Meiofauna Marina, Vol. 19, pp. 173–193, 14 figs., 1 tab., September 2011

Isthmiocaris laurae sp. nov. (Crustacea, Copepoda, Harpacticoida) from the Angola Basin – first deep-sea species of the genus with remarks on its copepodid development

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Abstract

The new species presented here contributes to the description of the community of Harpacticoida in the West-African Angola Basin and adds a new member to the few known deep-sea Canthocamptidae. *Isthmiocaris laurae* sp. nov. represents the first congener of *Isthmiocaris longitelson* George & Schminke, 2003 from the Patagonian continental shelf. In spite of the missing isthmion, a collar between the cephalothorax and the first free thoracic segment, the new species is placed in the genus *Isthmiocaris*. Three synapomorphies support the monophyletic status of the genus: the characteristical cylindrical, vermiform body shape, the elongated telson, and the elongated third endopodal segment in the third swimming leg of the male. *I. laurae* sp. nov. shares with *I. longitelson* and certain other marine canthocamptid species a sabre-like apophysis in the male enp2 P3 and the strongly derived outer seta and 2 apical setae in the male enp P4. In most characters *I. laurae* sp. nov. is more plesiomorphic than *I. longitelson*. The autapomorphies of the new species are an elongate enp2 P2 in the male; a gripper-like, twisted, highly ornamented, and twofold serrated element the male enp2 P4; rat-tailed setae in several mouthparts; and the sexually dimorphic body size with male being 3.4 times smaller than the female. Besides the pronounced differences in the body size of male and female, *I. laurae* sp. nov. shows sexual dimorphisms in the segmentation and setation of the swimming legs, and the relation of body size to the size of the swimming legs. Males and females of *I. laurae* sp. nov. can be matched by comparing the copepodid stages. The observed oligomerisation in the female enps of the swimming legs is manifested after the moult from CV to CVI.

Keywords: Abyssal plains, Meiofauna, Systematics, Sexual dimorphism, Developmental stages, Canthocamptidae, *Pyrocletodes* Coull, 1973

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Introduction

During the last years, deep-sea copepods came more into the focus of taxonomic studies. With an increasing number of deep-sea expeditions dedicated to taxonomy and biogeography and the success of the "Census of the Diversity of Abyssal Marine Life" (CeDAMar) programme many new species have been described. Some of the most recent articles on abyssal-plain Copepoda deal with new species from the Guinea and the Angola Basin (e.g., Seifried & Martínez Arbizu 2008, George 2008, Menzel & George 2009, Veit-Köhler & Drewes 2009, Willen & Dittmar 2009, Corgosinho & Martínez Arbizu 2010, Menzel 2010), or the South Atlantic, Cape Basin, and the Southern Ocean (e.g., Willen 2008, 2009; Gheerardyn & George 2010). Deep-sea species have also been described from other parts of the oceans, such as sea mounts (e.g., George & Plum 2009, Plum & George 2009, Gheerardyn & George 2010, Schulz & George 2010), the northeastern Brazilian continental slope and deep sea (e.g., Vasconcelos et al. 2008, 2009; Wandeness et al. 2009) or the Porcupine Seabight (e.g., Gheerardyn et al. 2008, Gheerardyn et al. 2009, Corgosinho & Gheerardyn 2009, Gheerardyn & George 2010). Further, new species from deep-sea chemosynthetic environments such as cold seeps and hydrothermal vents regularly contribute to enhance copepod diversity (e.g., Gollner et al. 2008, Plum & Martínez Arbizu 2009).

The almost 5500 m deep West-African Angola Basin is separated from the Guinea Basin in the north by the Ascension Fracture Zone and the Guinea Seamount Chain. In the west, the Mid Atlantic Ridge raises and builds a barrier towards the Brazilian Basin. In the south the Walvis Ridge separates the Angola Basin from the Cape Basin. Dinet (1973, 1974, 1975) carried out the first meiofauna studies for the Walvis Ridge. His studies included some stations in the Angola Basin from where he described new species of harpacticoid copepods (Dinet 1974, 1975).

The RV "Meteor" cruise M48/1 DIVA-1 in 2000 to the Angola Basin was one of the first deep-sea expeditions carried out during the 10-year CeDAMar programme. During this cruise, abyssal samples for meiofauna studies were taken at station 346 (northernmost sampling locality) and station 325 (southernmost sampling locality) in the central basin. Food availability and sediment structure differed between the two stations with higher total organic carbon and chlorophyll content in the northern part (Kröncke & Türkay 2003). Driven by these environmental factors abundance and diversity of benthic copepods was clearly distinguishable with higher values in the north (Rose et al. 2005).

The new species presented here was collected at both stations. The described harpacticoid copepod belongs to the Canthocamptidae Sars, 1906. It is placed in the so far monospecific genus *Isthmiocaris* George & Schminke, 2003. *Isthmiocaris longitelson* George & Schminke, 2003 represents its only congener. Contrary to the new deep-sea species, *I. longitelson* was collected at the Patagonian continental slope (55°26.4' S/66°14.0' W) at 101 m depth (George & Schminke 2003). The genus is, among other features, characterised by a long and cylindrical habitus, an elongated last abdominal segment (telson), and sexual dimorphisms and reductions in the swimming legs 2 to 4. Its most outstanding character is the isthmion, a collar between the cephalothorax and the first free prosomite. Our investigations on the new species show, that the isthmion is not a characteristic for the genus *Isthmiocaris*.

Material and methods

During the DIVA-1 campaign (RV "Meteor" cruise 48/1, from 6 July to 2 August 2000) sediment samples were taken with a multicorer at two different sites in the Angola Basin (station 325: 5447 to 5505 m depth, between 19°58.2' S/02°59.7' E and 19°58.4' S/02°59.8' E; station 346: 5389 to 5390 m depth, between 16°16.9' S/05°27.0' E and 16°17.0' S/05°27.0' E). Details on sampling strategy and sample treatment are described by Rose et al. (2005).

Presorted harpacticoid copepods were kept in glycerine on slides. Specimens of *Isthmiocaris laurae* sp. nov. were picked out and determined using a Leica MZ 12.5 stereomicroscope and a Leica DMR microscope. Before dissection, the female paratype 1 and the male allotype of *I. laurae* sp. nov. were drawn from the dorsal side. The holotype was dissected without previous habitus drawing. The dissected parts were mounted using glycerine as mounting medium. Drawings were made with the aid of a drawing tube on a Leica DMR microscope equipped with differential interference contrast (DIC) at 1000 × magnification. Scale bars in figures are indicated in millimetres

[mm]. The following abbreviations are used in the text: **exp**, exopod; **enp**, endopod; **aes**, aesthetasc; **benp**, baseoendopod; **P1–P6**, swimming legs 1–6; **"enp1 P2"**, the first segment of the endopod of P2; **CV**, copepodid V.

Results

Harpacticoida Sars, 1903
Canthocamptidae Sars, 1906

Isthmiocaris George & Schminke, 2003

Type species: *Isthmiocaris longitelson* George & Schminke, 2003

Additional species: *Isthmiocaris laurae* sp. nov

Generic diagnosis. *Isthmiocaris* George & Schminke, 2003. Body long, cylindrical and vermiform. Rostrum articulated with 2 sensilla at tip, with or without distinct dorsal ridge. Body somites of almost equal length, except for telson that is elongate of about same length as two preceding somites, and genital double somite in female. Body surface of female without spinules, male with or without spinules. Furcal rami ~3 times longer than broad with 6 setae. Female antennule 6- or 7-segmented, second segment carrying 1 small, transformed, bifid setal element. Antenna with 1-segmented enp and exp, enp with 2 lateral and 5 (sub)terminal, strong spines or setae, exp with 3 setae. Mandibular palp 2-segmented, basis armed or unarmed, 4 slender setae at enp. Maxillule praecoxal arthrite with 2 juxtaposed slender setae on anterior surface, oral margin with several strong spines, coxal endite with 1 strong geniculated and 1 slender seta, basis, enp and exp fused to single lobe with 6–7 (sub)apical setae, one of which geniculated, and 1–2 lateral slender setae. Maxilla with 2 endites, proximal endite with 2–3 setal elements, distal endite with 2–3 elements, basis drawn into strong claw, with 2 accompanying setal elements, reduced enp represented by 4–5 slender setae. Maxilliped prehensile, syncoxa (with 1 seta) and basis separate or fused, enp represented by strong claw longer than basis or syncoxa-basis. Swimming legs with exps and reduced, transformed or absent enps, furnished with strong spinules. P1 with strong inner basal seta, 2 or 3-segmented exp and 1 or 2-segmented enp. Terminal exopodal segment with 3–4 setal elements, enp terminally with 1–3 setal elements. P2 exp 2 or 3-segmented, enp absent, 1 or 2-segmented. P3 exp 3-segmented, enp absent, 1 or 2-segmented, male with distinct apophysis at enp2. P4 exp 3-segmented in the male and 2 or 3-segmented in the female, enp reduced or 1-segmented in the female, 2-segmented in the male with transformed seta at second segment. P5 reduced in female, with distinct exp or transformed to single plate in the male; P6 represented by 1 seta or small outgrowth in the female, in the male completely reduced or represented by 2 small setae on either side.

Isthmiocaris laurae sp. nov.

Species diagnosis as following description.

Locus typicus: Angola Basin (South Atlantic Ocean). Sampling dates: station 325 7/14/2000; station 346 7/27/2000.

Type material: The examined specimens are registered and deposited in the collection of the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (SMF), Germany (full details in the SeSam online database sesam.senckenberg.de; Brandis et al. 2007). Station numbers indicate "station/multicorer deployment – core number".

Female holotype: SMF (37019), dissected adult female, mounted on 20 slides; DIVA-1 station 325/5-3, 19°58.2' S/02°59.6' E, 5505 m.

Male allotype: SMF (37020), dissected adult male, mounted on 13 slides; DIVA-1 station 325/6-3, 19°58.3' S/02°59.8' E, 5448 m.

Female paratype 1: SMF (37021), adult female, not dissected, 1 slide; DIVA-1 station 325/4-3, 19°58.2' S/02°59.8' E, 5449 m.

Female paratype 2: SMF (37022), adult female, not dissected, 1 slide; DIVA-1 station 346/8-8, 16°17.0' S/05°27.0' E, 5390 m.

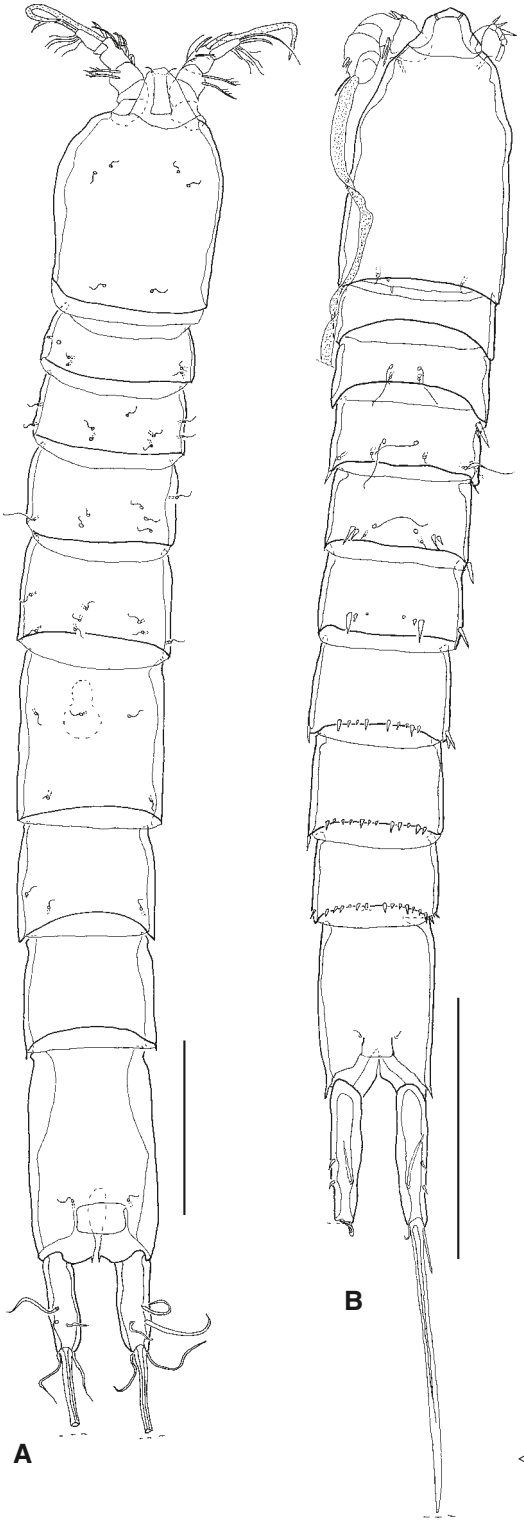
Copepodid paratypes:

CV male: SMF (37023), 1 slide; DIVA-1 station 325/7, 19°58.4' S/02°59.8' E, 5448 m.

CV male: SMF (37024), 1 slide; DIVA-1 station 346/1-9, 16°17.0' S/05°27.0' E, 5389 m.

CV male: SMF (37025), 1 slide; DIVA-1 station 346/5-4, 16°16.9' S/05°27.0' E. 5389 m.

CV female: SMF (37026), 1 slide; DIVA-1 station 346/8-3, 16°17.0' S/05°27.0' E, 5390 m.



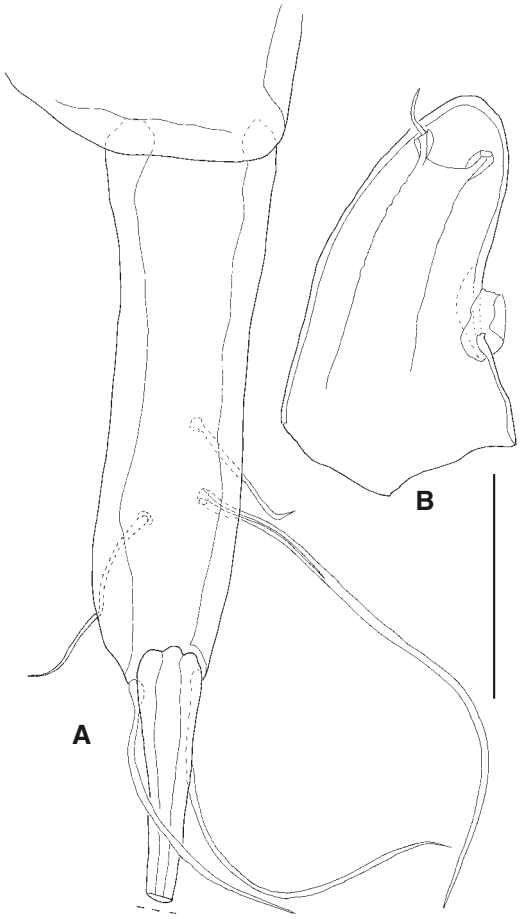


Fig. 2. *Isthmiocaris laurae* sp. nov., female holotype. **A.** left furcal branch, ventral view; **B.** rostrum, dorsal view, slightly damaged on right side. Scale bar 0.05 mm.

Etymology. The species is dedicated to Laura Glatzel, the daughter of Dr. Thomas Glatzel.

Description of female. Total body length measured from anterior tip of rostrum to posterior margin of telson: 1.42 mm; including caudal rami: 1.53 mm (paratype 1). Body elongate, slender, cylindrical and vermiform (Fig. 1 A); rostrum articulated with 2 sensilla at tip and distinct dorsal ridge (Fig. 2 B); telson elongate of about same length as two preceding somites combined with small anal operculum; body surface without

◁ **Fig. 1.** *Isthmiocaris laurae* sp. nov., habitus dorsal. **A.** female paratype 1; **B.** male allotype. Scale bars: A, 0.2 mm; B, 0.1 mm.

Fig. 3. *Isthmiocaris laurae* sp. nov., female holotype: Antennula. **A.** armature omitted; **B.** separated segments with armature. Scale bar 0.05 mm.

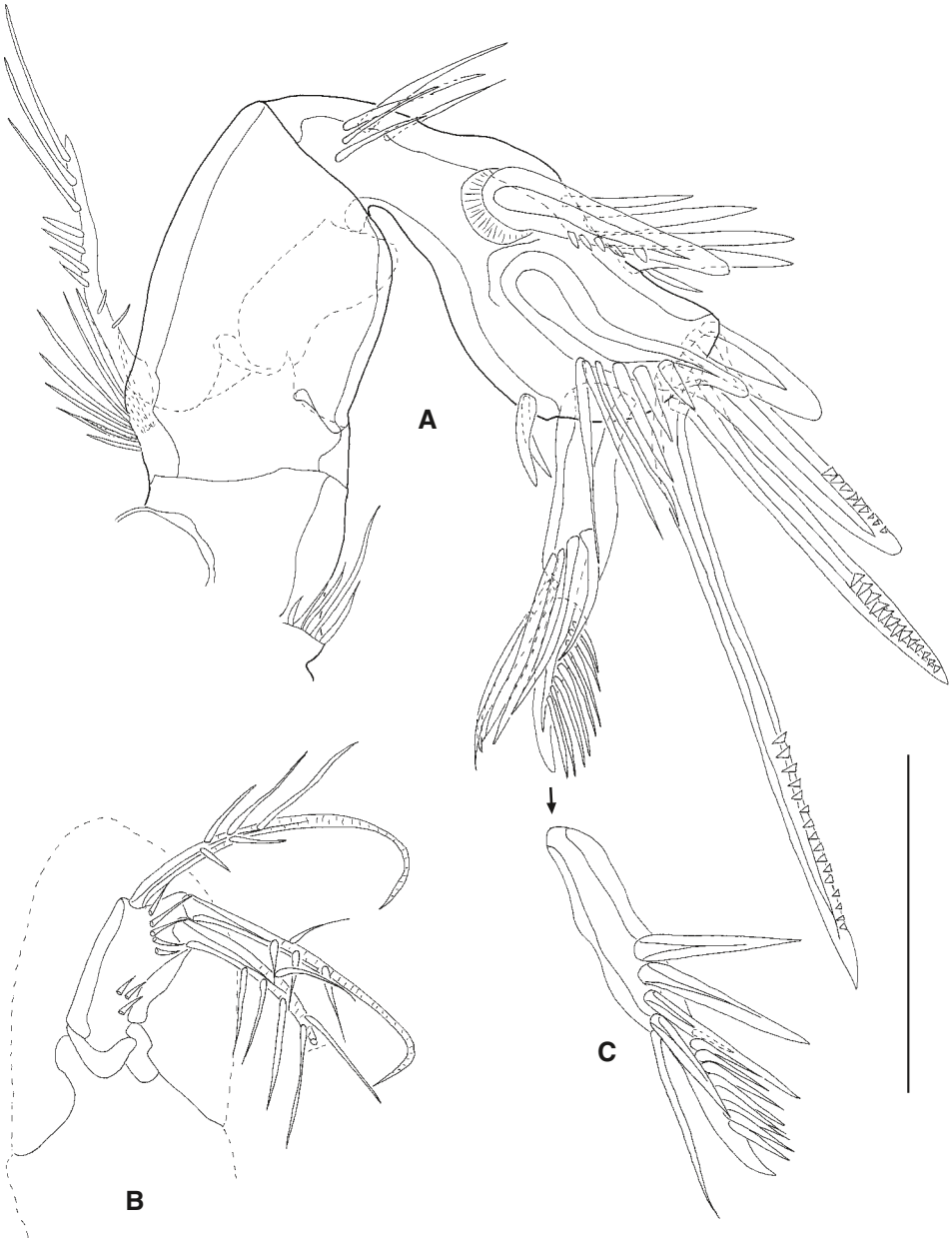


Fig. 4. *Isthmiocaris laurae* sp. nov., female holotype: Antenna. **A.** coxa, allobasis and one-segmented enp, exp is depicted with a dashed line; **B.** exp; **C.** opposite view of strongest endopodal, apical spine. Scale bar 0.05 mm.

spinules; free body somites with posterior hyaline frill; sensilla and pores as in Fig. 1 A; furca (Fig. 2 A) with 6 setae (enumeration after Gómez & Conroy-Dalton 2002): II and III dorsally on distal half; III longer than II; IV nearly as long as III, subapical on outer side; V terminally, longest; VI as small as IV, subapical on inner side; VII on distal half, dorsally displaced.

Antennule (Fig. 3): Short and sturdy, gradually tapering distally, 6-segmented, segment I with spinules on the lower fringe of the inner margin, segment III with distal outgrowth on inner mar-

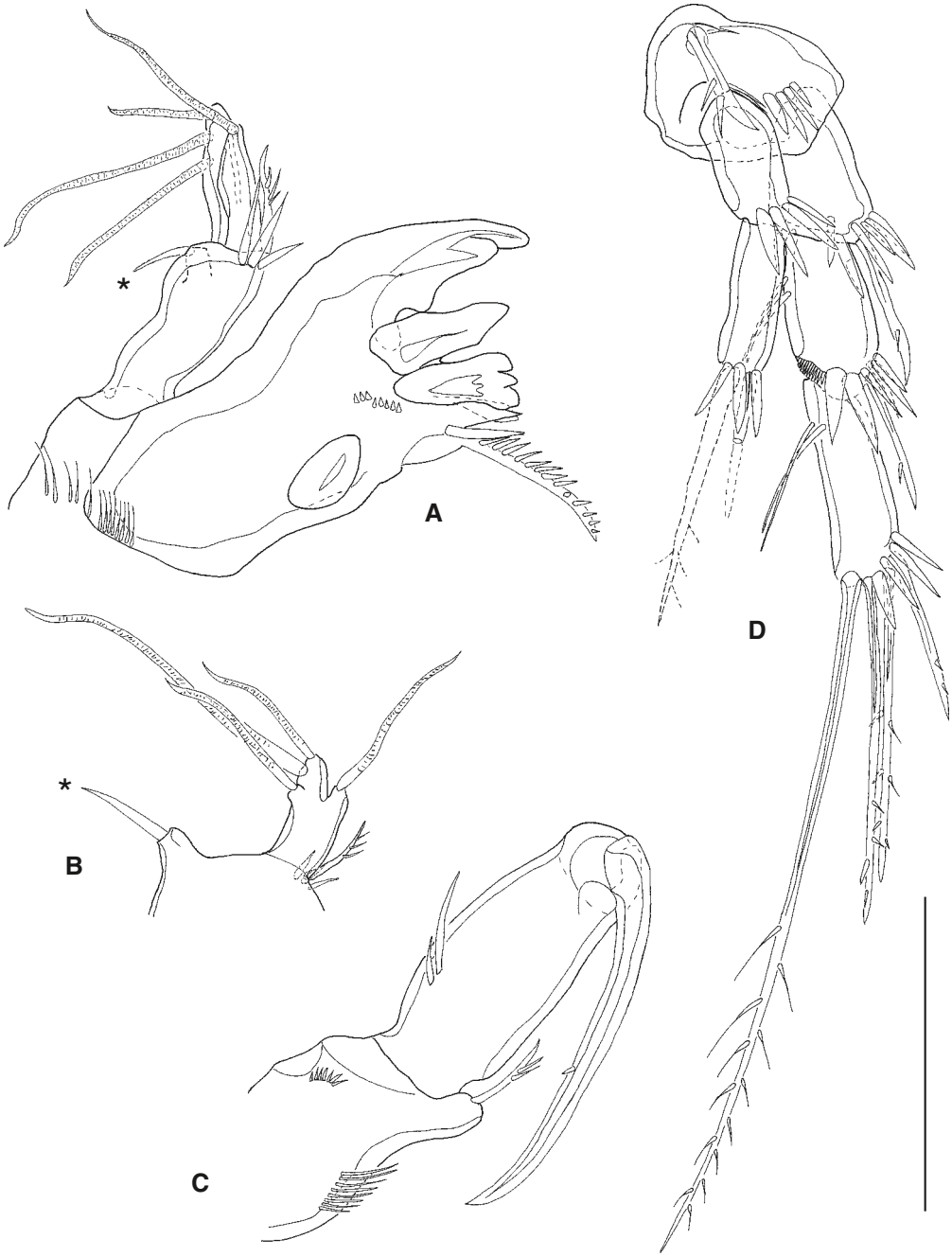


Fig. 5. *Isthmiocaris laurae* sp. nov., female holotype. **A.** mandible; **B.** mandibular palp after paratype 1 (A, B: seta on elevation representing exp marked with asterisk for orientation); **C.** maxilliped; **D.** P1. Elements as dashed line added according to undissected paratype 1. Scale bar 0.05 mm.

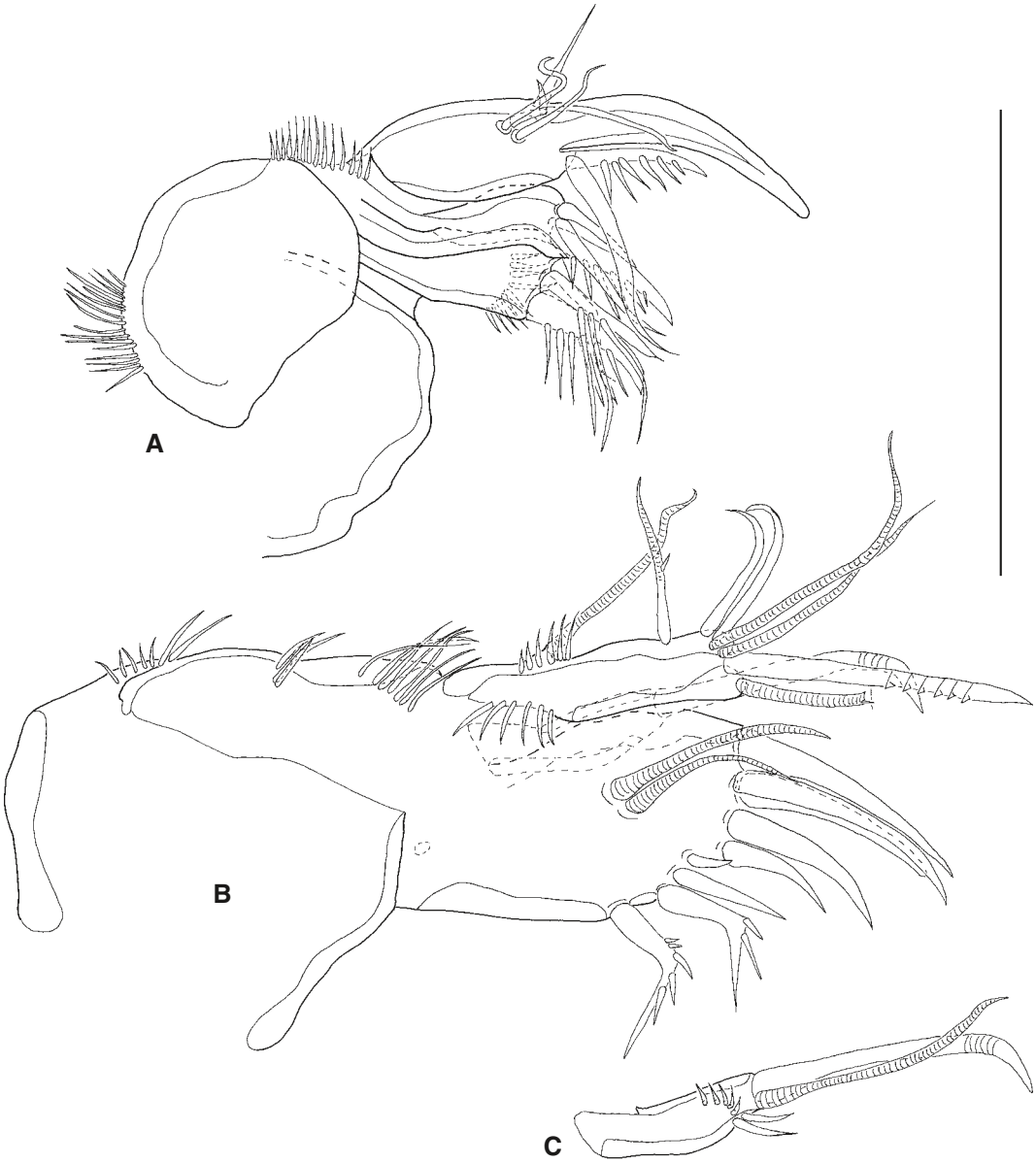


Fig. 6. *Isthmiocaris laurae* sp. nov., female holotype. **A.** maxilla; **B.** maxillule, coxalendite as dashed line; **C.** coxal endite of maxillule. Scale bar 0.05 mm.

gin; armature from proximal to distal segment: 1/6/5+aes /0/1/8+aes. Characteristics of setae per segment: I, 1 pinnate seta; II, 4 pinnate and 1 slender (rat-tailed) seta, 1 small, transformed, bifid setal element; III, 3 rat-tailed, slender setae, 1 stout spine, 1 pinnate spine, 1 aesthetasc; IV, no elements; V, 1 slender, naked seta; VI, 3 small naked setae located on small protrusions (2 more protrusions where setae are presumably lost), 2 slender, naked apical setae (rat-tailed in upper part), 1 long slender rat-tailed seta, 1 aesthetasc.

Antenna (Fig. 4): Robust, with coxa and allobasis, coxa with distal spinule row; allobasis with a spinulose seta and spinule row proximally; enp

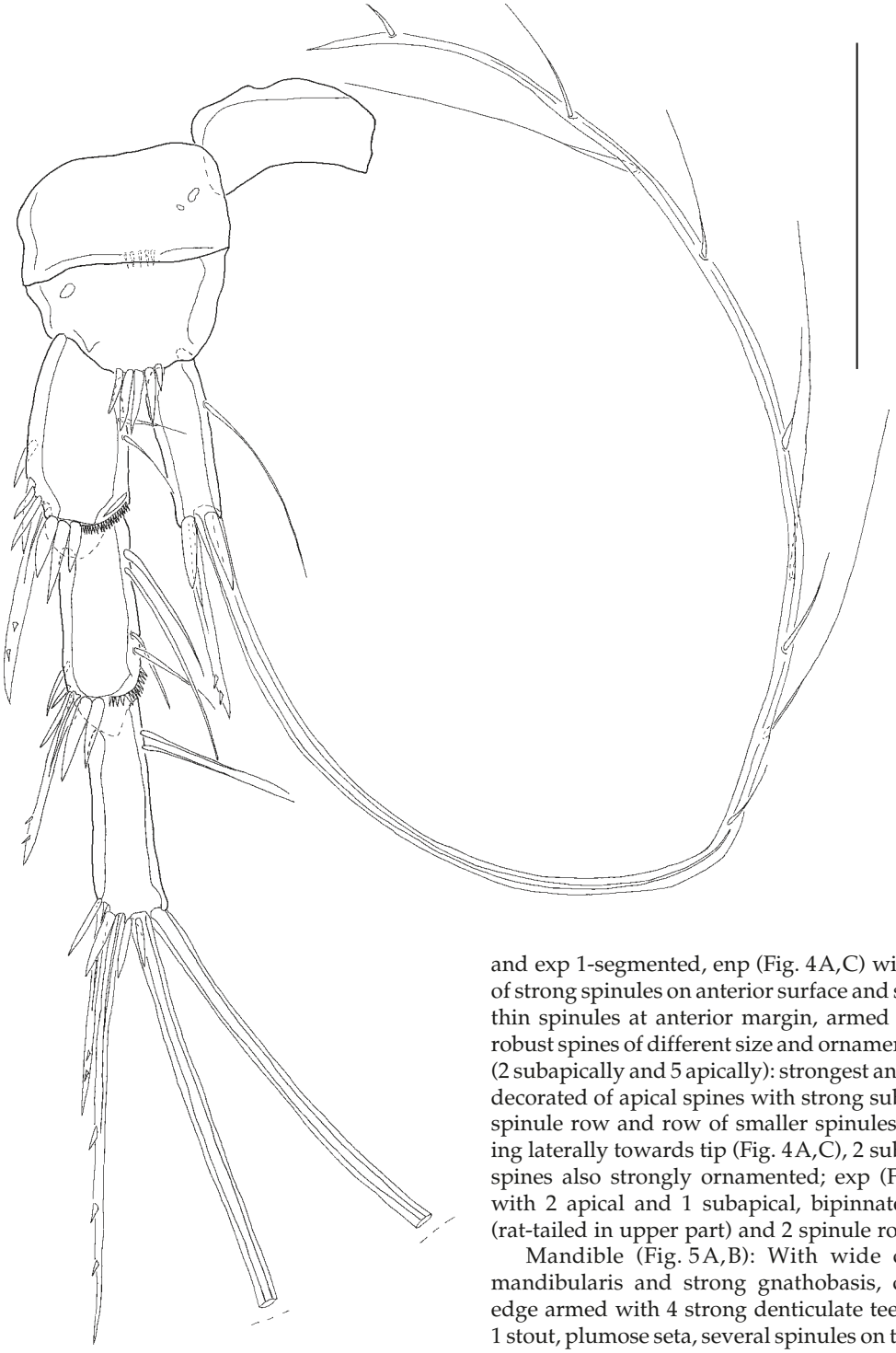


Fig. 7. *Isthmiocaris laurae* sp. nov., female holotype: P2. Scale bar 0.05 mm.

and exp 1-segmented, enp (Fig. 4A,C) with row of strong spinules on anterior surface and several thin spinules at anterior margin, armed with 7 robust spines of different size and ornamentation (2 subapically and 5 apically): strongest and most decorated of apical spines with strong subapical spinule row and row of smaller spinules tapering laterally towards tip (Fig. 4A,C), 2 subapical spines also strongly ornamented; exp (Fig. 4B) with 2 apical and 1 subapical, bipinnate setae (rat-tailed in upper part) and 2 spinule rows.

Mandible (Fig. 5A,B): With wide corpus mandibularis and strong gnathobasis, cutting edge armed with 4 strong denticulate teeth and 1 stout, plumose seta, several spinules on the oral surface; mandibular palp composed of basis, enp and reduced exp (Fig. 5B), basis with 1 plumose

seta accompanied by several spinules, enp unisegmented and bilobed with 4 slender, naked, rat-tailed setae, exp fused with basis and reduced to a small elevation with 1 slender seta (Fig. 5B).

Maxillule (Fig. 6B,C): Praecoxal arthrite with 2 juxtaposed, slender, rat-tailed setae on the anterior surface, oral margin of arthrite with 9 strong spines (2 armed and 7 naked, one of which small); coxal endite (Fig. 6C) with subapical spinule row with 1 strong, geniculated seta and 1 slender, rat-tailed seta; basis, exp and enp fused (Fig. 6B), with 2 rows of spinules, 6 setae apically (5 slender and 1 strong with short spinules), and 2 slender setae distally (1 with small pinnule), several of which rat-tailed.

Maxilla (Fig. 6A): Syncoxa with spinule rows on outer margin, carrying 2 endites; proximal endite with row of small spinules, 1 bare slender seta and 2 pinnate spines, distal endite with 2 bare setae and 1 pinnate spine; basis drawn into strong claw, apically with 1 strong naked seta and 1 pinnate spine, subapically with 5 slender setae (one of which small) representing the reduced endopod.

Maxilliped (Fig. 5C): Prehensile; syncoxa furnished with 2 spinule rows and carrying 1 pinnate seta; basis longer than syncoxa, proximally ornamented with 2 strong spinules; enp reduced to a vestige with strong

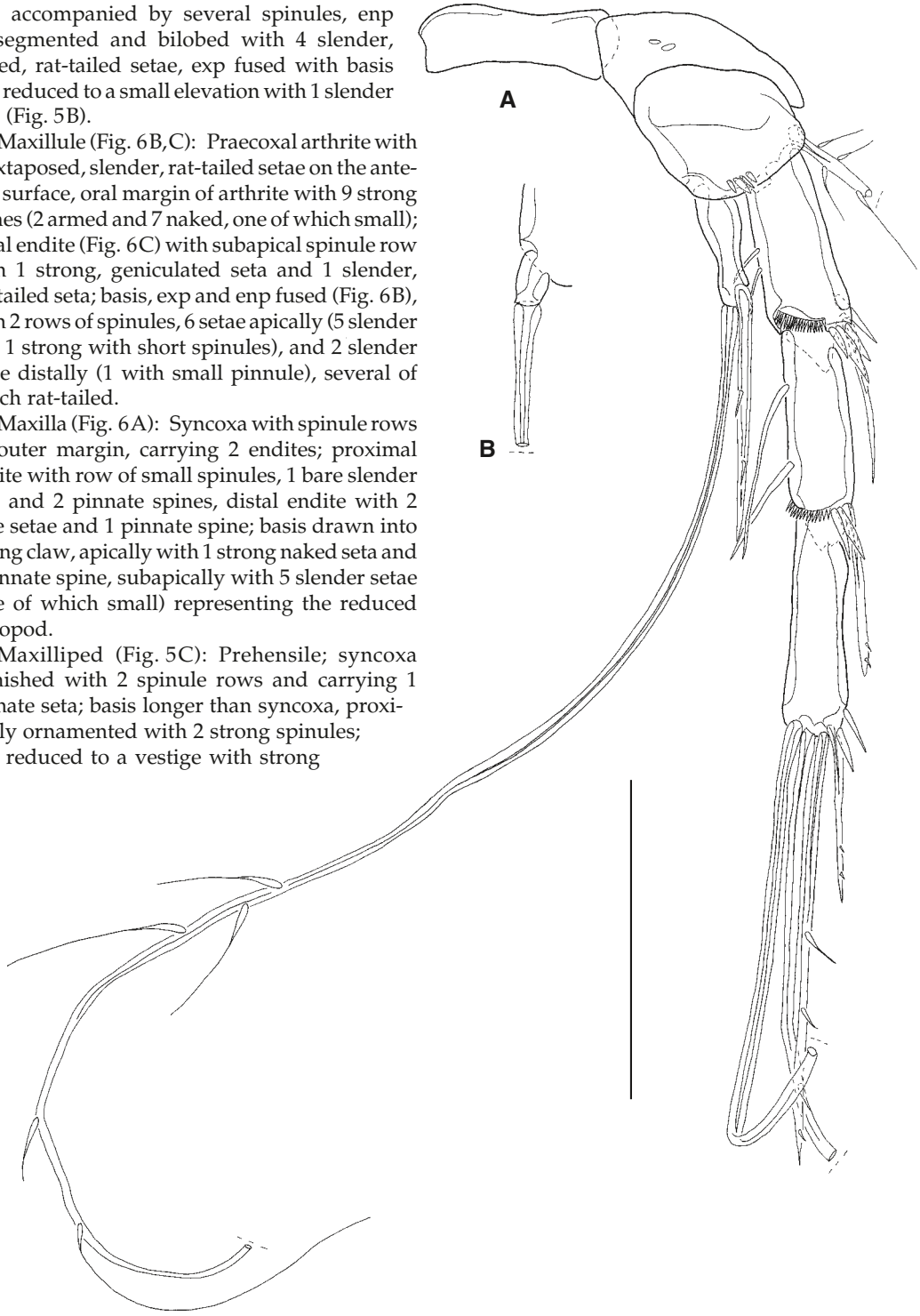
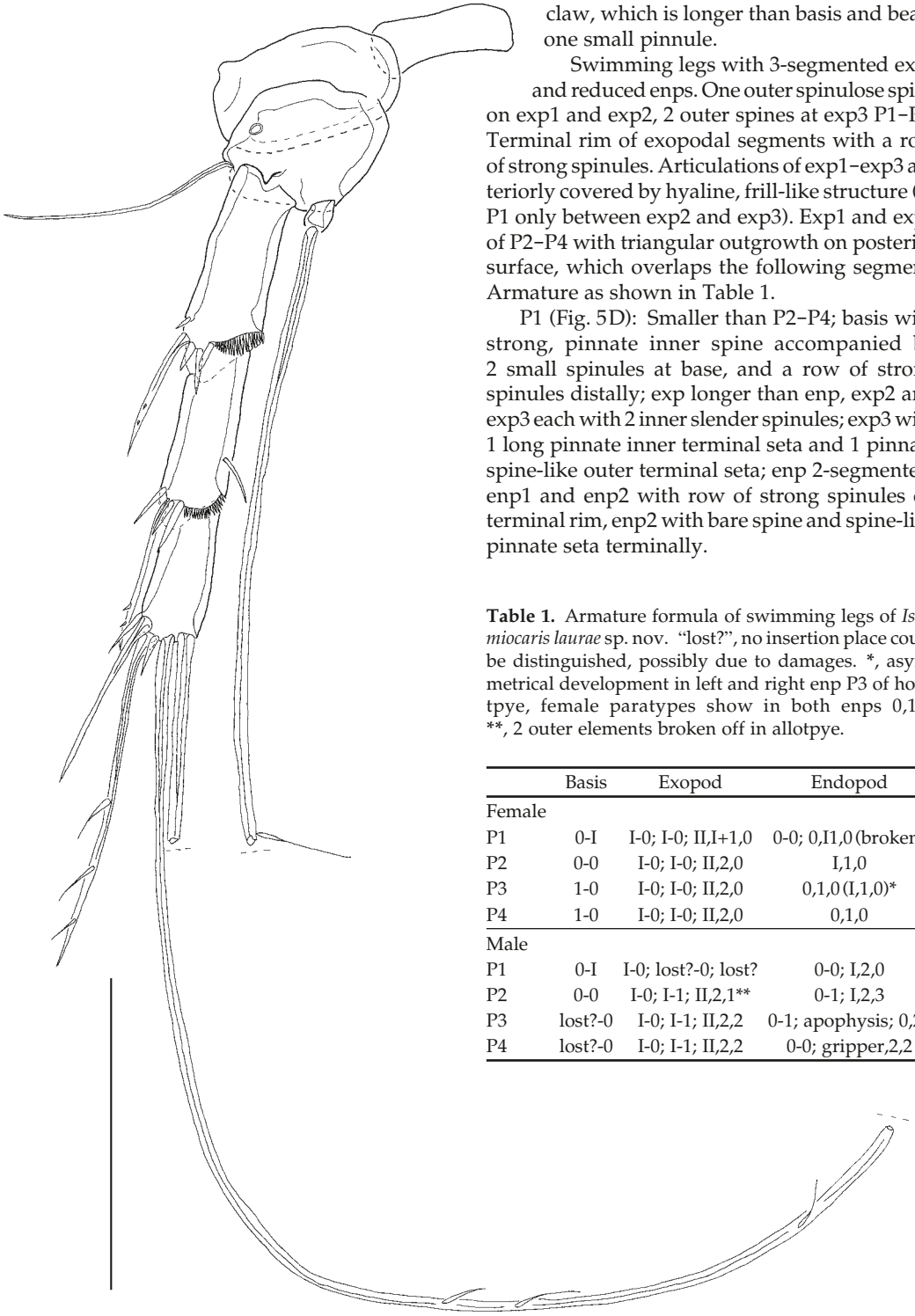


Fig. 8. *Isthmiocaris laurae* sp. nov., female holotype. **A.** P3; **B.** enp of right leg. Scale bar 0.05 mm.



claw, which is longer than basis and bears one small pinnule.

Swimming legs with 3-segmented exps and reduced enps. One outer spinulose spine on exp1 and exp2, 2 outer spines at exp3 P1–P4. Terminal rim of exopodal segments with a row of strong spinules. Articulations of exp1–exp3 anteriorly covered by hyaline, frill-like structure (in P1 only between exp2 and exp3). Exp1 and exp2 of P2–P4 with triangular outgrowth on posterior surface, which overlaps the following segment. Armature as shown in Table 1.

P1 (Fig. 5D): Smaller than P2–P4; basis with strong, pinnate inner spine accompanied by 2 small spinules at base, and a row of strong spinules distally; exp longer than enp, exp2 and exp3 each with 2 inner slender spinules; exp3 with 1 long pinnate inner terminal seta and 1 pinnate spine-like outer terminal seta; enp 2-segmented, enp1 and enp2 with row of strong spinules on terminal rim, enp2 with bare spine and spine-like pinnate seta terminally.

Table 1. Armature formula of swimming legs of *Isthmiocaris laurae* sp. nov. "lost?", no insertion place could be distinguished, possibly due to damages. *, asymmetrical development in left and right enp P3 of holotpye, female paratypes show in both enps 0,1,0. **, 2 outer elements broken off in allotpye.

	Basis	Exopod	Endopod
Female			
P1	0-I	I-0; I-0; II,I+1,0	0-0; 0,I1,0 (broken)
P2	0-0	I-0; I-0; II,2,0	I,1,0
P3	1-0	I-0; I-0; II,2,0	0,1,0 (I,1,0)*
P4	1-0	I-0; I-0; II,2,0	0,1,0
Male			
P1	0-I	I-0; lost?-0; lost?	0-0; I,2,0
P2	0-0	I-0; I-1; II,2,1**	0-1; I,2,3
P3	lost?-0	I-0; I-1; II,2,2	0-1; apophysis; 0,2,0
P4	lost?-0	I-0; I-1; II,2,2	0-0; gripper,2,2

Fig. 9. *Isthmiocaris laurae* sp. nov., female holotype: P4. Scale bar 0.05 mm.

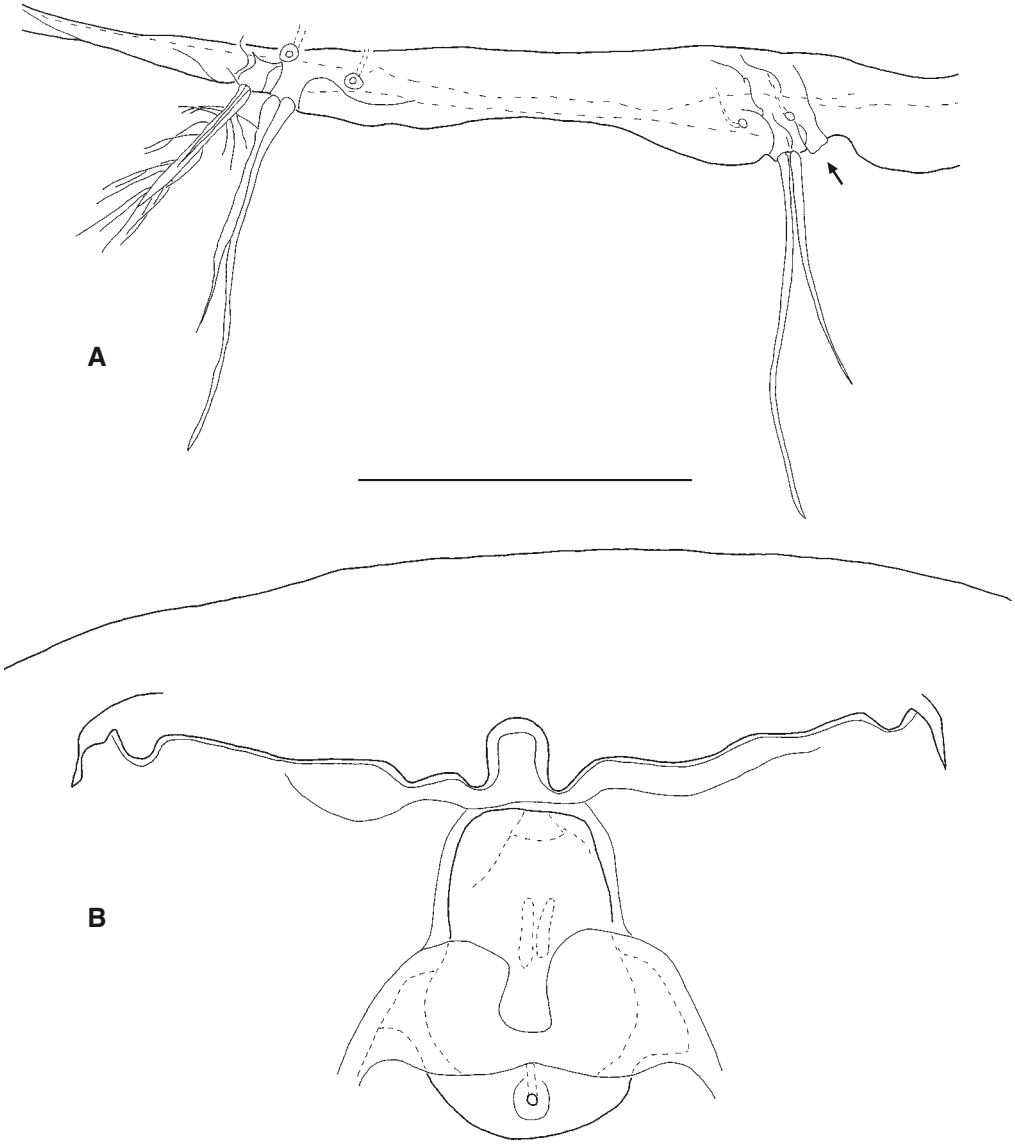


Fig. 10. *Isthmiocaris laurae* sp. nov., female holotype. **A.** P5, arrow indicates seta which is broken off; **B.** P6 and genital complex. Scale bar 0.05 mm.

P2–P4 (Figs. 7–9): Exp3 with two very long plumose terminal setae. Setae much longer than exp plus basis.

P2 (Fig. 7): Basis with row of strong spinules distally between insertion of enp and exp; exp1 and exp3 with 2 long and slender inner spinules, exp2 with 4 long and slender inner spinules; enp 1-segmented with 1 very long plumose, terminal seta, 1 spinulose outer spine, 1 very long inner spinule, and 2 strong spinules on terminal rim.

P3 (Fig. 8): Basis with row of short and strong spinules and with 1 plumose outer seta; exp1 and exp2 with 2 long inner spinules; enp very small, 1-segmented with 1 very long plumose, terminal seta (right leg of holotype and both legs of the paratypes, Fig. 8B), enp of left leg of holotype larger with additional subterminal spinulose outer spine (Fig. 8A).

P4 (Fig. 9): Basis with pore and long slender outer seta; exp2 with 1 inner spinule; enp reduced to small lobe with 1 very long plumose, terminal seta.

P5 (Fig. 10A): Benp reduced to a very narrow plate with 2 large pores on either side, 2 juxtaposed setae and 1 plumose seta at the former basis, in the holotype lost on the left side.

Genital complex and P6 (Fig. 10B): Last thoracic and first abdominal somite fused to form genital double somite; copulatory pore located ventrally in middle of somite; P6 very small, forming genital operculum, with short outgrowth on both sides.

Description of male. Habitus (Fig. 1B) as in female but 3.4 times smaller. Second and third urosomite not fused. Differs from female in 4th to 8th body somite that are ornamented with dorsal spinules of different sizes. Abdominal somites with additional ventral spinules of different sizes. Total body length measured from anterior tip of rostrum to posterior margin of telson: 0.4 mm; including caudal rami: 0.45 mm (Allotype). Furcal rami with 6 setae, II and II reduced to small spines, VII relatively longer than in female.

Swimming legs in relation to body size much larger in male than in female. Antenna, gnathobasis of mandible, maxillule, and maxilliped as in female. Mandibular palp broken. Maxilla as in female except for distal endite that carries only 2 elements instead of 3. Sexual dimorphisms in antennule and in P1–P6.

Antennule: broken, most setae lost, not drawn.

Swimming legs with 3-segmented exps, 2-segmented enps in P1, P2, and P4, and a 3-segmented enp in P3. Outer spines on exp1–exp3 spinulose (partly lost in P1, completely lost in P2).

P1 (Fig. 11A): Smaller than P2–P4; basis with strong inner pinnate seta accompanied by 2 spinules at base, row of strong spinules distally; terminal rim of exopodal segments with a row of strong stout spinules; exp1 with 3 setules on inner margin, exp2 with 2 setules; outer spine of exp2 and outer spines and terminal setae of exp3 probably broken off; enp1 with spinule on terminal rim; enp2 with 1 pinnate outer spine and 2 long and pinnate terminal setae.

P2–P4 (Figs. 11B, 12A–C): Exp1 and exp2 with posterior triangular outgrowth, which overlaps the following segment. Articulations of exp1–exp3 anteriorly covered by hyaline, frill-like structure.

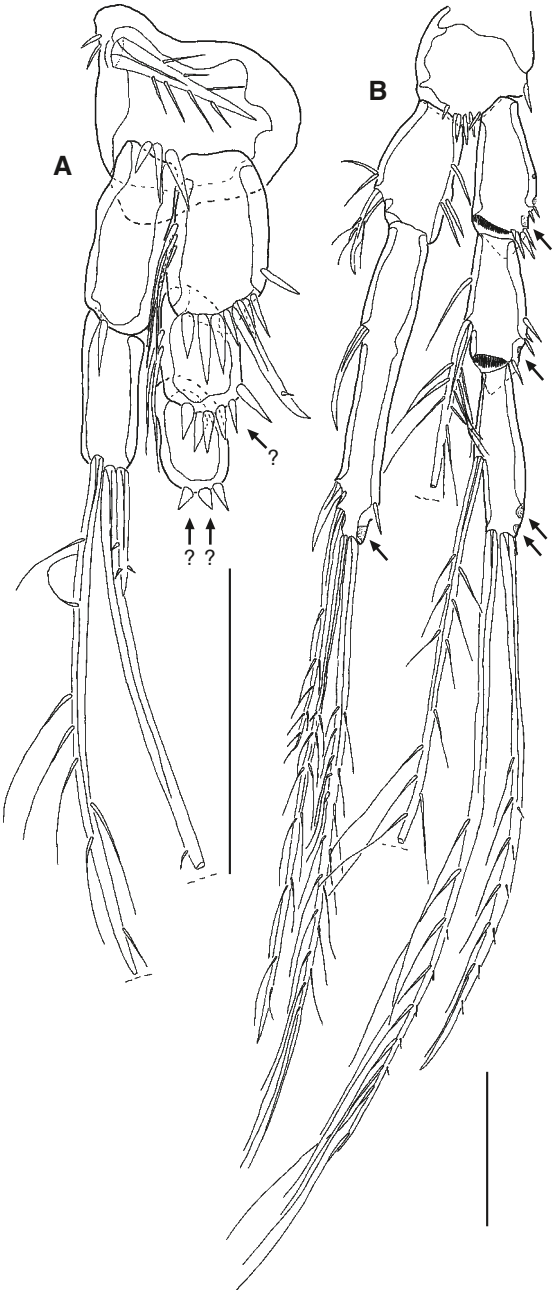


Fig. 11. *Isthmiocaris laurae* sp. nov., male allotype. **A.** P1; **B.** P2; arrows indicate lost or probably lost elements. Scale bars 0.05 mm.

Exp3 with 2 outer pinnate spines (broken off in P2) and 2 long terminal pinnate setae.

P2 (Fig. 11B): Basis with row of strong spinules on lower fringe and small outer spinule; outer

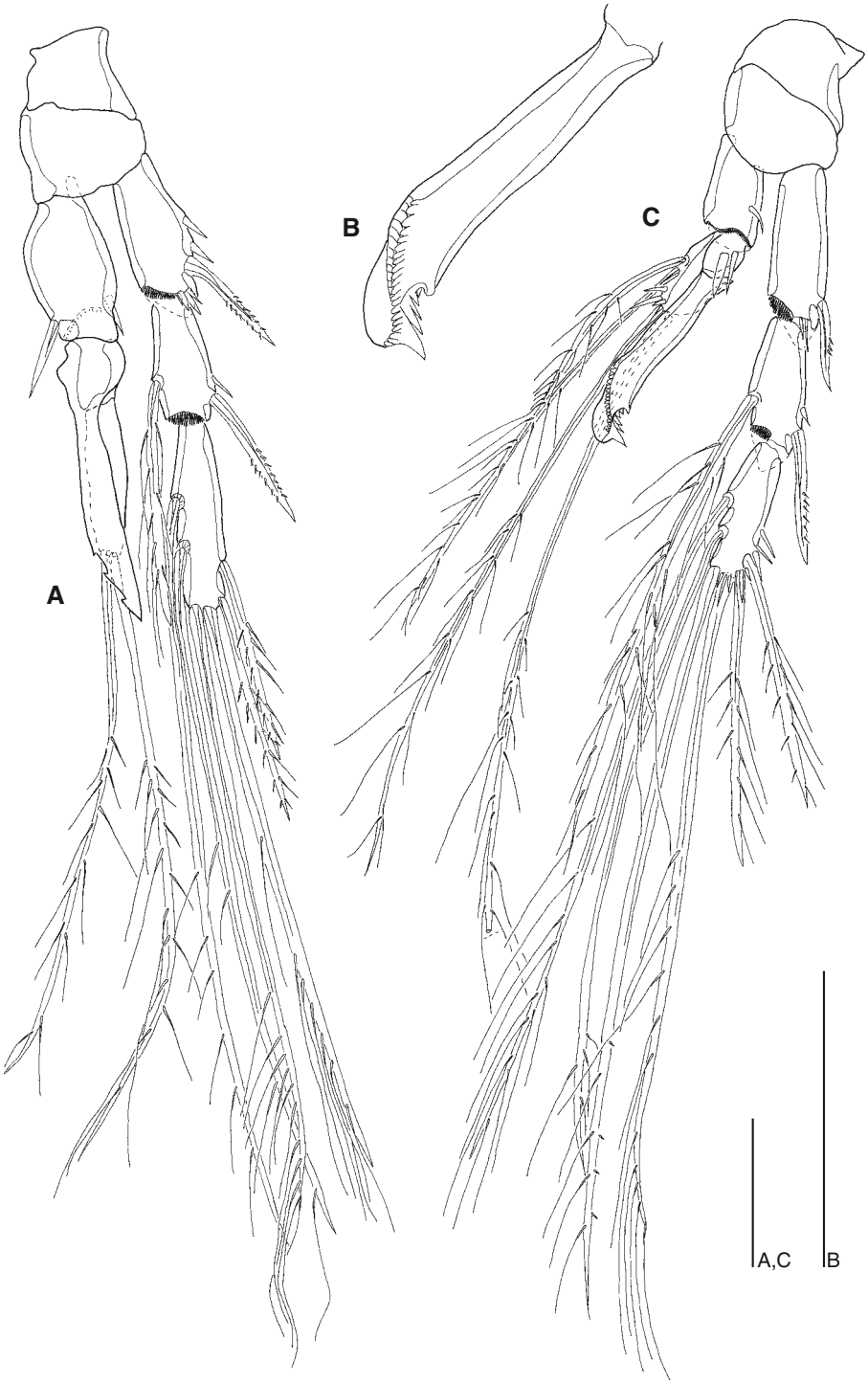


Fig. 12. *Isthmiocaris laurae* sp. nov., male allotype. **A.** P3; **B.** gripper-like element of enp2 P4; **C.** P4. Scale bars 0.05 mm.

spines of exp1–exp3 lost in this specimen; exp1 and exp2 with spinules on terminal and outer rim; exp2 with one inner spinule, exp2 and exp3 with 1 strong inner pinnate seta; enp1 with several spinules on the outer and inner margin and 1 plumose inner spine; enp2 elongate, 2 short naked inner spines, 1 inner subterminal pinnate, spine-like seta, and 2 terminal long, pinnate setae. Subterminal outer element broken off.

P3 (Fig. 12A): Basis naked, outer seta possibly lost but no insertion place visible; exp1 with strong spinules on the outer margin and terminal rim; exp2 with spinule on outer margin and strong plumose inner seta; exp3 with 2 long and plumose inner setae; enp strongly sexually dimorphic; enp1 with strong inner spine, spinule on outer margin and hyaline frill-like structure posteriorly over articulation with enp2; enp2 drawn out into strong, serrate apophysis with 3 barbs on inner side; enp3 slender, elongate, bearing 2 long, pinnate terminal setae.

P4 (Fig. 12B,C): Basis naked, outer seta possibly lost but no insertion place visible; exp1 with spinules on terminal rim; exp2 with strong spinule on outer margin and 1 long, strong inner plumose seta; exp3 with row of strong spinules along outer and terminal margin, 2 long and plumose inner setae; enp1 small, with strong outer spinule and hyaline frill on terminal rim; enp2 formed by 2 parallel parts that are fused in the proximal region of enp2, shorter part with 2 strong outer spinules and a highly modified, curved, and serrated gripper-like outer spine, longer part with 2 plumose inner setae and 2 terminal setae.

P5 (Fig. 13A): Benps of left and right legs confluent, forming small plate with 2 strong unarmed spines on endopodal lobe and plumose basal outer seta; exp with plumose inner seta, followed by a strong spine and 3 small spines (2 bare and 1 spinulous).

P6 (Fig. 13B) represented by 3 small spines situated on small outgrowth on either side of body.

Abdominal somites (Fig. 13B) contrary to female with additional ventral spinules of different sizes.

Comparison of copepodid V and adult swimming legs. Several copepodids of the new species were found in the investigated samples. There were no male copepodids belonging to stage CIV therefore the setation and segmentation of P1–P4 of the male and female CV stages are presented (Fig. 14).

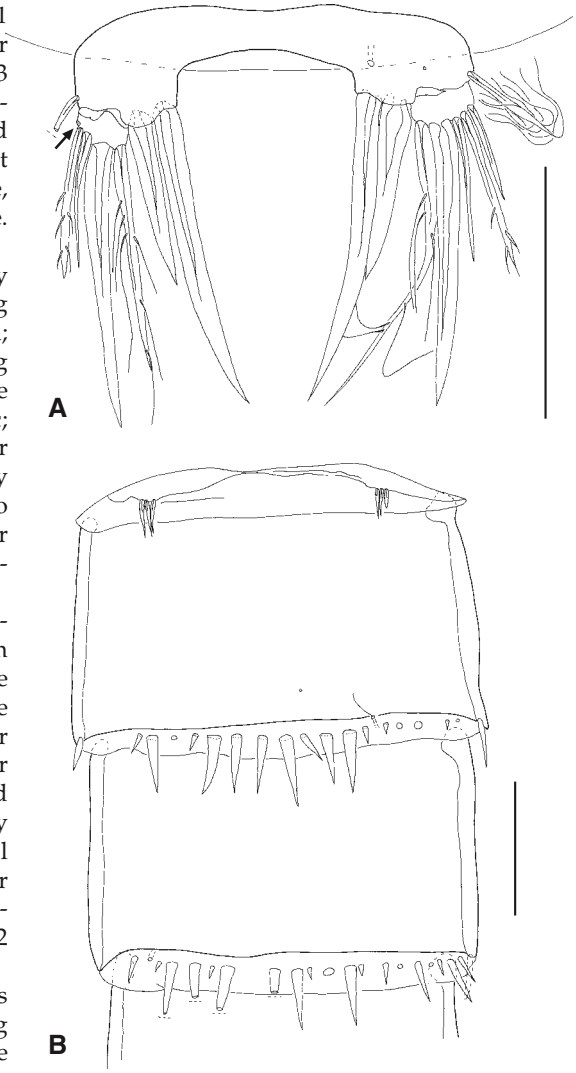


Fig. 13. *Isthmiocaris laurae* sp. nov., male allotype. **A.** P5; **B.** P6 and abdomen. Scale bars 0.05 mm.

It is obvious that the P1 in the male and female CV are identical, while in the adult female the innermost spine on enp2 is missing (Fig. 5) and in the male it is transformed into a long bipinnate seta (Fig. 11A).

In the P2 enps male and female CV both show 1 apical spine but they are distinguishable by the number of long apical setae (1 in the female, 2 in the male). The number of apical elements is kept in the adult female (Fig. 7), while the number of segments is reduced to one. During the moult to the adult male the number of elements in

enp2 rises to 6 and in enp1 appears 1 inner seta (Fig. 11B). In the exp P2 only the male CV shows inner setae at exp2 and exp3 (Fig. 14). These setae are kept in the adult male (Fig. 11B).

In both sexes the spinules at P3 and P4 are distinctly smaller than in the previous legs (Fig. 14). No basal setae were distinguishable at the P3 and P4 of the adult male (Fig. 12). This may indicate a reduction of these elements from the CV to the adult.

The exps P3 of the CV of both sexes are comparable to the P2 exps of the according sex. In the male an additional inner seta develops at the exp3 P3 during final moult. The enps P3 of the male and female CV differ in the number of segments and apical elements. The P3 of the adult female (Fig. 8) shows a reduced number of endopodal segments and apical elements compared to the P3 of the CV. However, one leg of the female holotype had still the complete setation of the female CV.

At the enp3 P3 of the male CV an apical, transformed setal element is present. Whether this element is a precursor of the apophysis at the enp2 in the adult, which would require a shift from the enp3 CV and to an insertion point at enp2 in the adult (Figs. 12A, 14), remains to be determined.

The P4 of the adult female differs from the CV P4 only by its distinctly smaller enp. In the male 2 additional inner setae develop at the exp3 during the final moult from the CV to the adult. The male enp P4 is 2-segmented in the CV and the adult. The adult carries 3 more seta (2 inner, 1 apical) at the enp2 than the CV. A transformed seta that rises at an apical position in the enp2 of the male CV (Fig. 14) is further transformed into a gripper-like element and shifts to a proximal position at the enp2 in the adult (Fig. 12B).

Discussion

Sexual dimorphism, matching of male and female and asymmetrical development. The sexual dimorphism of *I. laurae* sp. nov. is pronounced. It is not only evident in the setation and ornamentation of the swimming legs, but also in body size. The female is 3.4 times larger than the male but the relation of leg size to body size is much larger in the male than in the female.

The strongly differing males and females can be matched by comparing the segmentation and setation of the swimming legs of copepodid stages CV. The P1 in the male and female CV are identical, in the P2 enps male and female CV both show 1 apical spine, the pattern and sizes of spinules at P1–P4 are identical, and male and female CV show outer basal setae in P3 and P4. Females perform the last step of the marked oligomerisation in their enps of the swimming legs only after the moult from copepodid stage CV to the adult stage CVI.

However, there still remain several differences regarding setation and segmentation in the legs of the male and female CV such as the inner setae at exp2 and exp3 of P2 and P3 in the male, 2 long, apical seta in the male enp P2, or the sexually dimorphic enps of P3 and P4.

The observation of the development of the apophysis in the male enp2 P3 showed that this element may originally not be an outgrowth of the enp2 (Fig. 12A). During ontogeny a transformed seta appears apically at the enp3 (Fig. 14). How the element is relocated to the enp2 during the final moult to the adult stage or whether the transformed seta from enp3 CV is lost while a new transformed element is built at the enp2 in the adult, remains unclear.

Besides sexual dimorphism, asymmetrical development was observed in the female enp P3. During the final moult the 2 endopodal segments (Fig. 14) fuse and the outer apical spine is lost (Fig. 8B). The adult holotype retained the setation of the CV on one side of the body (Fig. 8A). This phenomenon of contralateral variability due to malformation on single specimens seems to be relatively common in deep-sea copepods, e.g. Seifried and Martínez Arbizu (2008) report it for *Bradya kurtschminkei* Seifried & Martínez Arbizu, 2008. They found several specimens with setal and segment numbers differing between right and left side of leg-pairs or mouthparts.

The genus *Isthmiocaris* George & Schminke, 2003. George and Schminke (2003) erected the genus *Isthmiocaris* to allocate the species *Isthmiocaris longitelson*. To date, the genus *Isthmiocaris* remained monospecific and was only collected at the Patagonian continental slope (101 m depth) during the RV "Polarstern" cruise ANT XIII/4 in 1996.

The genus was then characterised by a long and cylindrical habitus, the possession of extremely long sensilla on the dorsal and lateral body parts, a 2-segmented enp P4 in the male with 2 apical setae on enp2 and a saw-like derived seta, and the

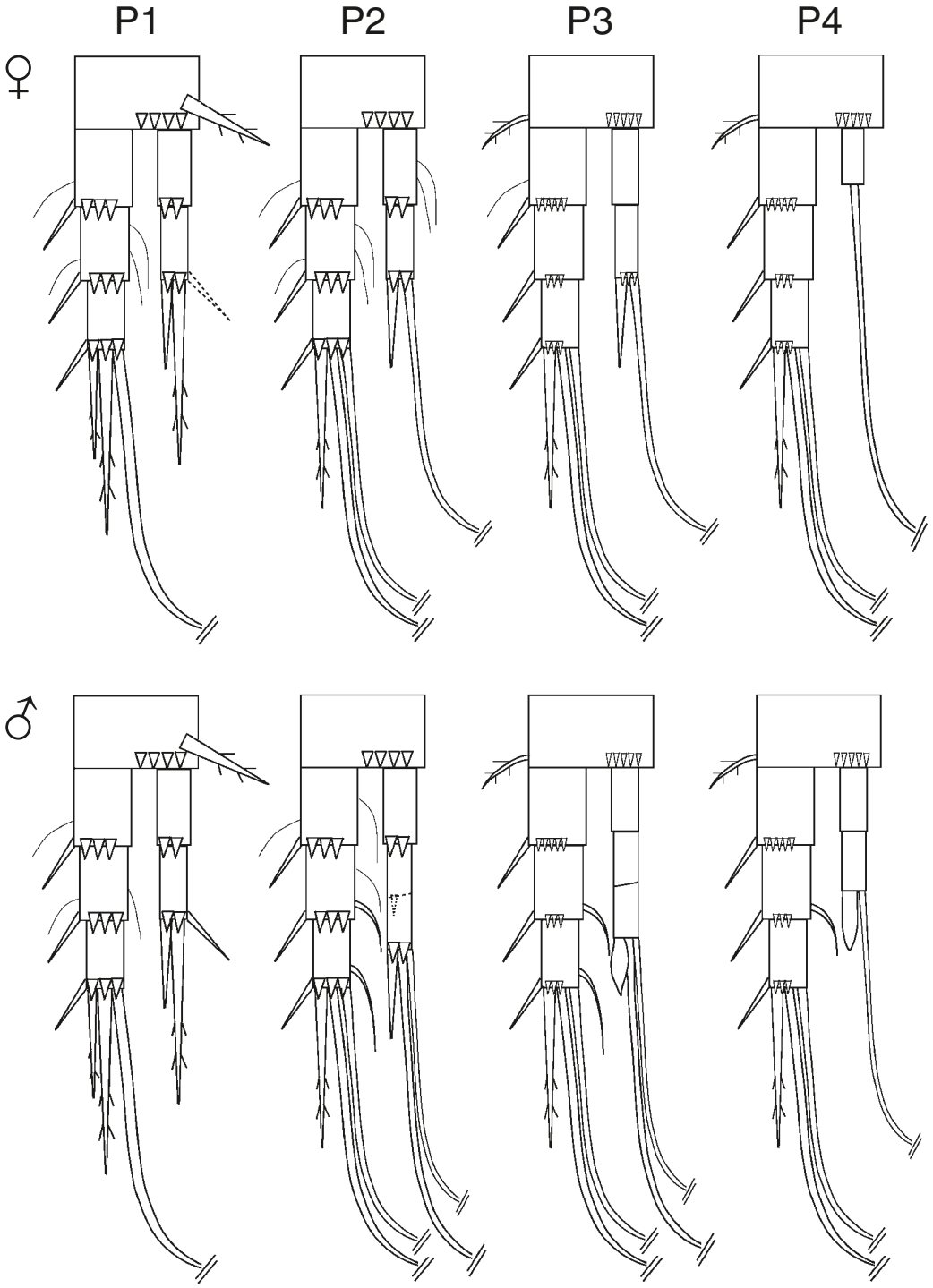


Fig. 14. *Isthmiocaris laurae* sp. nov., setation and segmentation of swimming legs P1–P4 of female and male copepodid V; schematic drawings. Elements depicted with a dashed line added according to other body side or paratypes.

following autapomorphies (George & Schminke 2003): (1) the isthmion, a collar between the cephalothorax and the first free thoracic somite; (2) an elongated telson; (3) a sexually dimorphic reduction of the outer spine in the female exp2 P2; (4) a sabre-like apophysis in the male enp2 P3 exceeding the length of exp with 2 small outer hooks instead of 1; (5) the transformation of the male enp3 P3 to a long paddle-like segment; (6) a reduced female P5 forming a very small plate with only 1 seta at each side; (7) a reduced male P5 with only 1 cuticular apophysis, 2 setae and 1 tube pore at each side; (8) the loss of the male P6.

Placement of *Isthmiocaris laurae* sp. nov. and differentiation from *I. longitelson*. *I. laurae* sp. nov. does not possess the typical collar or pseudosomite of *I. longitelson* [former autapomorphy (1) of *Isthmiocaris* after George & Schminke 2003, see above] but it shares the characteristically prolonged telson [former autapomorphy (2)], which is approximately as wide as the prosome. The male enp3 P3 is transformed to a paddle-like segment in *I. longitelson* [former autapomorphy (5)] and although it is not as large in *I. laurae* sp. nov. it is still longer than in the other canthocamptid species. The new species shows that the isthmion is not a requisite characteristic of the genus *Isthmiocaris* but the detected synapomorphies of the two species indicate the monophyletic status of the genus.

Synapomorphies of *I. longitelson* and *Isthmiocaris laurae* sp. nov.:
(A) long, slender, cylindrical and vermiform body shape
(B) prolonged telson
(C) elongated male enp3 P3

The following characteristics of *I. laurae* sp. nov. are more plesiomorphic than in *I. longitelson* and not shared with the latter: the outer spine lacking in the female exp2 P2 of *I. longitelson* is present in the new species [former autapomorphy (3)]; the sabre-like apophysis on the enp2 of the male P3 is only as long as the exp P3 in *I. laurae* sp. nov. and carries three barbs on the inner side; this is different to *I. longitelson*, where a distinctly longer apophysis can be observed that has two barbs on the outer rim [former autapomorphy (4)]; the male and female P5 of *I. longitelson* are more reduced than in *I. laurae* sp. nov., while *I. longitelson* possesses only 1 plumose seta on the former basal part of the female P5 [former autapomorphy (6)], *I. laurae* sp. nov. shows 1 plumose seta and 2 bare juxtaposed setae on either side of the body; the plesiomorphic P5 of the male of *I. laurae* sp. nov. consists of a benp with two strong unarmed endopodal spines, a basal outer plumose seta and an exp with 5 elements, the male endopodal lobe of the P5 in *I. longitelson* shows only one strong cuticular apophysis which is fused with the benp, and has a reduction in the number of setal elements at the exopodal part which is fused to the benp [former autapomorphy (7)]; the P6 is lost in the male of *I. longitelson* [former autapomorphy (8)], while *I. laurae* sp. nov. still shows the remnants of the leg represented by 3 small setae on either side of body.

The modified outer spine in the male enp2 P4 is a characteristic that several other canthocamptid species show (see George & Schminke 2003), but in *I. laurae* sp. nov. it is more derived than in *I. longitelson*: this spine in the male enp2 P4 is a gripper-like, twisted, highly ornamented, and twofold serrated element in *I. laurae* sp. nov. while it is smaller and more unadorned in *I. longitelson* and other Canthocamptidae.

Male and female *I. longitelson* are of the same body size (0.68 mm), while in *I. laurae* sp. nov. the male (0.45 mm) is 3.4 times smaller than the female (1.53 mm). Contrary to *I. longitelson*, *I. laurae* sp. nov. possesses a small anal operculum.

Autapomorphies for *Isthmiocaris laurae* sp. nov.:
(A) Enp2 P2 in the male of *Isthmiocaris laurae* sp. nov. is elongated and as long as exp2 and exp3 together.
(B) The modified outer spine in the male enp2 P4 is typical for Canthocamptidae, but in *I. laurae* sp. nov. it is a gripper-like, twisted, highly ornamented, and twofold serrated element.
(C) Rat-tailed setae have not been reported before for any of the closely related species of *I. laurae* sp. nov. These setae are found at the antennule, antenna exp, mandible palp, and maxillule of *I. laurae* sp. nov.
(D) The male is 3.4 times smaller than the female.

The enigmatic genus *Pyrocletodes* Coull, 1973. The genus *Pyrocletodes* was established by Coull (1973) with the description of the species *Pyrocletodes desuramus* Coull, 1973 from the deep sea off North Carolina and provisionally assigned to the family Cletodidae T. Scott, 1904. Dinet (1975) doubted this affiliation when he described

a second species of the genus, *Pyrocletodes coulli* Dinet, 1975 from the West-African Angola Basin. Further discussions about the systematic status of the genus are documented by Bodin (1997) who lists the genus as "Harpacticoida *gen. incertae sedis*". Both species were described from females only. The lack of males evidently hampered a justified allocation to any family.

However, the Canthocamptidae and *Isthmiocaris* share many characteristics of mouth parts, swimming legs and caudal rami with *Pyrocletodes*. Examples are the articulated rostrum with two sensilla at the tip and a distinct dorsal ridge in *P. coulli* and *I. laurae* sp. nov.; the shape of the setal elements of the antenna in *Pyrocletodes* and the Canthocamptidae; the nearly identical maxilliped; the segmentation, spinulation and setation of the P1 which is except for the setation at the enp1 (1 more seta in *P. coulli*, 2 more setae in *P. desuramus*) and 1 seta at the exp3 identical between *Pyrocletodes* and *I. laurae* sp. nov.; the female P3 in *Pyrocletodes* and *I. longitelson* where only 2 elements are lacking in the exp3 of *I. longitelson*; the comparable state of reduction of P5 in the females of *Pyrocletodes* and *I. laurae* sp. nov.; and the furcal rami that are of a distinct shape in *Pyrocletodes* and *Isthmiocaris*.

Unluckily, to date no males of *Pyrocletodes* have been described. Therefore important characters such as the apophysis at the male enp2 P3 and the transformed seta at the enp2 P4 could not be verified until now.

Whether *Isthmiocaris* has to be considered as a junior synonym of *Pyrocletodes*, and *Pyrocletodes* should be allocated to the family Canthocamptidae remains to be determined. The recent focus on deep-sea biodiversity and the available samples from abyssal plains world wide allow for a search for the males of *Pyrocletodes* in order to resolve this unsatisfactory situation.

Distribution of deep-sea Canthocamptidae. Canthocamptidae is the dominant family of benthic copepods in freshwater habitats but the family is found as well in the marine realm (Boxshall & Halsey 2004). Some members of Canthocamptidae have been described from the deep sea: *Perucamptus rapiens* (Becker, Noodt & Schriever, 1979) from the Peru Trench, *Heteropsyllus serratus* Schriever, 1983 from the Iceland-Faroe Ridge, *Selenopsyllus abyssalis* (Becker, 1979) and *Selenopsyllus profundus* (Becker, 1979) from the Iberian deep sea, and *Selenopsyllus antarcticus* Moura & Pottek 1998 as well as *Selenopsyllus dahmsi* Moura & Pottek, 1998 from the deep Weddell Sea (CeDAMar data base; Becker et al. 1979, Schriever 1983, Moura & Pottek 1998). *Isthmiocaris longitelson*, however, has been described from only 101 m depth on the Patagonian continental shelf. It is astonishing, that the closest relative to *I. longitelson* has been collected from the West-African Angola Basin separated from Patagonia by the Mid-Atlantic ridge and the Argentine Basin. However, benthic deep-sea copepod species have recently been found to surmount ridges as well as abyssal plains and populate vast geographic regions on large scales (Gheerardyn & Veit-Köhler 2009, Menzel 2011, Menzel et al. 2011).

More samples from the CeDAMar expeditions have to be considered in the future in order to determine how far the distribution range of *I. laurae* sp. nov. reaches.

Acknowledgements

The authors would like to thank Dr. Elke Willen and Dr. Kai Horst George (Senckenberg am Meer – DZMB) for sampling the material on board RV Meteor. Sample treatment and meiofauna sorting was carried out by Dr. Sybille Seifried and supported by Iris Zaehle and students of the former AG Zoosystematik und Morphologie, C.v.O. Universität Oldenburg. Gisela Moura is thanked for the determination of the systematic status and the allocation of male and female of the new species. This study is a contribution to CeDAMar (Census of the Diversity of Abyssal Marine Life, www.cedamar.org), a field project of the Census of Marine Life (CoML). Dr. Kai Horst George and Dr. Hendrik Gheerardyn are thanked for their comments that improved the manuscript considerably.

References

Becker, K.-H., W. Noodt & G. Schriever (1979). Eidonomie und Taxonomie abyssaler Harpacticoidea (Crustacea, Copepoda) Teil II. Paramesochridae, Cylindropsyllidae und Cletodidae. Meteor Forschungsergebnisse D 31: 1–37.

Bodin, P. (1997). Catalogue of the new marine harpacticoid copepods (1997 Edition). Documents du travail de l'Institut Royal des Sciences Naturelles de Belgique 8: 1–304.

Boxshall, G. A. & S. H. Halsey (2004). An introduction to copepod diversity. The Ray Society, London.

Brandis, D., A. Allspach, L. Menner & M. Türkay (2007). The collection management system SeSam of the Senckenberg Research Institute, Frankfurt a. M., Germany. Zoology 110: 161–162.

CeDAMar data base. All published benthic species records deeper than 2000 m gathered by CeDAMar.

Corgosinho, P. H. C. & H. Gheerardyn (2009). A new species of *Parameiropsis* Becker, 1974 (Copepoda: Harpacticoida) from the Porcupine Seabight (Northeast Atlantic Ocean). Marine Biodiversity 39: 83–93.

Corgosinho, P. H. C. & P. Martínez Arbizu (2010). Ameiridae Boeck and Argestidae Por revisited, with establishment of Parameiropsidae, a new family of Harpacticoida (Crustacea, Copepoda) from deep-sea sediments. Helgoland Marine Research 64: 223–255.

Coull, B. C. (1973). Meiobenthic Harpacticoida (Crustacea, Copepoda) from the deep sea off North Carolina IV. The families Cletodidae T. Scott and Ancorabolidae Sars. Transactions of the American Microscopical Society 92 (4): 604–620.

Dinet, A. (1973). Distribution quantitative du méiobenthos profond dans la région de la dorsale de Walvis (Sud-Ouest Africain). Marine Biology 20: 20–26.

— (1974). Espèces nouvelles de Copépodes harpacticoïdes (Crustacea) des sédiments profonds de la dorsale de Walvis. Archives de Zoologie Expérimentale et Générale 115: 549–577.

— (1975). Sur une nouvelle forme du genre *Pyrocletodes* Coull, 1973 (Copepoda, Harpacticoida) à position systématique incertaine. Bulletin de la Société Zoologique de France 100 (4): 437–442.

George, K. H. (2008). *Argestes angolaensis* sp. nov. (Copepoda: Harpacticoida: Argestidae) from the Angola Basin (Southeast Atlantic), and the phylogenetic characterization of the taxon *Argestes* Sars, including the rediscription of *A. mollis* Sars, 1910, and *A. reductus* (Itô, 1983). Zootaxa 1866: 223–262.

George, K. H. & C. Plum (2009). Description of two new species of *Dorsiceratus* Drzycimski, 1967 (Copepoda: Harpacticoida: Ancorabolidae) from Sedlo and Seine Seamounts (Northeastern Atlantic) and remarks on the phylogenetic status of the genus. Zootaxa 2096: 257–286.

George, K. H. & H. K. Schminke (2003). *Isthmiocaris longitelson* gen. et sp. nov., a strongly derived harpacticoid (Crustacea, Copepoda) from the Magellan Region, and its systematic affinities to certain "canthocamptid" taxa. Journal of Crustacean Biology 23(1): 119–130.

Gheerardyn, H. & K. H. George (2010). New representatives of the genus *Ancorabolina* George, 2006 (Copepoda, Harpacticoida, Ancorabolidae) including remarks on ancorabolid phylogeny. Zoological Journal of the Linnean Society 158: 16–55.

Gheerardyn, H. & G. Veit-Köhler (2009). Diversity and large-scale biogeography of Paramesochridae (Copepoda, Harpacticoida) in South Atlantic abyssal plains and the deep Southern Ocean. Deep-Sea Research I 56 (10): 1804–1815. doi:10.1016/j.dsr.2009.05.002

Gheerardyn, H., S. Seifried & A. Vanreusel (2008). A new species of *Halophytophilus* Brian, 1919 (Copepoda: Harpacticoida: Ectinosomatidae) from cold-water corals in the Porcupine Seabight (NE Atlantic). Zootaxa 1761: 1–16.

Gheerardyn, H., P. Martínez Arbizu & A. Vanreusel (2009). Discovery of Novocriniidae (Copepoda, Harpacticoida) from cold-water corals in the Porcupine Seabight (NE Atlantic), with description of a new species of *Atergopedia* Martínez Arbizu & Moura, 1998. Organisms, Diversity & Evolution 9: 248.e1–248.e12.

Gollner, S., V. N. Ivanenko & P. Martínez Arbizu (2008). A new species of deep-sea Tegastidae (Crustacea: Copepoda: Harpacticoida) from 9°50' N on the East Pacific Rise, with remarks on its ecology. Zootaxa 1866: 323–336.

Gómez, S. & S. Conroy-Dalton (2002). Description of *Ancorabolus hendrickxi* sp. nov. (Copepoda: Harpacticoida: Ancorabolidae) from the neotropics and notes on caudal ramus development within oligoarthran harpacticoids. Cahiers de Biologie Marine 43: 111–129.

Kröncke, I. & M. Türkay (2003). Structure and function of benthic communities in the deep Angola Basin in relation to food availability. Marine Ecology Progress Series 260: 43–53.

Menzel, L. (2010). A new species of *Eurycletodes* Sars, 1909 (Copepoda: Harpacticoida: Argestidae) from the Southern hemisphere including remarks on the phylogeny of and within this genus. Helgoland Marine Research, doi:10.1007/s10152-010-0237-9.

— (2011). First descriptions of copepodid stages, sexual dimorphism and intraspecific variability of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae), including the description of a new species with broad abyssal distribution. ZooKeys 96: 39–80, doi: 10.3897/zookeys.96.1496.

Menzel, L. & K. H. George (2009). Description of four new species of *Mesocletodes* Sars, 1909 (Copepoda, Harpacticoida, Argestidae) and redescription of *Mesocletodes robustus* Por, 1965 from the South Atlantic, including remarks on the phylogeny of the *Mesocletodes abyssicola*-group. Zootaxa 2096: 214–256.

Menzel, L., K. H. George & P. Martínez Arbizu (2011). Submarine ridges do not prevent large-scale dispersal of abyssal fauna: a case study of *Mesocletodes* (Crustacea, Copepoda, Harpacticoida). Deep-Sea Research I 58: 839–864, doi: 10.1016/j.dsr.2011.05.008.

Moura, G. & M. Pottek (1998). *Selenopsyllus*, a new genus of Cylindropsyllinae (Copepoda, Harpacticoida) from Atlantic and Antarctic deep waters. Senckenbergiana maritima 28: 185–209.

Plum, C. & K. H. George (2009). The paramesochrid fauna of the Great Meteor Seamount (Northeast Atlantic) including the description of a new species of *Scottopsyllus (Intermedopsyllus)* Kunz (Copepoda:

Harpacticoida: Paramesochridae). Marine Biodiversity 39: 265–289.

Plum, C. & P. Martínez Arbizu (2009). Discovery of *Smacigastes* Ivanenko & Defaye, 2004 (Copepoda: Harpacticoida: Tegastidae) in a deep-sea cold seep, with the description of a new species from the Gulf of Mexico. Zootaxa 2096: 338–355.

Rose, A., S. Seifried, E. Willen, K. H. George, G. Veit-Köhler, K. Bröhldick, J. Drewes, G. Moura, P. Martínez Arbizu & H. K. Schminke (2005). Comparing abyssal harpacticoid within-core species diversities in the Angola Basin at local and regional scale (Crustacea: Copepoda). Organisms, Diversity and Evolution 5: 3–17.

Schriever, G. (1983). New Harpacticoidea (Crustacea, Copepoda) from the North-Atlantic Ocean. III. New species of the family Cletodidae. Meteor Forschungsergebnisse 36: 65–83.

Schulz, M. & K. H. George (2010). *Ancorabolus chironi* sp. nov., the first record of a member of the *Ancorabolus*-group (Copepoda: Harpacticoida: Ancorabolidae) from the Mediterranean. Marine Biodiversity 40: 79–93.

Seifried, S. & P. Martínez Arbizu (2008). A new and exceptional species of *Bradya* Boeck, 1873 (Copepoda: Harpacticoida: Ectinosomatidae) from the abyssal plain of the Angola Basin and the variability of deep-sea Harpacticoida. Zootaxa 1866: 303–322.

Vasconcelos, D. M., K. H. George & P. J. P. Santos (2008). First record of the genus *Pseudomesochra* T. Scott (Harpacticoida: Pseudotachidiidae) in the South Atlantic with description of a deep-sea species: *Pseudomesochra longiseta* sp. nov. Zootaxa 1866: 337–348.

Vasconcelos, D. M., G. Veit-Köhler, J. Drewes & P. J. P. Santos (2009). First record of the genus *Kliopsyllus* Kunz, 1962 (Copepoda Harpacticoida, Paramesochridae) from Northeastern Brazil with description of the deep-sea species *Kliopsyllus minor* sp. nov. Zootaxa 2096: 327–337.

Veit-Köhler, G. & J. Drewes (2009). *Kliopsyllus schminkei* sp. n. (Copepoda, Harpacticoida, Paramesochridae) – a new copepod from the southeast Atlantic deep sea (Angola Basin). Zootaxa 2096: 313–326.

Wandeness, A. P., K. H. George & P. J. P. Santos (2009). First record of the taxon *Echinopsyllus* (Copepoda, Harpacticoida, Ancorabolidae) from the deep sea of Campos Basin, Brazil, with the description of three new species and their contribution to phylogenetic analysis. Zoological Journal of the Linnean Society 156: 52–78.

Willen, E. (2008). Pseudotachidiidae (Copepoda: Harpacticoida) from the Angola Basin and the Antarctic deep sea, with the description of a new species of *Paradanielssenia* Soyer, 1970. Organisms, Diversity and Evolution 8: 249–250 and electronic supplement.

— (2009). *Nyxis rostrocularis*, a new genus and species of Paranannopinae Por, 1986 (Copepoda, Harpacticoida) from the Southern Atlantic deep sea. Zootaxa 2096: 299–312.

Willen, E. & J. Dittmar (2009). A new genus of *Pseudomesochrinae* Willen, 1996 (Copepoda, Harpacticoida, Pseudotachidiidae) from the Guinea Basin. Zootaxa 2096: 287–298.