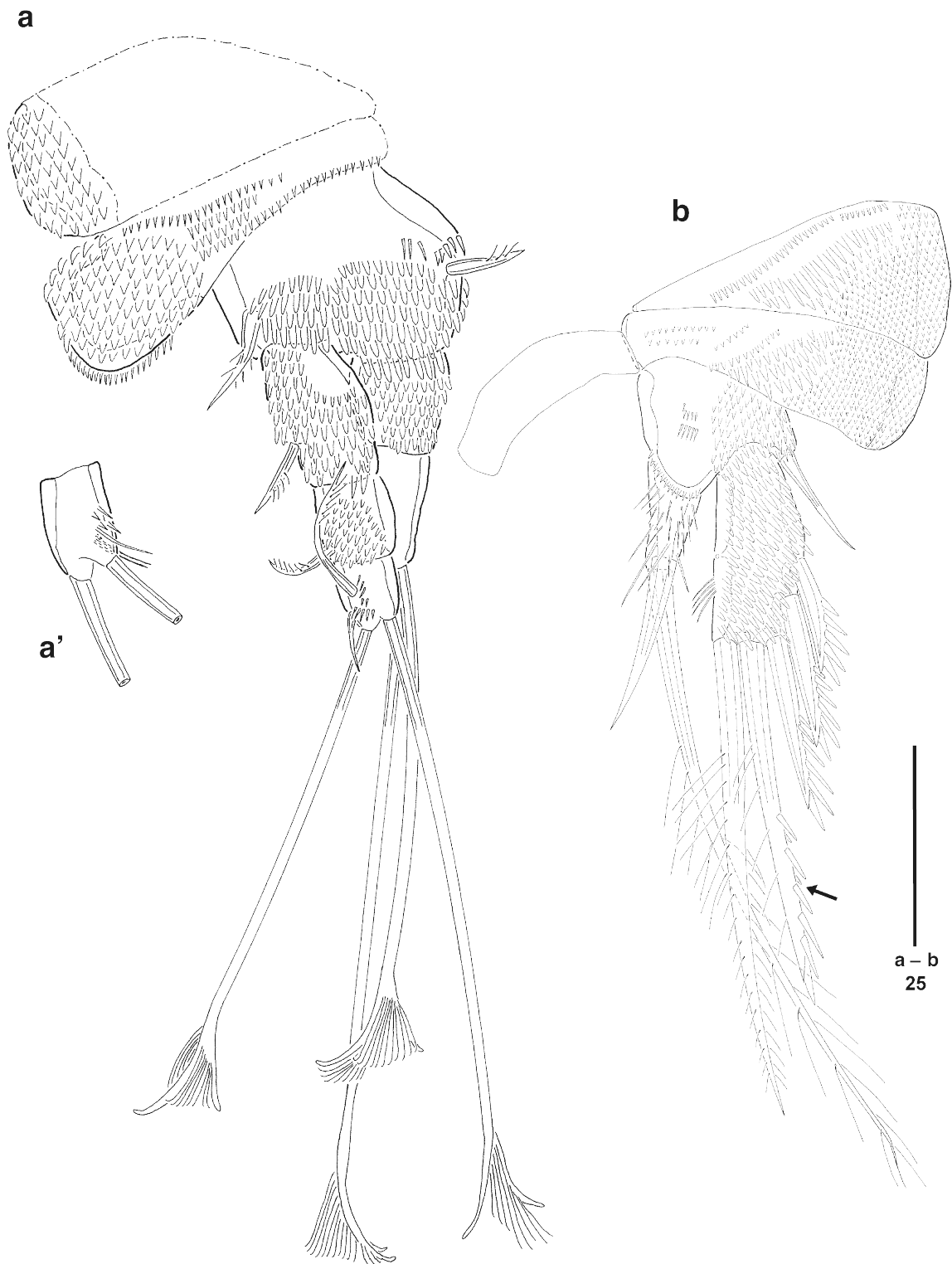


Fig. 11 *Tryphoema wernerii* sp. nov., female. **a** P1 (praecoxa and coxa partially broken), **a'** P1 distal segment of enp (from counterpart), **b** P2 (arrow indicates laterally shifted spinules). **a, a'** paratype 3, **b** paratype 2. Scale bar in μm

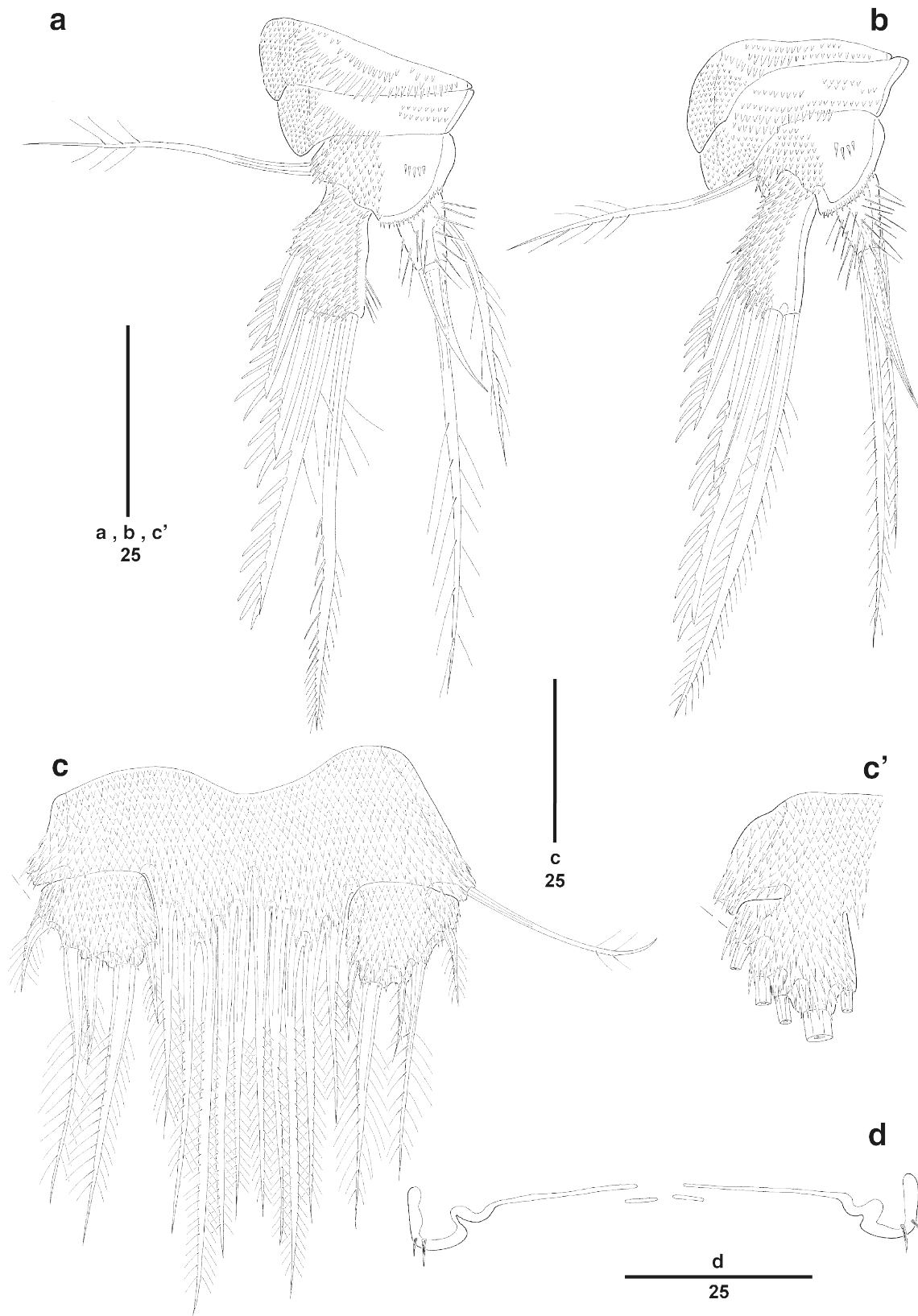


Fig. 12 *Tryphoema weneri* sp. nov., female. **a** P3, **b** P4, **c** P5, **c'** variability of P5, exp partially fused to benp, **d** GF. **a** paratype 2, **b**, **c'** paratype 1, **c**, **d** paratype 3. Scale bars in μm

Table 2 *Tryphoema weneri* sp. nov., setation of P1–P4

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

broad denticles and patches of smaller setules. Basis bare, with short row of denticles at outer margin. Enp 2-segmented; enp-1 bare and small; enp-2 forming claw with distal row of spinules and proximally 2 short, bare setae (one inserting anteriorly, one posteriorly).

P1 (Fig. 11a, a') not prehensile. Outer margin of coxa and praecoxa laterally widened. Basis with 1 inner and 1 outer seta, both plumose. Enp 2-segmented, enp-1 slightly shorter than enp-2 and without setation. Enp-2 with several setules at outer distal margin (Fig. 11a'), apically with 2 long setae with brush-like tip. Exp 3-segmented, exp-1 longest, exp-3 slightly shorter than exp-2. Exp-1 and exp-2 each with 1 uniplumose outer spine. Exp-3 with 1 uniplumose and 1 bare outer spine, apically with 2 long setae with brush-like tip. Except enp-2, exp-3 and intercoxal sclerite, all segments of P1 largely covered with denticles.

P2–P4 (Figs. 11b, 12a, b) outer margin of coxa and praecoxa laterally widened. Basis with 1 outer seta, (short and bare in P2, remarkably longer and biplumose in P3 and P4). Basis, coxa and praecoxa mostly covered with denticles. Enp 1-segmented, apically with 1 bare, strong and short seta and 1 long, biplumose seta, in P3 and P4 additionally with 1 biplumose seta, inserting near middle of inner margin. Exp 1-segmented with 5 spines in total; 2 spinulose outer spines and 3 spines apically (2 outermost spines spinulose, innermost spine biplumose). Exp and enp completely covered with denticles, slender and long at enp, broader at exp. Setation of P1–P4 is summarized in Table 2.

P5 (Fig. 12c, c'). Exp distinct, slightly broader than long, with 5 biplumose setae, fourth seta (counted from outer margin) longest and strongest. Left and right benps fused, each with 1 biplumose basal seta and 5 biplumose endopodal setae, fused to segment. Benps and exps completely covered with denticles.

GF (Fig. 12d). P6 strongly reduced, with 2 setae. GF not covered.

Description of male:

Sexual dimorphism expressed in following characters: body and appendages smaller, body length 430 μm (Fig. 13a), last thoracic and first abdominal somites not fused, shape and setation of A1 and P5.

A1 (Fig. 13b) 7-segmented, chirocer with geniculation between segments 6 and 7. First segment partly covered with denticles and with 1 plumose seta. Second segment with 9 setae; 6 biplumose, 1 bipinnate and articulated, 2 multiplumose. Third segment very small, with 9 setae; 7 bare (one of which articulated), 2 biplumose. Fourth segment swollen, with 10 setae and 1 aes; 8 setae bare (one of which fused with aes) and 2 uniplumose. Fifth segment short, bare and largely enclosed by segment 4. Sixth segment bare. Seventh segment claw-shaped, with 8 setae and 1 aes; 3 setae bare (two of which fused with aes (acrothek)), 5 plumose (four of which articulated). Setal formula: 1/1, 2/9, 3/9, 4/10 + aes, 5/0, 6/0, 7/8 + aes.

P5 (Fig. 13c). Exp incorporated in benp. Left and right benp distinct. Each P5 with 6 biplumose setae in total; 1 basal seta, 2 endopodal setae, 3 exopodal setae. All setae of P5 distinct in contrast to benp of female's P5, which are fused to segment. Entire P5 covered with slender, long denticles.

Intraspecific variation:

Several individuals of *T. weneri* sp. nov. show intraspecific variation in some spinulose spines of the exopods of P2 to P4. A few spinules of these spines are not positioned in a perfect row, but are shifted laterally (e.g. arrow Fig. 11b). Furthermore, the right exopod of the P5 of paratype 1 is partially fused with the baseoendopod (Fig. 12c').

Key to the species of the genus *Tryphoema*

1. P2–P4 exp 1-segmented.....
..... *T. weneri*, new species
- P2–P4 exp 2-segmented.....2
2. P2–P4 enp with 1 seta; P5 ♀ exp with 6 setae
..... *T. ramabula* (Pennak, 1942)
- P2–P4 enp with at least 2 setae; P5 ♀ exp with
at most 5 setae.....3
3. P1 enp-2 with 3 setae, P2–P4 enp with 4 setae
.....*T. irmgardae* new species
- P1 enp-2 with 3 setae, P2–P4 enp with 3 setae
.....*T. porca* Monard, 1926
- P1 enp-2 with at most 2 setae.....4
4. P5 ♀ benp with 3 endopodal setae; P5 ♂ exp distinct,
left and right P5 fused.....*T. riedli* Coull, 1971
- P2–P4 exp-2 with setation 4:3:3; P5 ♂ exp
incorporated, left and right P5 fused.....
.....*T. bocqueti* (Bözić, 1954)
- These characters not combined.....5
5. P1 exp-3 without outer spine; P2–P4 exp-2
with setation 3:3:3.....
.....*T. lusitanica* (Wells and Clark, 1965)
- P1 exp-3 with outer spine; P2–P4 exp-2 with setation
4:3:4.....*T. scilloniensis* (Wells, 1968)

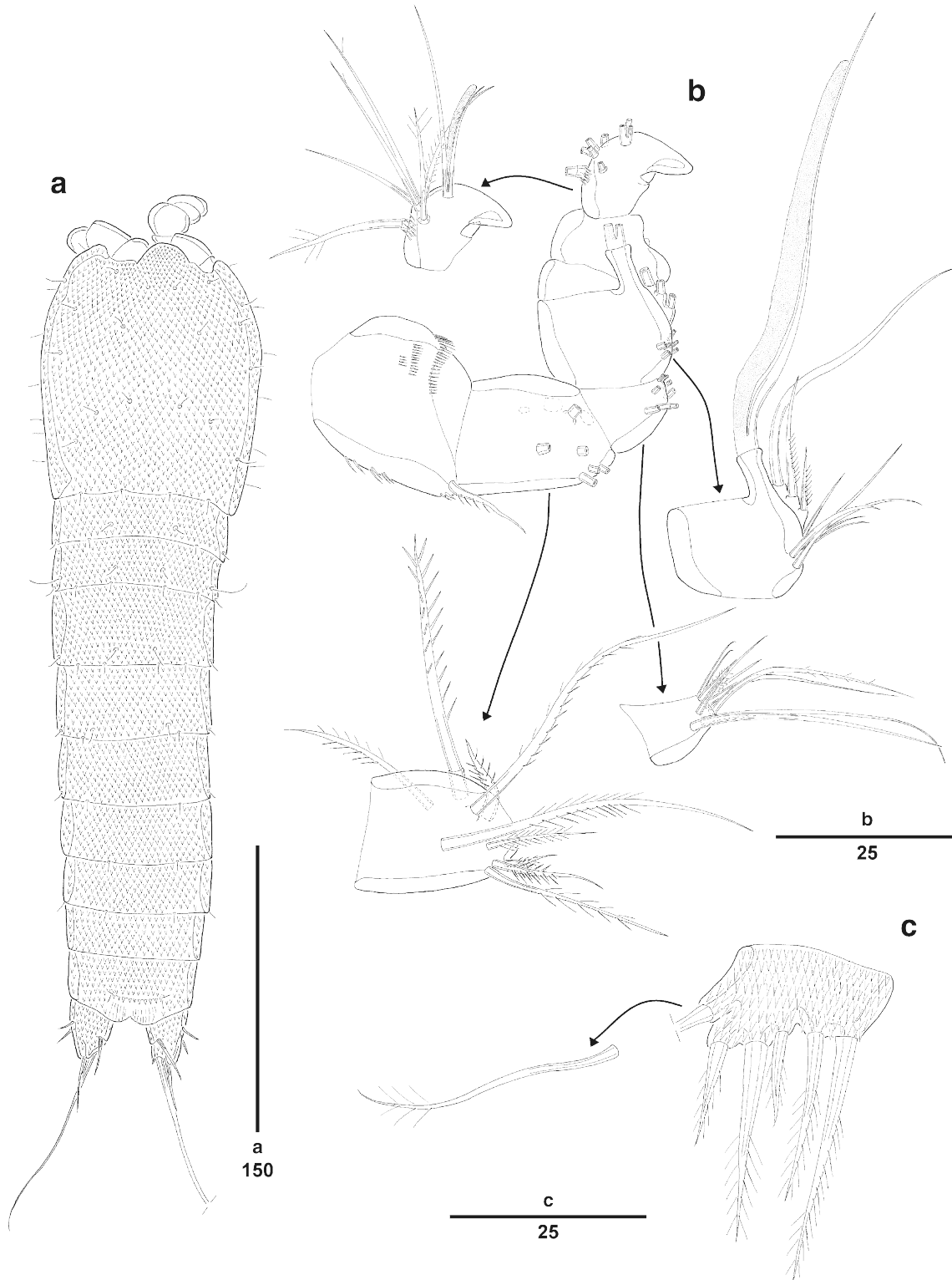


Fig. 13 *Tryphoema weneri* sp. nov., male. **a** Habitus dorsal, **b** A1, ventral (arrows indicate detailed drawings of segments 2–4 and 7), **c** P5 (outer basal seta broken, drawing from paratype 6). **a** paratype 5, **b**, **c** paratype 4. Scale bars in μm

Discussion

The Rhizotrichidae Por, 1986, which comprise 18 species to date (11 in *Rhizothrix* and 6 + 2 new in *Tryphoema*), are well characterised by four apomorphic characters (Por 1986) (plesiomorphies in square brackets):

1. Body covered by a dense pubescence [body not completely covered with setules or denticles]
2. A1 ♀ distal segment apically with 1 remarkably short, strong, spinulose spine [setae of A1 ♀ distal segment not remarkably short and thickened]
3. P1 exp distal segment with 2 long setae with apical brush [P1 setae without apical brush]
4. P1 enp distal segment with 2 long setae with apical brush [P1 setae without apical brush]

Character 1: The entire body surface and parts of the appendages are completely and squamous covered with slender or broad denticles in most species of Rhizotrichidae (except six species with unknown texture of their body surface; namely *Rhizothrix curvata* (Brady, 1880), *R. gracilis* (T. Scott, 1903), *R. scotti* (Lang, 1936), *R. tenella* (Wilson, 1932) *R. reducta* Noodt, 1952, *R. wilsoni* Bodin, 1979 and *Tryphoema ramabula* (Pennak, 1942)). In most taxa of the Harpacticoida, the body surface is smooth with a particular ornamentation of setules or spinules. Even closely related taxa, like the Cletodidae T. Scott, 1905, lack such an overall coverage of the body surface, which supports the recognition of this character as apomorphic for the Rhizotrichidae (however this character needs to be checked in the six species mentioned above).

Character 2: All representatives of the Rhizotrichidae display a remarkably strong and short spine, equipped with broad spinules, which is positioned apically at the distal segment of the female's antennule. The development of short spines instead of long setae is proposed to be a derivation because setae tend to be long and slender in most harpacticoid copepods and especially in basal families (like the Aegisthidae Giesbrecht, 1892 and Rometidae Seifried and Schminke, 2003; (Seifried 2003)). The remarkably strong and spinulose spine at the antennule of the Rhizotrichidae is assumed to be apomorphic for the family since there is no comparable spine of this shape at the distal segment of the antennule of presumably related families (e. g. Cletodidae, Huntmaniidae Por, 1986).

Characters 3 and 4: All species of the Rhizotrichidae display long and slender setae with an apical brush distally on the endopods and exopods of the P1. Similar setae can only be found in very few taxa of the Harpacticoida like for example the genus *Orthopsyllus* Brady and Robertson, 1873. *Orthopsyllus* is included in the supra-familiar taxon Laophontoidea T. Scott, 1905 (Huys 1990) and displays

none of the apomorphic characters of the Rhizotrichidae. Therefore, it appears to be likely, that this type of seta has evolved several times independently within the Harpacticoida. In case of the Rhizotrichidae, it can be recognized as an apomorphic character of the family.

Tryphoema irmgardae sp. nov. and *Tryphoema weneri* sp. nov. show all four apomorphies of the Rhizotrichidae and can easily be classified within this family. The Rhizotrichidae comprise the genera *Rhizothrix* Sars, 1909 and *Tryphoema* Monard, 1926. To date, *Rhizothrix* cannot be justified as a monophylum because it is not characterised by any apomorphic character. On the contrary, representatives of *Tryphoema* display six apomorphies (Monard 1926, Lang 1948) (plesiomorphies in square brackets):

5. P2 enp 1-segmented [P2 enp 2-segmented]
6. P3 enp 1-segmented [P3 enp 2-segmented]
7. P4 enp 1-segmented [P4 enp 2-segmented]
8. P2 exp 2-segmented [P2 exp 3-segmented]
9. P3 exp 2-segmented [P3 exp 3-segmented]
10. P4 exp 2-segmented [P4 exp 3-segmented]

The reduced number of endopodal and exopodal segments of legs 2–4 are assumed to be apomorphic characters based on the oligomerisation principle (Huys and Boxshall 1991). Due to the fact, that all six morphological characters of the genus are fulfilled, *T. irmgardae* sp. nov. can surely be placed within *Tryphoema*. *Tryphoema weneri* sp. nov. shows a further reduction of the number of the exopodal segments at P2–P4, and is the only representative of the family with 1-segmented exopods. *T. weneri* sp. nov. complies with morphological characters 5–7, whereas it displays an even progressed state of derivation in the characters 8–10. Besides the reduced number of exopodal segments, *T. weneri* sp. nov. displays no further autapomorphic characters. Therefore, this species is placed within *Tryphoema* as well, instead of establishing a new genus. This requires a rephrasing of the apomorphic characters 8–10, i. e. the exopods of P2–P4 are 1- to 2-segmented (this adaptation has been adopted in the advanced generic diagnosis of *Tryphoema*, provided in this publication).

Most species of *Tryphoema* display at most 3 setae at the endopods of P2–P4. Only exception is *T. irmgardae* sp. nov., which bears 4 setae at the endopods of P2–P4. Following the oligomerisation principle (Huys and Boxshall 1991), a reduction of setae is more likely than the development of an additional seta. Therefore, the setation of the endopods of *T. irmgardae* sp. nov. must be considered as a plesiomorphy. Comparing the endopods P3 and P4 of *T. weneri* sp. nov. and *T. irmgardae* sp. nov., it is likely that, counted from the inner margin, seta 2 of *T. irmgardae* sp. nov. is lost in *T. weneri* sp. nov.. For the P2 endopod, the homologisation of setae is

Table 3 Main differences between *Tryphoema irmgardae* sp. nov. and *Tryphoema weneri* sp. nov.

	<i>T. weneri</i>	<i>T. irmgardae</i>
Rostrum	Rounded	Bifid
Furca	Sensillum laterally besides seta II Seta V more than 3 times longer than FR	Spinules between seta I and II Seta V only slightly longer than FR
Mxl	Basis with 6 setae	Basis with 5 setae
Mxp	Basis bare	Basis completely covered with denticles
P1	Enp-2 with 2 setae Outer basal seta short and bifid	Enp-2 with 3 setae Outer basal seta remarkably thickened and multi-spinulose
P2	Exp 1-segmented Enp with 2 setae Outer basal seta bare Exp outer spines only slightly thickened Enp cylindrical Enp with slender and long setules	Exp 2-segmented Enp with 4 setae Outer basal seta short and spinulose Exp outer spines remarkably short and thickened Enp broadend Enp with short and broad denticles
P3 and P4	Exp 1-segmented Enp 3 setae Enps cylindrical Enp with slender and long setules Exp outer spines short	Exp 2-segmented Enp 4 setae Enps as broad as long and flattened Enp with short and broad denticles Exp outer spines remarkably short and thickened
P5 ♀	Exp as long as broad Benp 5 setae Benp setae fused to the segment Exp setae 4 (counted from outer margin) only slightly thickened	Exp longer than broad Benp 4 setae Benp setae distinct Exp setae 4 remarkably thickened and short
P5 ♂	Benp distinct	Benp fused
GF	P6 strongly reduced with 2 setae	P6 strongly reduced with 1 seta

difficult; the innermost seta as well as one of the apical setae are lost in *T. weneri* sp. nov..

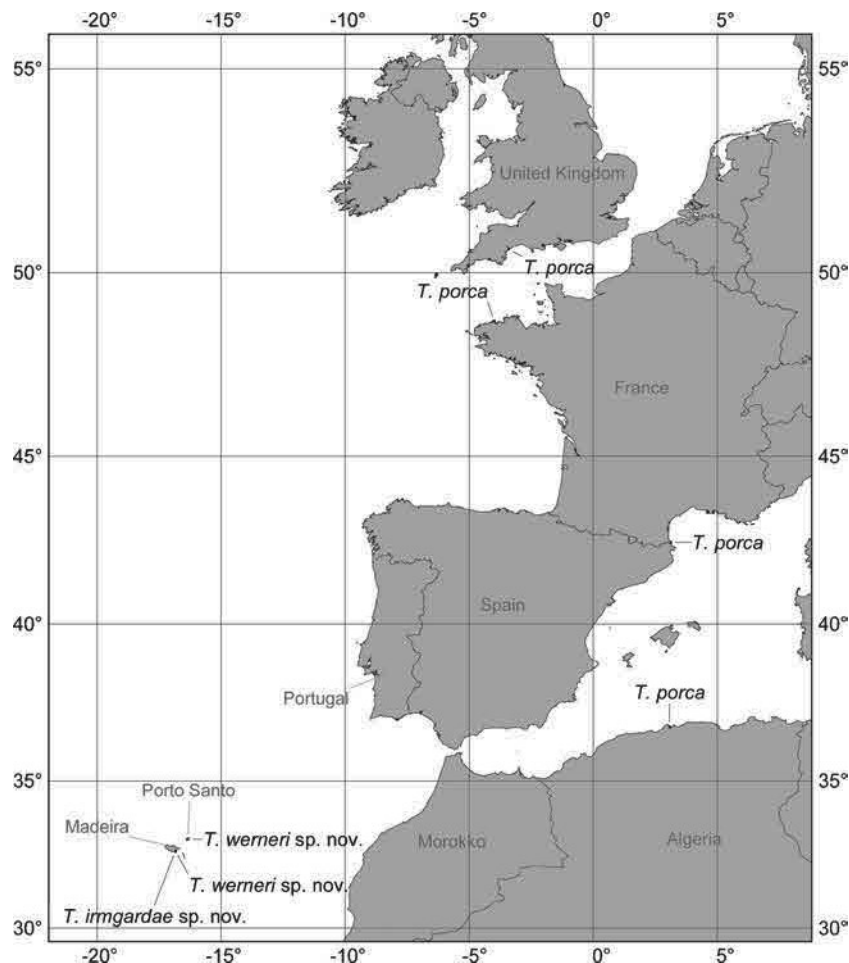
T. weneri sp. nov. and *T. irmgardae* sp. nov. differ from each other in many morphological characters which is shown in Table 3. The characters both new species have in common can be found in at least one or more other species of the genus: for example, the outer margin of the coxa and praecoxa of P1–P4 is remarkably laterally widened, which they have in common with *T. lusitanica* (Wells and Clark, 1965), *T. ramabula* (Pennak, 1942) and *T. scilloniensis* (Wells, 1968) (the coxa and praecoxa have unfortunately not been considered in the remaining species descriptions). On the other hand, *T. irmgardae* sp. nov. shares several similarities with the type species *T. porca* Monard, 1926, which has been found along the south and north coast of France (Monard 1926, 1928 and 1935), at the coastline of Algeria (Monard 1937) and at the estuary of the River Exe (United Kingdom, Wells 1963) (Fig. 14). Both species display the plesiomorphic character state of a third seta at the distal segment of the P1 endopods, while all remaining species of the genus possess 2 setae. Synapomorphic characters of *T. irmgardae* sp. nov. and *T. porca* are (plesiomorphies in square brackets):

11. P2 to P4 exp outer spines remarkably thickened [outer spines not remarkably thickened]
12. P5 ♀ benp with 4 inner setae [P5 ♀ benp with 5 inner setae]
13. Mxp basis completely covered with denticles [Mxp basis bare]

Character 11: As already mentioned above, short setae are assumed to be derivative compared with long and slender setae and the same development is assumed for spines. All representatives of the genus *Tryphoema* display comparatively short spinulose outer spines at the exopods of P2 to P4, but the outer spines of *T. irmgardae* sp. nov. and *T. porca* are remarkably short and thickened, which is assumed to be an apomorphic character for both species.

Character 12: *T. irmgardae* sp. nov. and *T. porca* bear only 4 endopodal setae at the baseoendopods of the female's P5 while the remaining representatives of the family Rhizotrichidae display 5 endopodal setae (only exception is *T. riedli* with solely 3 setae). It is likely that in these two species (*T. irmgardae* sp. nov. and *T. porca*) one endopodal seta of the baseoendopod is lost and the presence of only four instead of five setae is considered an apomorphy of both species.

Fig. 14 Finding locations of *Tryphoema irmgardae* sp. nov., *Tryphoema weneri* sp. nov. and *Tryphoema porca* Monard. (Map-Source: Pangaea PanMap)



Character 13: The basis of the maxilliped is completely covered with tiny denticles in *T. irmgardae* sp. nov. and *T. porca*, whereas in all other representatives of the genus or even of the family Rhizotrichidae it is at most ornamented with one or several rows of spinules (in some species the ornamentation of the appendages is unfortunately unknown). Additionally, a squamous coverage of the basis of the maxilliped cannot be found in closely related families like for example the Cletodidae. For that reason, the ornamentation of the basis of the maxilliped is assumed to be an apomorphy of *T. irmgardae* sp. nov. and *T. porca*.

The similarities of *T. irmgardae* sp. nov. and *T. porca* indicate, that both species are closely related. The large amount of differences between the Madeiran species *T. irmgardae* sp. nov. and *T. weneri* sp. nov. and the close relation between *T. irmgardae* sp. nov. and *T. porca* might indicate, that representatives of Rhizotrichidae settled the island of Madeira twice, independently of one another. A second possibility is that the two different Madeiran species of Rhizotrichidae evolved through radiation. Nonetheless the history and mechanisms of the colonisation of Madeira (concerning Rhizotrichidae) remains unclear to date and

further information is needed for valid hypothesis. For profound statements on the phylogeny and biogeography of the genus *Tryphoema* and the Rhizotrichidae comprehensive revisions of the whole family are urgently needed. The majority of original species descriptions concerning this family do not comply with contemporary standards and are therefore hardly comparable. For that reason, many morphological characters could not be used in a comparison of the species.

All species of Rhizotrichidae were found in shallow-water habitats, except a single specimen from deep-sea sediments of the Angola basin (Rose et al. 2005) at a depth of 5,448 m (not yet described). *T. irmgardae* sp. nov. and *T. weneri* sp. nov. were both found in sandy sediments in shallow water depths (*T. irmgardae* sp. nov. from 10 to 13 m, *T. weneri* sp. nov. from 2 to 3 m and 13 m). While *T. weneri* sp. nov. occurs on Madeira and Porto Santo, *T. irmgardae* sp. nov. was found at one sampling location at the south coast of Madeira (Reis Magos). At this sampling location both species were present. *T. weneri* sp. nov. occurs in low abundances (single specimens up to 5 adult individuals per sample) whereas *T. irmgardae* sp. nov. was found in comparatively higher abundances (up to 44 adult specimens per sample).

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