PARACRENHYDROSOMA OCEANIAE SP. NOV. (COPEPODA: HARPACTICOIDA), FROM KONGSFJORDEN, NORTHWEST SVALBARD (ARCTIC)

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Abstract.— Both sexes of a new species of Cletodidae belonging to the *Acrenhydrosoma*lineage are described from material collected at Kongsfjorden (Svalbard) and attributed to the genus *Paracrenhydrosoma* Gee, 1999. *Paracrenhydrosoma oceaniae* **sp. nov.** is easily distinguished from its congeners by the reduced setal formula of the natatorial legs, lacking the inner subdistal seta on segment 3 of legs 3 and 4. Several other characteristics *viz*. antennular and antennal armature, and the free leg 5 exopodite in both sexes, are indications of its basal position in the genus.

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Key words.— Paracrenhydrosoma, new species, Harpacticoida, Arctic fjord, Svalbard.

INTRODUCTION

Despite increasing interest in the role of biodiversity in the functioning of marine ecosystems, detailed taxonomic faunal studies are surprisingly rare. Our knowledge of the species composition of Svalbards (Spitsbergen) littoral meiofauna in general, and of the Harpacticoida in particular, is not an exception. Although Svalbards marine meiobenthos has been subject to a series of investigations, most reports only provide information on abundance and biomass at higher taxa level (Szymelfenig et al. 1995, Weslawski et al. 1997, Weslawski et al. 1999, Weslawski and Szymelfenig 1999, Soltwedel et al. 2000). Occasionally and for a few localities only, the meiofauna composition has been described in detail (Radziejewska and Stankowska-Radziun 1979, Kendall et al. 1997).

The first accounts on the harpacticoid fauna from the Arctic in general, and from Svalbard in particular, were published by Scott and Scott (1901) and Lang (1936). Additional reports, dealing with detailed species descriptions, are of much more recent date (Mielke 1974, Gee and Huys 1994, Gulliksen et al. 1999).

Based upon re-examination of the cotypes of Acrenhydrosoma perplexa (T. Scott, 1899) and addi-

tional material Gee (1999) recently recognized the separate status of the *Acrenhydrosoma*-lineage within the Cletodidae. To date this lineage comprises 4 well defined genera: *Acrenhydrosoma* Lang, 1944, *Dyacrenhydrosoma* Gee, 1999, *Paracrenhydrosoma* Gee, 1999 and *Neoacrenhydrosoma* Gee and Mu, 2000.

In the present contribution, the harpacticoid *Paracren-hydrosoma oceaniae* sp. nov., an abundant meiofaunal component at Kongsfjorden (Kotwicki et al. 2004), is described in detail and its intrageneric relationships discussed.

MATERIALS AND METHODS

Meiofauna samples from 25 stations located throughout Kongsfjorden (west coast of Spitsbergen Island at 79°N and 12°E) were taken during the cruises of the r/v "Oceania" in July 1999 and July 2000. Triplicate subsamples were collected from the contents of a van Veen grab. Sediments were preserved in 4% formaldehyde-seawater solution. For further details on sample treatment and for biological and physical data of the fjord see Hop et al. (2002), Svendsen et al. (2002) and Kotwicki et al. (2004). Material studied here was preserved in alcohol dissected in glycerine. Observations and illustrations were made using a Leitz Diaplan light microscope, equipped with phase contrast and a drawing tube. Terminology and abbreviations used are in accordance with Huys and Boxshall (1991). The type-series is deposited in the copepod collection of the Royal Belgian Institute of Natural Sciences, Brussels. Additional material forms part of the senior authors personal collection at the Institute of Oceanology Polish Academy of Sciences

Systematics

Paracrenhydrosoma oceaniae sp. nov. (Figs 1–5)

Etymology. The specific name, *oceaniae* refers to the research vessel *Oceania*, and honors its crew on the two field campaigns in which the specimens were collected.

Type material. Holotype: female, dissected and mounted on 3 slides, reg. no. COP 5000a-c; allotype male: dissected on 3 slides, reg. no. COP 5001a-c; para-types: 2 females and 1 male mounted on slides (reg. nos. COP 5002, 5003, 5004, respectively); 3 females and 3 males preserved in alcohol (reg. no. COP 5005).

Type-locality. Svalbard (Spitsbergen) The type-series was collected from station 20 (E4) at Kongsfjorden; 78.59.100 N and 11.31.677 E; 23 July 2000. Station 20 has a mud percentage up to 93% (fraction<63 μ m) and was characterized by: salinity – 34.2 PSU; temperature – 2°C and organic matter content – 3%.

Diagnosis. Paracrenhydrosoma oceaniae sp. nov. is easily distinguished from *Paracrenhydrosoma karlingi* (Lang, 1965,) *Paracrenhydrosoma maccalli* (Schizas and Shirley, 1994) and *Paracrenhydrosoma normani* Gee, 1999 by the reduced setal formula of the natatorial legs, lacking the inner subdistal seta on segment 3 of legs 3 and 4 and by the presence of 3 elements on the leg 5 exopodite in the female (2 seta in the other species). Several other characteristics viz. antennular and antennal armature, and the free leg 5 exopodite in both sexes, are indication of its basal position in the genus.

Description. Female. Body (Figs 1A, B) cylindrical, gently tapering posteriorly, without pronounced demarcation between prosome and urosome. Length: 335 μ m (holotype); ranging from 324–341 μ m. Head bell-shaped in dorsal view, with longitudinal internal cuticular ridges. Other somites well demarcated, with rigid transverse internal ridges in anterior half. Pleural region of leg-bearing somites rounded, of urosomites triangular, slightly expanded laterally and directed posteriorly. Genital double somite (Figs 1A–B, 2A) with distinct transverse ridges marking original segmentation: complete and external dorsally; nearly complete but internal ventrally. Anal somite slightly longer than wide with rounded smooth anal operculum.

Cephalothorax and other body somites with strong internal chitinous ridges. Posterior margin of cephalothorax with 3 pairs of sensillum-bearing socles. First free pedigerous somite with 3 pairs of sensillum-bearing socles along posterior margin, and two latero-dorsal sensillae arising in posterior third of somite, between medial and first lateral socle. Second and third free pedigerous somite with 4 pairs of sensillum-bearing socles along the posterior margin, and 1 pair of sensillum-bearing socles located close to, and at the medial site, of the dorsalmost pair of socles. Fifth-leg bearing somite with 4, first genital somite with 2, second one with 4, and successive somite with 3 pairs of sensillum-bearing socles. Penultimate somite without sensillae. Anal somite with 1 pair of sensillae-bearing socles, flanking operculum.

Ventral surface of genital double somite (Fig. 2A) and successive somite with a single pair of sensillum-bearing socles, penultimate somite without socles. Ventral surface of abdominal somites ornamented with minute spinules arranged transversally, close to posterior margin.

Rostrum (Fig. 3C) bell-shaped with pair of subdistal sensillae, and a central tube pore ventrally. Distal edge of rostrum hyaline with central depression.

Caudal rami (Figs 1A, B, 2A) conical, tapering posteriorly, 8 times as long as maximum width. Dorsal seta VII triarticulate at base, arising in proximal half of ramus, close to inner margin. Both proximal lateral setae I and II arising in anterior third, and seta III in median third. Outer and median terminal setae IV and V fused at base, the latter 1.5 times as long as ramus. Inner terminal seta VI slightly swollen at base. Surface ornamentation largely invisible, except for a short row of spinules along the ventral distal margin of ramus. Tube pores present (Fig. 2A) along outer margin: 1 proximal and 1 distal to setae I and II and 2 distal to seta III.

Antennule (Figs 3A, B) five-segmented, armature formula as follows: 1-8-7+ae-1-11+ae. All elements pinnate or serrate, except for single seta on segment 4, and on segment 5 the posterior directed setae and one of the elements forming thritek. Segment 2 dorsal seta apically pinnate, arising from a wide circular membranous depression.

Thritek. First segment with spinules near the distal edge and a semi-transparent (chitinous?) process with 3 to 4 cusps on the anterior margin, located close to the articulation of the antennule with the cephalothorax.

Antenna (Figs 3D–E), allobasis bearing a one-segmented exopodite and 2 abexopodal setae: proximal one short and sparsely pinnate, distal one long and strongly pinnate. Exopodite with 1 lateral plumose and 1 distal 1 pinnate seta. Endopodite with following armature: 3 lateral (2 spines, 1 minute seta) and 5 terminal (3 spines and 2 geniculate setae). Spinules on coxal segment, on



Figures 1A–C. Paracrenhydrosoma oceaniae sp. nov. (A) Female habitus, dorsal view; (B) female habitus, lateral view; (C). Male habitus, dorsal view. (A–B: holotype; C: paratype).



Figures 2A–C. *Paracrenhydrosoma oceaniae* sp. nov. (A) Female urosome (excluding P5 – bearing somite), ventral view; (B) male urosome, ventral view; (C) female genital field. (A, C: holotype; B: allotype).

allobasis near insertion of abexopodal setae, along outer and distal margin of endopodite, and parallel with the distal margin of exopodite.

Mandible (Figs 3F-G) with slender gnathobase ornamented with several teeth and a slender seta. Palp onesegmented with four pinnate setae: 1 inner, 2 distal and 1 on anterior surface. Spinule row on palp and on coxa near insertion of palp.

Maxillule (Fig. 3H) with 9 elements on arthrite. Coxal endite with 2 setae, not fused to basis. Basis without dis-



Figures 3A–K. *Paracrenhydrosoma oceaniae* sp. nov. (A) Female antennule, disarticulated; (B) Female antennule (armature omitted); (C) female rostrum, ventral view; (D) female antenna, outer view; (E) female antennal endopod; (F) female mandible, posterior view; (G) female mandibular palp, anterior view; (H) female maxillule; (I) female maxilla; (J) female maxilliped; (K) male antennule (armature omitted). (A–F, I–J: holotype; G–H: paratype; K: allotype).

tinct rami, bearing 6 elements: 2 inner, 2 medial and 2 outer ones.

Maxilla (Fig. 3I) with 2 syncoxal endites, each bearing 3 elements: 1 smooth and 2 pinnate setae. Allobasis drawn out intro smooth claw, bearing 2 accessory setae. Endopodite vestigial, represented by 2 setae.

Maxilliped (Fig. 3J) well developed, prehensile. Syncoxa with spinule rows on outer and inner margins, and a long inner distal pinnate element. Basis with strong spinules along palmar margin. Endopodal claw long and strongly recurved, with long accessory seta.

Leg 1 (Figs 4A, B) with well developed triangular praecoxa, ornamented with spinules on anterior surface. Intercoxal sclerite long, narrow, and bare. Coxa and basis furnished with dense pattern of long spinules. Outer basal seta bare, and reaching beyond second



(A, C-D: holotype; B: paratype).

exopodal segment. Inner basal spine pinnate and as long as endopodite. Outer margins of exopodal and endopodal segments with long spines, inner margins with fine setules. Terminal seta(e) of exopodite and endopodite penicillate.

Legs 2–4 (Figs 4C–D, 5A) with 3-segmented exopodites and 2-segmented endopodites. Praecoxa, coxa and basis with anterior spinule rows, posterior surface smooth. Endopodites short; reaching beyond articulation between exp-1 and -2 (P2), to length of exp. 1 and -2 combined (P3) or just beyond length exp-1 (P4). All rami with strong spinules.

Chaetotaxy of legs 1-4:

	Exopodite	Endopodite
leg 1:	0-0-022	0-111
leg 2:	0-0-022	0-020
leg 3:	0-0-022	0-021
leg 4:	0-0-022	0-021

Inner distal seta on exp-3 penicillate (P2, P3) or plumose (P4). Subdistal outer endopodal spine of leg 3 as long as supporting segment, of leg 4 twice as long as supporting segment.



Leg 5 (Fig. 5B) baseoendopodal lobe produced into long, apical serrate mucroniform process, reaching towards middle of penultimate body somite; with a transverse spinule row posteriorly; proximal half with several transverse spinule rows anteriorly; with 2 pinnate inner spines distal 1.5 times as long as proximal one. Exopodite clearly separated from baseoendopodite, bearing 3 setae: a short subdistal outer one and 2 apical ones. Peduncle, bearing outer basal seta articulating with anterior face of baseoendopod medial to exopod. Three tubular pores present along inner margin, and 1 on frontal surface of mucroniform process. No pore or tubular element discernible on exopodite.

Leg 6 (Fig. 2C) vestigal, each with two long, slender setae, forming a transverse bar, covering gonopores. Copulatory pore minute, at level of median transverse ridge, leading to wide and oval seminal receptacle. Latter connected by thick walled duct leading towards genital slit below leg 6 vestiges. Pair of simple pores located posterior to leg vestiges.

Tube pores, sensillae on head surface, and fine ornamentation of somites hardy discernible because of the presence of a layer of fine coagulated brownish material.

Male. Body (Fig. 1C) as in female but more narrow. Length 328 μ m (allotype; between 328–335 μ m in other specimens). Urosomites 3 to 5, posterior margins with slender spinules ventrally (Fig. 2B). Sexual dimorphism in urosome, antennule, leg 3 endopodite, leg 5 and leg 6.

Antennule (Fig. 3K) 7-segmented with following complement: 1-9-8-2-11+ae-2-9+ae. Segment 1with 2 spinule rows and a semitransparent ridge with 4 teeth. Segment 2 dorsal seta arising from depression and setulose as in female. Segment 5 dorsal surface with row of rigid and large spinules; with robust cuspidate struc-

ture proximally. Segment 6 with expanded outer distal corner. Segment 7 with hook-shaped terminal half. Aesthetascs present on segments 5 and 7.

Legs 1–4 as in female, except for leg 3 endopodite (Figs 5C–D). P3 enp-2 with hook-shaped apophysis, with 2 blunt teeth in distal half of outer margin; with 2 terminal plumose setae.

Leg 5 (Fig. 5 E) general appearance as in female. Inner margin of mucroniform process with single, short, pinnate spine. Exopodite with only 2 apical pinnate setae.

Leg 6 vestiges (Fig. 2B) unarmed and asymmetrical; one member articulating with somite (right), other member (left) not differentiated.

DISCUSSION

The genera Acrenhydrosoma Lang, 1944, Dyacrenhydrosoma Gee, 1999, Paracrenhydrosoma Gee, 1999 and Neoacrenhydrosoma Gee and Mu, 2000 constitute a well defined lineage among the genera currently assembled in the family Cletodidae T. Scott, 1905 sensu Por, 1986 (see Bodin 1997). The strongly modified endopodal lobe of the fifth legs in both sexes, the position of the exopods in the fith legs when present, the armature of the female sixth legs, separate these four genera from all other known cletodids. Based on this combination of characters the new species described from Svalbard, undoubtedly, belongs to this lineage. On account of the rostral shape, mandibular palp with 4 setae, the absence of a pseudo-operculum on the preanal somite, segmentation of swimming leg rami and setal formula of the first leg, the new species is placed in the genus Paracrenhydrosoma. P. oceaniae, however, readily distinguishable from its congeners by the reduced setal formula of exopods of the third and fourth legs (subdistal inner seta on the exp-3 absent) and by the presence of 3 elements on the leg 5 exopodite in the female (2 seta in the other species).

Despite the obvious resemblances of the Svalbard species with the three species currently assigned to *Paracrenhydrosoma*, differences are observed in the antennules, the antennae and in the fifth legs.

Male and female antennules of *P. maccalli* (Schizas and Shirley, 1994) and *P. normani* Gee, 1999 appear to be identical with that of *Acrenhydrosoma perplexa* (T. Scott, 1988) with the second segment possessing 7 elements in the female and 9 in the male. One of the dorsal elements present on this segment typically arises from a circular depression (pit) and is represented by a modified tubular seta within the *Acrenhydrosoma*-line-age. The antennules of *P. oceaniae* however, bear 8 setae in the female segment 2. Additionally the dorsal pit-seta of segment 2 is unmodified bipinnate in both sexes.

Apparently, P. karlingi (Lang, 1965) also displays an unmodified, dorsal seta on antennulary segment 2, according to the original description and illustration. The number of elements on the segment 2 of the female of *P. karlingi* appears to be 7 instead of 8, but this has to be confirmed. Also, *Neoacrenhydrosoma zangli* Gee and Mu, 2000, has an antennulary armature formula similar to the species described here. However, both of these characters could be the results of errors made in the original description and need to be verified by re-examination of *N. zangli* and *P. karlingi*.

The general morphology of the antenna is similar in all species belonging to the *Acrenhydrosoma*-lineage. However, 3 types are recognizable based on the abexopodal armature of the allobasis: (1) completely devoid of setal elements as in *Dyacrenhydrosoma breviseta*; (2) with a single seta arising in the distal (endopodal) half of the segment as in *Acrenhydrosoma perplexa*, *Paracrenhydrosoma maccalli* and *P. normani*, and (3) with a single seta located in the proximal (basal) half as in *Neoacrenhydrosoma zhangi*.

In contrast, the antenna of *P. oceaniae* retains the plesiomorphic condition of the antennary allobasis with 2 setae (basal and endopodal) along the abexopodal margin.

With the exception of *Neoacrenhydrosoma zhangi* which completely lacks an exopodite (Gee and Mu 2000) the female fifth leg exopodite is similar in all other members of the *Acrenhydrosoma* - lineage. The quadrate expansion bears either 3 (*Acrenhydrosoma perplexa*) or 2 (the other species) setae in female. *P. oceaniae* bears three exopodal elements: 2 apically and one outer laterally. In this respect, the fifth leg exopodite of *P. oceaniae* resembles that of *A. perplexa*, more than that of *P. maccalli* or *P. normani*. The outer lateral element can not be confused with a lateral tube pore on the exopod, as seen in *P. maccalli*.

The fifth leg exopodal ramus of *P. karlingi* has been described by Lang (1965: p. 439) having: "one hair-like setula on outer edge and two plumose terminal setae". The exact nature of the lateral element is not discernable from the accompanying illustration. It may represent either a slender seta, or long slender setule or a tube pore. It should be re-examined in the future.

The Acrenhydrosoma-complex is largely defined by a series of apomorphic conditions of the fifth leg. Indeed, at least 2 autapomorphic characterstates are recognizable for this appendage: (1) the extension and narrowing into a mucroniform structure of the endopodal lobe; (2) the striking similarity of shape and dimension of the leg in the two sexes.

With the addition of the Svalbard species to the genus *Paracrenhydrosoma*, four species (*P. macalli* (Schizas and Shirley, 1994), *P. karlingi* (Lang, 1965) and *P. normani* Gee, 1999) are now unified within this taxon. However, *P. oceaniae* displays the plesiomorphic condition of several characteristics *viz.* the female antennule with on the second segment 8 setae, the antenna with a proximal and a distal element on the abexopodal margin, and the

leg 5 exopodite not fused with the baseoendopodite. This contrasts fundamentally with the more advanced aspect of these appendages in two of the previously described species (*P. macalli* and *P. normani*).

P. oceaniae is clearly a member of *Paracrenhydosoma* in which it takes a basal position. Crucial in the unraveling of the phylogenetics of this taxon is *P. karlingi*. The exact nature of several appendages and elements of this species have to be re-examined.

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References

- Bodin, Ph. 1997. Catalogue of the new marine Harpacticoid Copepods (1997 edition). Studiedocumenten van het K.B.I.N., 89: 1–304.
- Gee, J. M. 1994. Towards a revision of *Enhydrosoma* Boeck, 1872 (Harpacticoida: Cletodidae *sensu* Por): a re-examination of the type-species, *E. curticauda* Boeck, 1972, and the establishment of *Kollerua* gen. nov. Sarsia, 79: 83–107.
- Gee, J. M. 1999. A revision of Acrenhydrosoma (Copepoda, Harpacticoida) with the establishment of Dyacrenhydrosoma gen. nov. and Paracrenhydrosoma gen. nov. and descriptions of two new species. Cahiers de Biologie Marine, 40: 337–357.
- Gee, J. M. and R. Huys. 1994. Paranannopidae (Copepoda: Harpacticoida) from sublittoral soft sediments in Spitsbergen. Journal of Natural History, 28: 1007–1046.
- Gee, J. and Mu. 2000. A new genus of Cletodidae (Copepoda: Harpacticoida) from the Bohai Sea, China. Journal of Natural History, 34: 809–822.
- Gulliksen, B., Palerud, R., Brattegard, T. and J. Sneli (eds.). 1999. Distribution of marine benthic macro-organisms at Svalbard (including Bear Island) and Jan Mayen. Research Report for DN 1999-4. Directorate for Nature Management., 148pp.
- Hop, H., Pearson, T., Hegseth, E. N., Kovacs, K. M., Weslawski, J. M., Wiencke, C., Kwasniewski, S., Eiane, K., Leakey, R., Cochrane, S., Zajaczkowski, M., Lønne O. J., Mehlum, F., Lydersen, C., Gulliksen, B., Falk-Petersen, S., Poltermann, M., Wangberg, S. A., Kendall,

M., Bischof, K., Voronkov, A., Kovaltchouk, N. A., Gabrielsen, G. W., Wlodarska-Kowalczuk, M., Wiktor, J., di Prisco, G., Estoppey, A., Pappucci, C. and S. Gerland. 2002. The marine ecosystem of Kongsfjorden, Svalbard. Polar Research, 21: 167–208.

- Huys, R. and G. A. Boxshall 1991. Copepod evolution: 1–468 (The Ray Society, London).
- Kendall, M. A., Warwick R. and P. J. Somerfield. 1997. Species size distribution in Arctic benthic communities. Polar Biology, 17: 389–392.
- Kotwicki, L., Szymelfenig, M., de Troch, M. and M. Zajaczkowski. 2004. Meiofauna distribution in Kongsfjorden, Spitsbergen. Polar Biology, 27: 661–669.
- Lang, K. 1936. Die wahrend der Schwedischen Expedition nach Spitzbergen 1899 eingesammelten Harpacticiden. Kungliga Svenska Vetenskapsakademiens Handlingar, (3) 15 (4): 1–55.
- Lang, K. 1965. Copepoda Harpacticoidea from the Californian Pacific coast. Kunglia Svenska Vetenskaps Akademiens Handlinger, 10(2): 1–560.
- Mielke, W. 1974. Eulitorale Harpacticoida (Copepoda) von Spitzbergen. Mikrofauna des Meeresbodens, 37: 161–210.
- Radziejewska, T. and M. Stankowska-Radziun. 1979. Intertidal meiofauna of Recherchefjorden and Malbukta, Vest Spitsbergen. Sarsia, 64: 253–258.
- Scott, T. and A. Scott. 1901. On some Entomostraca collected in the Arctic Seas in 1898 by William S. Bruce. Annals and Magazine of Natural History, Ser. 7, 8: 337–356.
- Soltwedel, T., Mokievsky V. and I. Schewe. 2000. Benthic activity and biomass on the Yermark Plateau and in adjacent deep-sea regions northwest of Svalbard. Deep Sea Research I, 47: 1761–1785.
- Svendsen, H., Beszczynska-Møller, A., Hagen, J. O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J. B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J. G. and W. Dallmann. 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fiord system in Svalbard. Polar Research, 21:133–166.
- Szymelfenig, M., Kwasniewski, S. and J. M. Weslawski. 1995. Intertidal zone of Svalbard 2. Meiobenthos density and occurrence. Polar Biology, 15: 137–141.
- Weslawski, J.M. and M. Szymelfenig. 1999. Community composition of tidal flats on Spitsbergen: Consequence of disturbance? *In*: Biogeochemical Cycling and Sediment Ecology, J.S. Gray et al. (eds.), 185–193.
- Weslawski, J.M., Szymelfenig, M., Zajaczkowski, M. and A. Keck. 1999. Influence of salinity and suspended matter on benthos of an Arctic tidal flat. ICES Journal of Marine Science, 56, Suppl.: 194–202.
- Weslawski, J.M., Zajaczkowski, M., Wiktor, J. and M. Szymelfenig. 1997. Intertidal zone of Svalbard 3. Littoral of a subarctic, oceanic island: Bjornoya. Polar Biology, 18: 45–52.

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