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The multiple faces of *Nannopus palustris auct.* reconsidered: A morphological approach (Copepoda: Harpacticoida: Nannopodidae)

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ABSTRACT

Specimens attributable to the genus *Nannopus* and sampled on three intertidal mudflats *e.g.* Longyearbyen (Spitsbergen, Svalbard archipelago), the river banks of "De Schelde" in Belgium and from its estuary, the "Oosterschelde", in the Netherlands are compared. This revealed the presence of a series of specific features allowing the discrimination of different species: *N. didelphis* spec. nov., *N. scaldicola* spec. nov., *N. procerus* spec. nov. and *N. hirsutus* spec. nov. In view of this, the poor original description of *Nannopus palustris* Brady, 1880 is reinterpreted and compared with the few descriptions available and the materials studied herein. "Norwegian" specimens identified by Sars as *N. palustris* turn out to be conspecific with *N. procerus* spec. nov., *N. flexibilis* (Lilljeborg) is re-instated as a separate species with *N. palustris tiberiadis* Por, 1968, *N. palustris* sensu Sars, 1927, Damian-Georgescu, 1970, and *Nannopus* spec. Hemsen, 1952 as junior synonyms. *Nannopus* may turn out to comprise of two different phylogenetic lineages each sustained by derived character states exhibited in the structure of the leg 4 armature and the morphology of the male leg 6 and the male genital apparatus.

1. Introduction

The outright vagueness of the original description of *Nannopus palustris* by Brady (1880) has generated considerable confusion (Willey, 1923). Subsequent descriptions (Canu, 1892; Scott, 1902; Lilljeborg, 1902; Sars, 1909a,b; Gurney, 1932) based on specimens claimed to represent *N. palustris* excelled in detail but discrepancies between the presentations initiated the general stigmatization of *N. palustris* as a morphological highly variable harpacticoid. For decades, deviations from these contributions have been emphasized and judged as additional evidences of its morphologic plasticity. Reports of *N. palustris* in different habitats, ranging from sublitoral to estuarine, in sandy to pure siltly sediments, from marine to freshwater, and from global locations have contributed significantly to the notion of *N. palustris* as a eurytopic harpacticoid (Wells, 1971).

The demonstration of genetic isolation in sympatric morphs inhabiting a South Carolina estuarine marsh challenged those longstanding assumptions (Staton et al., 2005). But, when the genetics provided a clear and promising signal for at least two out of three co-occurring morphs, the few and small visualized structural differences fed the suspicion of a species complex in which differentiation would be a matter of small and hardly discernible details. An expanded data set (Gárlitska et al., 2012) with specimens obtained from the North Sea, Black Sea and White Sea corroborated the findings of Staton et al. (2005) but failed largely to differentiate each of the morphs on morphological grounds.

Numerous reports on the occurrence of *N. palustris* have been published (see distribution map in Gárlitska et al., 2012) but very few provided structural details of the specimens examined. Text books often present a compilation of illustrations from different sources (Pesta, 1932; Lang, 1948; Borutzky, 1952; Wilson and Yeatman, 1959) maintaining the longstanding confusion as a consequence. The purpose of the present contribution is to document the morphology of specimens collected on three intertidal mudflats: Longyearbyen in Adventfjorden along the west coast of Spitsbergen (Svalbard), the estuary of the Oosterschelde in the Netherlands and from the river banks along the river De Schelde in Belgium. Although certain structures display variability, others appear to be constant and allow the differentiation of four different groups. Each of these groups is considered herein as a distinct species. Among them, none could be attributed to *N. palustris* as described by Brady (1880). Four new species, *N. didelphis* spec. nov., *N. hirsutus* spec. nov., *N. scaldicola* spec. nov. and *N. procerus* spec. nov. are thus introduced. The latter one could be identified with the Norwegian population of *N. palustris* described by Sars (1909a,b). Illustrated records referring to *N. palustris* are discussed in order to

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highlight their particularities currently annotated as expressions of the structural variability, but which are now assumed to be species specific characteristics. As a result, *N. flexibilis* (Lilljeborg, 1902) is reintroduced as a separate species. *N. palustris tiberiadis* Por, 1968, *N. palustris* sensu Sars, 1927, *N. palustris* sensu Damian-Georgescu, 1970 and *Nannopus* spec. Hemsen, 1952 are considered conspecific with *N. flexibilis* and sunk in synonymy. We refrain to introduce new names for certain morphs displaying significant, possibly species specific, differences. Such introductions appear ambiguous at the moment. A redescription of *N. palustris* based on topotypic material (desirably), eventually with the designation of a neotype, is a fundamental requirement before further attempts can be made to disentangle this species complex.

2. Methods

Material originated from three intertidal mudflats: (1) Longyearbyen in Adventfjorden (Spitsbergen, Svalbard archipelago), (2) the river banks of "De Schelde" (Belgium) and (3) the "Oosterschelde" estuary (the Netherlands). Samples were fixed in the field by adding formalin (resulting in a concentration of approx. 4%). Sorted specimens were preserved in 75% ethyl alcohol (*N. didelphis* spec. nov. and *N. scaldicola* spec. nov.) or pure glycerol (*N. procerus* spec. nov. and *N. hirsutus* spec. nov.). Dissected animals are mounted in glycerol, preserved ones in buffered ethyl alcohol (75%)/glycerol mixture. All are incorporated in the Crustacean collection at the Royal Belgian Institute of Natural Sciences (Brussels) and registered RBINSc COP #. The material from Norway, Birqet Quarum (Egypt) and the Caspian Sea identified as *N. palustris* by Sars (1909a,b, 1927), either preserved in alcohol or mounted on slides, is stored at the Zoological Museum in Oslo. Abbreviations used in text and tables: Aesth, aesthetasc, Exo, End, exopodite, endopodite, respectively; CII-CV, copepodid stages 2–5; Latin and Roman numerals in tables refer to spines and seta, respectively.

3. Systematics

3.1. Species descriptions

Family Nannopodidae Boeck, 1880
(ex Huntemanniidae Por, 1986)

Nannopus didelphis spec. nov.
(Figs. 1–11)

Nannopus palustris Brady, 1880 – Mielke, 1974: 198–200, Fig. 23.
Nannopus palustris Brady, 1880 – Kotwicki, 2002: tbl. 1.
? *Nannopus palustris* Brady, 1880 – Wojtasik and Kur, 2007: 97–108 [partial].

Type locality. Spitsbergen (Svalbard Archipelago), Adventfjorden (= southern branch of Isfjorden): intertidal mud flat in front of Longyearbyen (78°13′0″ N, 15°38″ E) and the affluents of the glacier-fed rivers Adventelva and Longyearelva: specimens collected between microphytobenthic diatom colonies (cfr. *Gyrosigma*). Leg. L. Kotwicki, July 2011)
Type material. Holotype (female) dissected on 3 slides, registered RBINSc COP 9906A-C, allotype, dissected on 3 slides, registered RBINSc COP 9909A-C; paratypes dissected: 6 females, registered RBINSc COP 9903A-C, 9904A-C, 9905A-C, 9907A-C, 9908A-B; 10.079A-C, 2 males, registered RBINSc COP 9910A-B, 10.078A-C; 1 female CV (RBINSc COP 9916A-B), 1 male CV (RBINSc COP 9915A-B), 1 female CIV (RBINSc COP 9917A-B), 1 male CIV (RBINSc COP 9918A-B); preserved paratypes (29 females, 13 males, 2 CV females, 2 CIV females, 1 CIV male, 2 CIII, 1 CII) registered RBINSc COP 10.080.
Etymology. *Didelphis* from the Greek prefix *dis* (pair or double) and *delphis* (womb), referring to the separated genital atria and associated structures in the female. Used as a noun in apposition.

Description. Female. Habitus (Fig. 1A–C) fusiform, prosome faintly depressed; cephalothorax widest along posterodorsal margin, bell-shaped, nearly as long as 1/4 of entire body length with crescent invagination in middle of ventral border; metasome gently narrowing caudally; podoplean flexure indistinct; urosome less than half entire body length; genital somite completely fused with following somite forming genital double-somite, ancestral posterodorsal and lateral margin of genital somite distinct; anterior half of genital double-somite (urosomite 2) wider than posterior half (urosomite 3); ventral surface of genital double-somite flat and undivided (Fig. 2A); urosomites 4–6 ovate in cross-section; integument of somites rather thick and rigidly sclerotized; presence of integumental windows unclear (dotted circle on pediger 2 in Fig. 1B); body length 538–698 μm (compact-expanded, and maximum width 215–220 μm.

Body ornamentation: posterodorsal and lateral margin of each pleurotergite coarsely serrate, with pleural margin hirsute; cephalothorax with smooth surface; surface of metasomites and urosomites furnished with dense carpet of minute spinules (not illustrated); posteroventral margin of genital double-somite and abdominal somites coarsely serrate, with (Fig. 2A inserts with arrow) or without (Fig. 2A general illustration) slender spinules located midventrally or along the entire margin; posterolateral edges of urosomites with dense cluster of long flexible setules; ventral surface of genital double-somite smooth, of following somites with minute spinules.

Anal somite (Fig. 3A–E) with crescent operculum, densely covered with long and slim setules; surface of somite with minute spinules (not illustrated) and lacking obvious pore orifices; ventral surface with (Figs. 2A and 3C), rarely without (Fig. 3E), transverse row of long spinules along posteroventral margin, on either side of closure of anal sinus.

Caudal rami (Fig. 3A–E) cylindrical, with separation between anal somite and ramus hardly discernable ventrally; twice (in dorsal view) to three (in ventral view) times longer than wide, and bearing 7 setae; anterolateral accessory seta (I) short, less than ramal width, inserted close to ramal articulation with somite; anterolateral and posterolateral setae (II and III) both located at midlength of margin, former as long as ramus and half as long as the latter; outer terminal seta (IV) robust, without breaking plane, near to 3 times longer than ramus, ornamented with few short and widely spaced setules; median terminal seta (V) twice as long as outer one, without breaking plane, globular inflated at insertion and with circlet of fine setules located at caudal margin of inflation; anterior half of median terminal seta rather wide and smooth; caudal half distinctly more narrow, sparsely pinnate; inner terminal seta (VI) inserted at ventral side of margin below insertion of median terminal seta; half as long as ramus, and globular at insertion; dorsal seta (VII) located in median third near medial margin, and articulating on two basal parts; rami ornamented with rows of robust spinules along outer, posterodorsal and posteroventral margin; medial margin with an anterior row of setules and a posterior row of spinules; dorsal and lateral surface of rami covered with dense pattern of minute spinules (not illustrated), ventral surface smooth.

Rostrum (Fig. 4G) prominent, truncate, partially fused with cephalothorax, recurved ventrally nearly perpendicular with main body axis; lateral margins and distal area densely hirsute with long and slender setules (considerably more than illustrated);

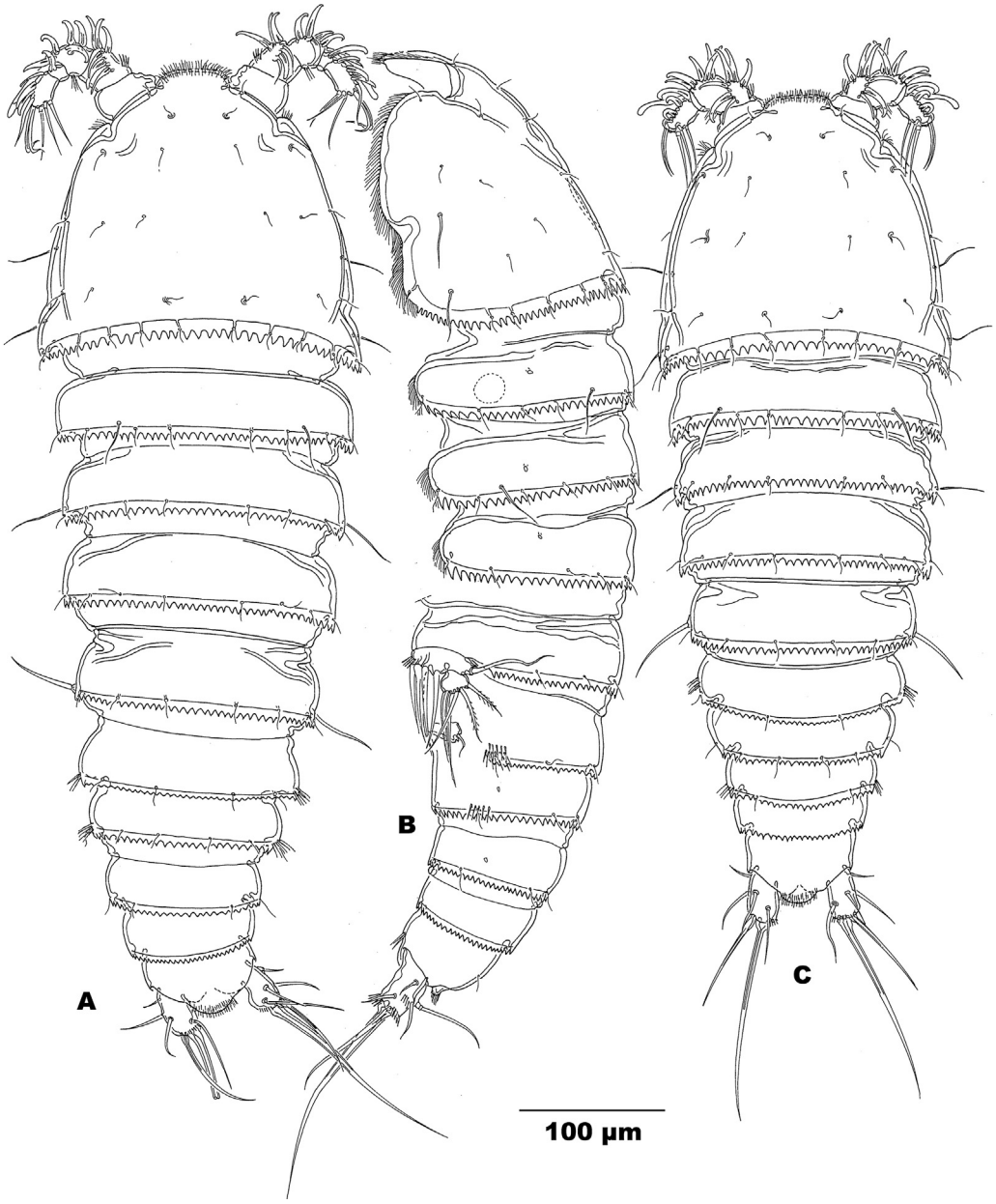

Fig. 1. *Nannopus didelphis* spec. nov., female (A–C). (A) Habitus, dorsal. (B) Habitus, lateral. (C) Habitus, dorsal. Note the length difference between expanded (A and B) and contracted specimens (C) co-occurring in the same sample.

2 dorsal sensillae located in anterior region; main surface of rostrum smooth.

Antennule (Fig. 4A and B) 5-segmented, short and compact; separation between first and second segment hardly discernable; arthrodial membrane between first and second segment formed wide and triangular; armament (from proximal to distal segment): 1, 9, 7+Aesth, 1, 10+Aesth; setal armament short and robust, partially pinnate (segment 2), partially devoid of ornament (segments 2, 3, 4 and 5); setae on posterodistal edge of ultimate segment articulating on basal part; first segment voluminous with blunt rigid ventral notch near anterior margin and a row of long spinules and a tubular pore extension (arrow in Fig. 4B) close to insertion of seta; second segment with dorsal spinular row in proximal half, third one with spinular row along posterior margin.

Antenna (Fig. 4C–E) composed of allobasis, 1-segmented endopodite and 1-segmented exopodite; outer margin of allobasis with proximal setular cluster and 2 abexopodal setae; endopodite widening distally, furnished with cluster of long setules in proximal half of outer margin, set of robust spinules on outer distal corner, and comb of slender spinules along inner distal edge; endopodal armament composed of 5 strong, short and rigid naked elements (2 sub-distal on outer margin, 3 on distal border) and 1 slender smooth element (inner distal corner); endopodal armature elements as long as segment, at the most; exopodite 1.5 times longer than wide, bearing 4 elements: 2 subdistal and 2 apical ones; proximalmost element pinnate with stout setules widely spaced along stem; subdistal and terminal element apparently smooth; integument of exopodite unadorned.

Mandible (Fig. 5A–C) with robust and rigidly sclerotized gnathobasis, furnished with an outer and a medially situated short row of slender spinules; cutting edge composed by 4 rigid, multicuspidate blunt teeth and a hyaline structure composed by a serrate seta and 2 laminate and multi-cuspidate expansions; basis well developed, rami obsolete, represented by 2 (Fig. 5B) or 3 (Fig. 5A and

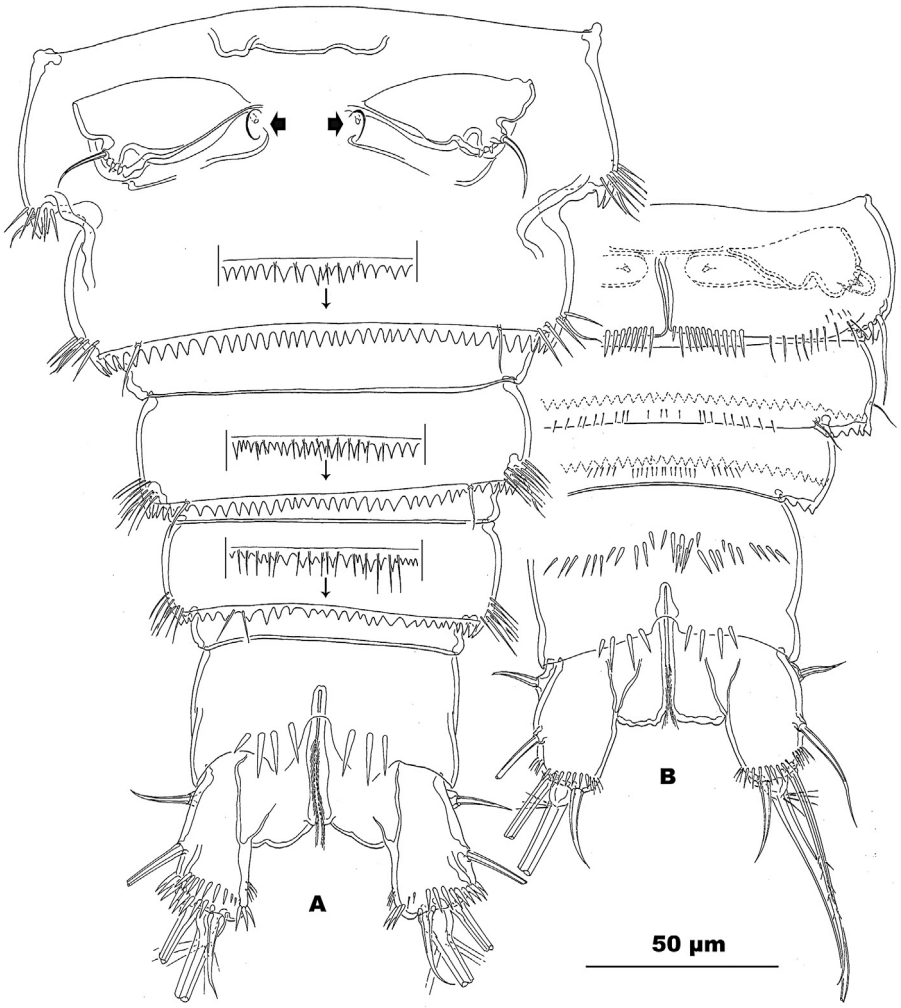

Fig. 2. *Nannopus didelphis* spec. nov., female (A–B). (A) Ggenital double-somite and abdomen, ventral (inserts depict variability of border ornamentation). (B) Female copepodid V urosomites 2–5, ventral (adult leg 6 complex and posterior margins of urosomites visible, represented with dotted lines).

C) setae; medial element of basis long; all setae with dense and rigid setular ornamentation (partially illustrated); surface of mandibular palp with a proximal setule comb, expanding from caudal to frontal face, and a double setule row parallel with distal margin.

Paragnath (Fig. 5D) large, semi-ovate, with dense clusters of thin setules along outer and distal margin. Labrum (Fig. 4F) wide; border with hyaline appearance, fitted between pair of blunt rigid expansions of labral plate; margin furnished with slender spinules and setules.

Maxillule (Fig. 5E–G) with prominent praecoxal arthrite armed with 2 slender and naked surface setae, 8 sturdy (serrate or smooth) medial spines, and 2 long recurved and heavily armed lateral elements; posterior surface with some spinules (Fig. 5G); syncoxa with cylindrical coxal endite bearing 2 elements (one geniculated, one hook-shaped); spinular rows on anterior syncoxal surface and along medial margin of coxal endite present; basis with 5 medial elements: 3 distal, 2 subdistal; dorsomedial ones armed with long and rigid spinules; subdistal ones pinnate; endopodite represented by 1, exopodite represented by 2 setae (outermost and innermost sparsely, middle one densely pinnate, only partially illustrated); surface of basis with spinules along medial margin.

Maxilla (Fig. 5H–J) with 2 endites on syncoxa, outer border with few spinules, surface smooth; each endite with 3 elements, confluent with segment; one prominent and voluminous, both others half as wide; each element furnished with large and rigid spinules proximally, smooth ventrally; basis with narrow, unarmed claw, 1 accessory seta, and a spinular comb on frontal surface; endopodite confluent with basis, represented by a short elevation bearing two setae.

Maxilliped (Fig. 4H–I) 3-segmented; syncoxa shorter than basis with single short distal seta, located halfway frontal face; syncoxal frontal surface with proximal row of short and slender spinules; outer margin and inner distal area of caudal syncoxal surface with row of long and slender spinules; basis ovate, twice as long as wide, with frontal and caudal spinular comb parallel with inner margin, spanning entire length, and crown of long and slender spinules distally near articulation of endopodite; endopodite 2-segmented with 2 setae and claw on distal segment; claw confluent with distal segment and armed with long and rigid spinules in distal half.

Leg protopodites well defined with wide and concave intercoxal sclerites (Figs 6B, 7C and 8B), smooth on both sides, except for some hairy ornament on leg 2 intercoxal lamella (Fig. 6F); frontal face of preacoxa narrow, expanding along entire width of leg, with spinular row in outer third of distal border; caudal region of praecoxa narrow, represented as large semi-ovate expansion partially covering coxa and armed with a spinular row parallel to outer margin (example leg 2 see Fig. 6E); frontal surface of coxa with 2 spinular rows: one composed of wide and robust spinules arranged parallel with outer margin and one of narrow spinules on surface near outer half in leg 1, in medial half in legs 2–4; caudal surface of coxa unadorned; leg 1 basis with short setiform outer seta and prominent rigid and pectinate medial spine; spinular rows on frontal surface: near

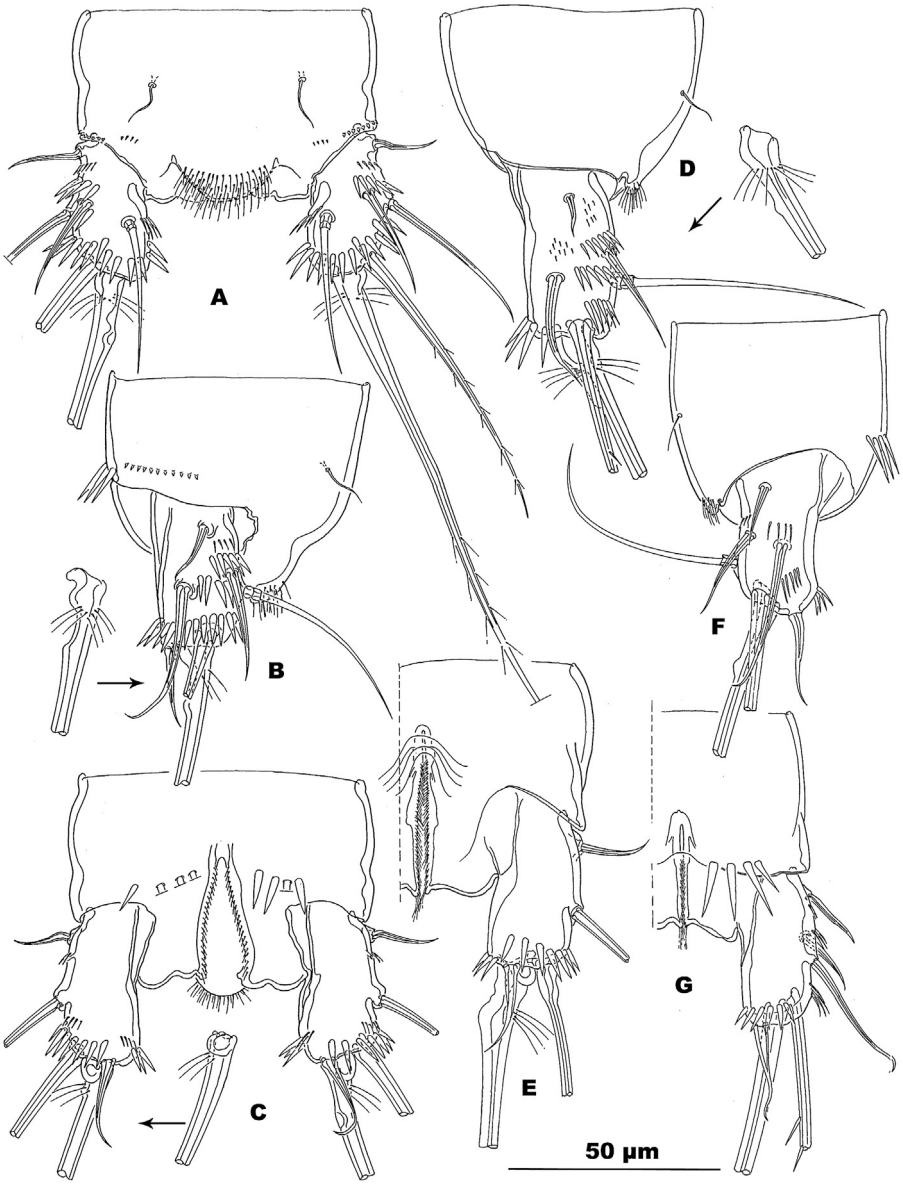

Fig. 3. *Nannopus didelphis* spec. nov., female (A–E), male (F–G). (A) Anal somite in dorsal view. (B) Idem, lateral. (C) Idem, ventral. (D) Idem, lateral. (E) Idem, ventral. (F) Anal somite, lateral. (G) Idem, ventral (profile of principal terminal seta separately depicted laterally in A and D, ventrally in C).

articulation with exopodite (robust spinules) and near articulation of endopodite (slender spinules) in legs 1–4 and at insertion of medial spine in leg 1; caudal surface of basis smooth; ornamentation of basis in legs 2–4 comparable, but spinular ornament at inner distal corner more slender and considerably longer than in leg 1; outer seta of leg 2 basis short, of leg 3 and 4 about twice as long as in legs 1 and 2.

Legs 1–3 with 3-segmented exopodite and 2-segmented endopodite; leg 4 with 3-segmented exopodite and one-segmented, dwarfed, endopodite (Figs. 6A, 6D, 7A and 8A, respectively); endopodites of legs 1–3 rather short, at the most as long as first and second exopodite segment combined; proximal endopodite segment of leg 2 with truncate expansion on outer distal corner, unmodified in legs 1 and 3 (Table 1).

Outer exopodite spines long, robust, blunt and smooth, except for single subdistal sharp tooth on spine of second segment of leg 1, on both terminal spines of leg 3, and on terminal spine of leg 4; outer terminal spine on leg 1 exopodite long, smooth along outer margin, armed with long rigid setules medially; inner terminal element on leg 1 exopodite twice as long as outer one, setiform and pinnate; outer terminal elements on leg 2–4 exopodite 2 to 2.5 times longer than outer subdistal outer spine, rigid, and furnished with widely spaced robust setules on both sides (outer element) or along outer margin only (inner element); medial elements of leg 2–4 exopodite setiform and sparsely pinnate except for subdistal medial stout element on leg 4 exopodite being pectinate in distal third and being half as long as proximal seta; exopodal segments with, frontally, wide and robust spinules along outer margin and along outer distal edge, a tuft of long and slender spinules in middle of inner margin,

Table 1
Leg armature distribution in *N. didelphis* spec. nov.

		EXO	END
Leg 1	Fig. 6A	I,0-I,1-II,I+1,0	0,0-I,1,1
Leg 2	Fig. 6B	I,0-I,1-III,I+1,1	0,0-I,1,1
Leg 3	Fig. 7A	I,0-I,1-III,I+1,2	0,0-I,1,1
Leg 4	Fig. 8A	I,0-I,1-III,I+1,2	020

Fig. 4. *Nannopus didelphis* spec. nov., female (A–I). (A) Antennule, dorsal. (B) Idem, ventral. (C) Antenna. (D) Antennary endopodite, inner view. (E) Antennary exopodite. (F) Labrum, ventral. (G) Rostrum, dorsal. (H) Maxilliped, frontal. (I) Idem, caudal.

and a short hyaline serrate fringe along medial half of distal border; caudal surface of exopodite segments with comb of long and flexible setules lined up parallel to outer margin (example: leg 3 exopodite in Fig. 7B).

Leg 1 endopodite (Fig. 6C) with outer terminal element on second segment as long as endopodite segments combined, smooth except for single subdistal tooth (arrowed in Fig. 6C); median terminal element slightly longer than endopodite, robust and set with rigid, widely spaced, setules; inner seta short, slender with subdistal flagel; leg 1 endopodite segments with spinular row on frontal surface and cluster of long setules along medial margin; leg 2 endopodite (Fig. 6D) with medial and outer terminal elements subequal, median one 3 times longer; outer spine smooth, median and medial one pinnate; leg 3 endopodite (Fig. 7A) with inner terminal and medial element subequal, setiform, and pinnate (not illustrated); outer terminal spine smooth; proximal endopodite segment of legs 2 and 3 with long spinules along distal frontal border, and with (leg 2) or without (leg 3) tuft of setules along inner margin; second endopodite segment with spinular row along distal frontal border (leg 2) or in middle of frontal surface (leg 3) and with cluster of setules along medial margin (legs 2 and 3); leg 4 endopodite (Fig. 8C) dwarfed, slightly wider than long, with few spinules along distal margin, bearing a long pinnate outer element and short pinnate inner one.

Leg 5 (Fig. 9A–C) with baseoendopodite represented as a narrow triangular transverse plate, widest at outer side, slimmest medially; intercoxal sclerite absent; margins and surface furnished with a variable number of (slender and rigid) spinules; three or four endopodal elements with outermost one the longest and being pinnate; innermost element, second longest, invariably pectinate distally distal end; median ones either pectinate (Fig. 9B and C) or completely pinnate (Fig. 9A); exopodite, articulating with baseoendopodite, square, bearing 5 elements: 1 medial, 2 distal, and 2 outer ones; medial element most prominent, voluminous, pinnate, and confluent with segment; distal ones lanceolate; distal and outer setae variable in length, sparsely pinnate with short setules; frontal surface of exopodite with transverse spinular rows of variable spinular robustness and number.

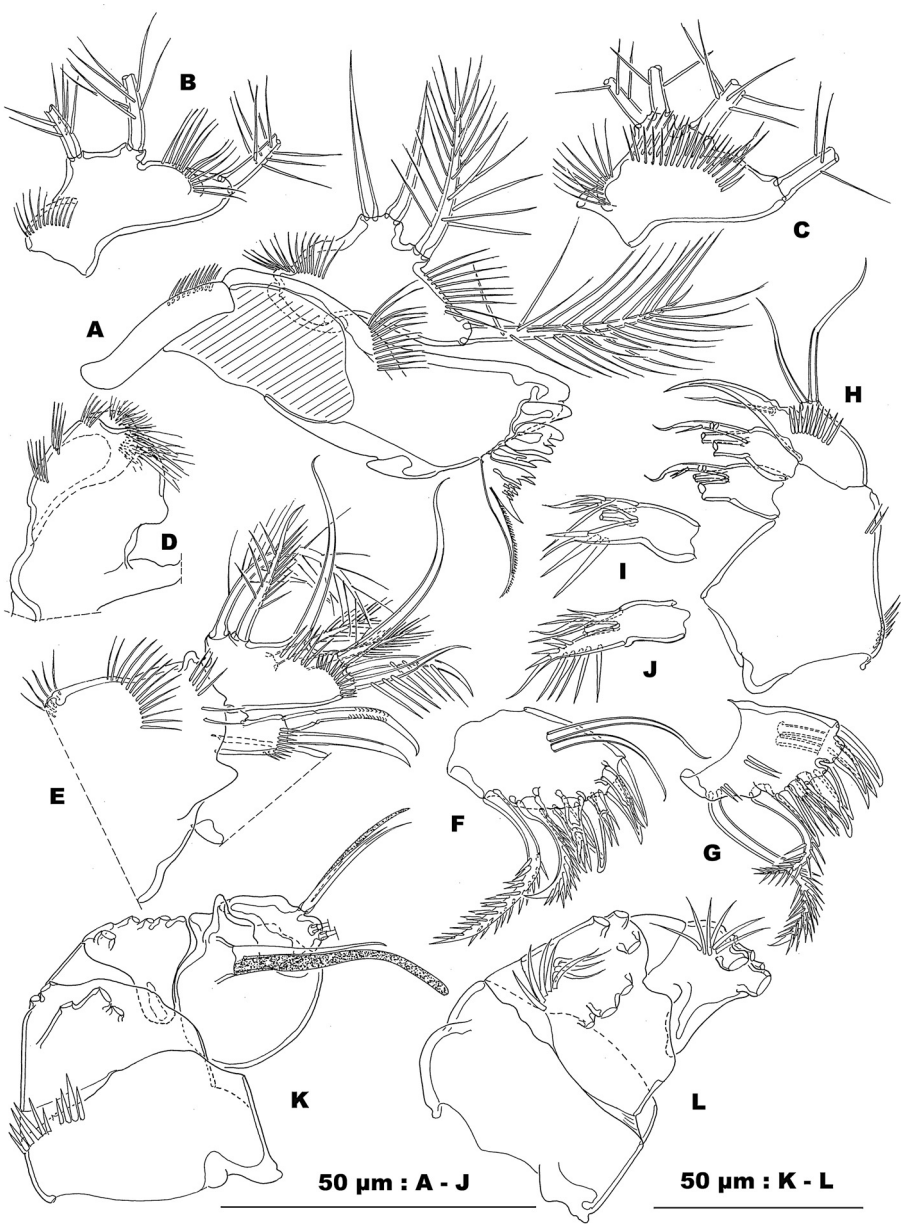

Fig. 5. *Nannopus didelphis* spec. nov., female (A–G), male (K–L). (A) Mandible, caudal view. (B) Mandibular palp with reduced armament (caudal view). (C) Mandibular palp, frontal view. (D) Paragnath. (E) Maxillula, frontal (gnathobasis omitted). (F) Maxillary gnathobasis, frontal. (G) Idem, caudal. (H) Maxilla, frontal. (I) Distal maxillary endite, caudal. (J) Proximal maxillary endite, caudal. (K) Antennule contour with aesthetsacs, ventral. (L) Antennulary proximal segments, dorsal.

Leg 6 and genital atria (Fig. 2A) separate; leg 6 vestiges semi-triangular with prominent outer distal edge bearing 1 long setiform element and 2 (middle and medial one) hyaline remnants of ancestral armature; copulatory pore located near medial edge of leg 6 vestiges outside the operculum, opening in shallow ovate depression; two egg-sacs, each with 6–10 eggs, carried below urosome.

Male

Habitus (Fig. 10A) fusiform; metasome nearly parallel sided, urosome tapering caudally; podoplean flexure indistinct; length 514 µm (505–528 µm); dorsal ornamentation of somites as in female; posteroventral margin of postgenital urosomites coarsely serrate and ornamented with complete transverse spinular row on urosomites 3 and 5, midventrally interrupted on urosomite 4 (Fig. 10B); ventral surface of postgenital urosomites with irregular pattern of minute spinules (not illustrated); anal somite as in female, with set of 2, 3 or 4 spinules at either side of ventral closure of anal sinus.

Caudal rami (Figs. 3F–G and 10A, B) as in female, except (1) outer and median terminal elements (IV and V) furnished with widely spaced rigid spinules, and (2) median terminal seta (V) with slender appearance, not inflated at insertion with ramus and lacking setular crown.

Antennule (Fig. 5K–L) haplocer, distinctly 5-segmented, considerably compact, with first and second segment large resembling those in female but lacking blunt structure on dorsal surfcae of first segment; first, second and third segment with spinular row, on ventral, dorsal and dorsal side, respectively; armature distribution: 1, 9, 4, 7+Aesth, 9+Aesth; armature as in female on segments 1 and 2; third segment robust, triangular, bearing 2 thick and short elements, 2 slender ones; segment 4 inflated, semi-ovate, with blunt triangular outgrowth along inner margin of palm; principal aesthetasc wide and long, fused with accompanying seta,

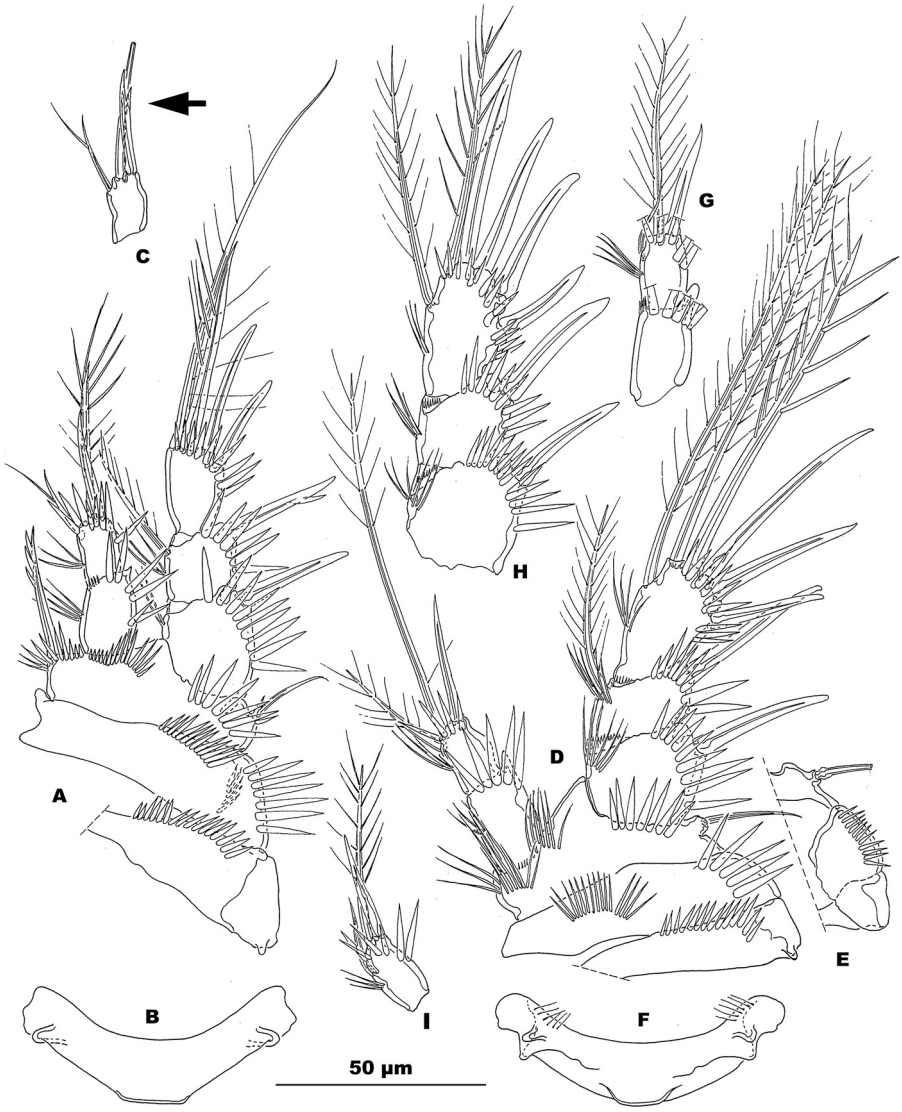

Fig. 6. *Nannopus didelphis* spec. nov., female (A–F), male (G–I). (A) Leg 1, frontal. (B) Leg 1 intercoxal sclerite, frontal. (C) Terminal endopodite segment of leg 1, spinule pattern omitted. (D) Leg 2, frontal. (E) Outer region of protopodal components of leg 2, caudal. (F) Leg 2 intercoxal sclerite, frontal. (G) Leg 2 endopodite, spinule pattern partially illustrated, frontal. (H) Leg 2 exopodite, frontal. (I) Terminal segment of leg 2 endopodite, frontal.

and arising from short pedestal; fifth segment with triangular apex and slender tubular aesthetasc fused to both accompanying setae; exact armature not illustrated because of compact detritus cover.

Mouthparts and leg 1 as in female

Leg 2 (Fig. 6G–I) with outer exopodal spines unadorned, shorter and stouter than in female; terminal outer element modified in rigid smooth and blunt spine, slightly longer than outer subdistal one; inner terminal and medial elements short, with sturdy setules (terminal one) or simply pinnate (medial one); first endopodite segment and spinular ornament of first and second endopodite segment as in female; medial and distal seta on distal endopodite segment shorter than in female with the medial one sigmoid, less long than segment and naked, the distal one twice as long as subdistal outer spine.

Leg 3 (Fig. 7D–G) with exopodal armature modified as described for leg 2; first endopodite segment as in female; second one with outer spiniform and sharp apophysis, either armed with single subdistal tooth or partially serrate along medial border; median terminal element twice as long as outer apophysis, pinnate; inner subdistal element half as long as outer element, smooth, recurved at apex.

Leg 4 (Fig. 8D and E) resembling female leg 4 closely; outer element on proximal exopodite segment slim (flexible?) and outer spines on middle and terminal exopodite segment unadorned; distal elements slightly shorter than in female, outer one unmodified; outer seta on endopodite reaching distal margin of exopodite only; inner element apparently smooth.

Leg 5 baseoendopodite (Fig. 9D–F) confluent with somite with opposite legs either interconnected midventrally (Fig. 9E–F) or with medioventral remnant of medial border (Fig. 9D); distal margin with 3 or 4 slender and short elements, pectinate or pinnate, and variable number of spinules; exopodite confluent with baseoendopodite, represented by small elevation bearing 5 elements; medial one short, less than half as long as distal ones, and smooth; distal setae longest, sparsely pinnate, and subequal; outer lateral ones as long as medial one, smooth or sparsely pinnate; surface of exopodal expansion smooth.

Leg 6 (Figs. 9G and 10B) forming a continuous concave transverse plate interconnecting both opposite leg 6 vestiges; distal margin completely set with spinules, with wide and robust caudally

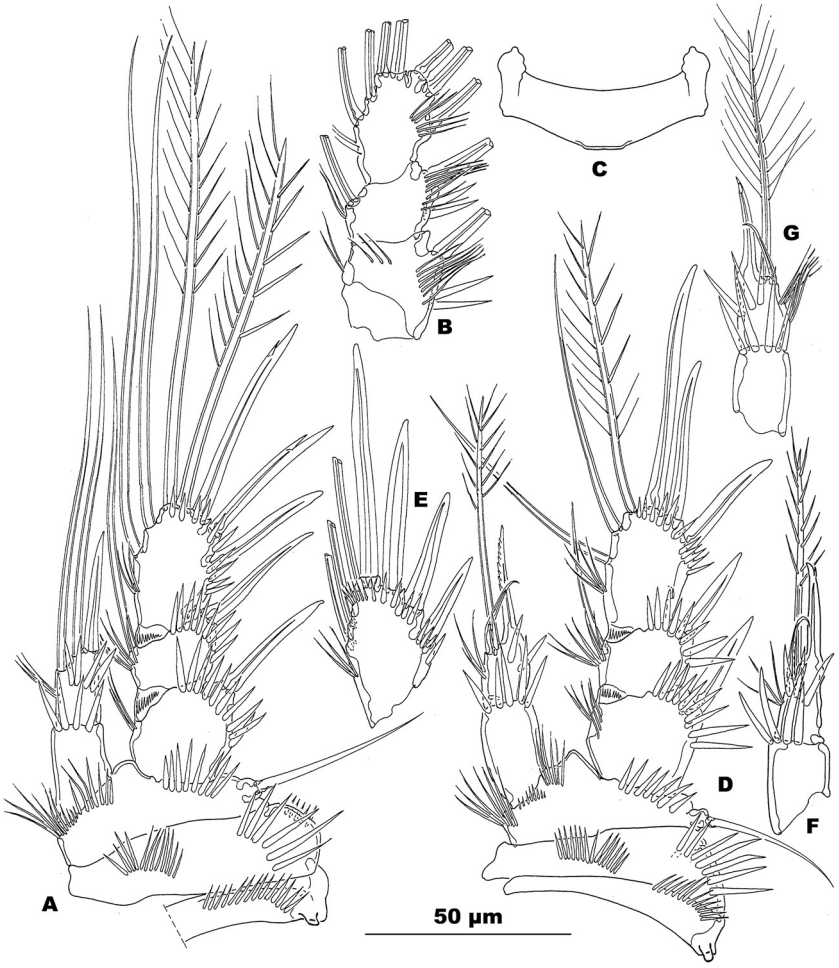

Fig. 7. *Nannopus didelphis* spec. nov., female (A–C), male (D–F). (A) Leg 3, frontal. (B) Leg 3 exopodite, caudal. (C) Leg 3 intercoxal sclerite, frontal. (D) Leg 3 with aberrant spine number on terminal segment, frontal. (E) Terminal exopodite segment of leg 3 with complete armature, frontal. (F) Leg 3 endopodite, opposite side, frontal.

directed spinules along middle part, and long and slender, medially directed, spinules laterally; leg 6 vestige armature setiform; outer and middle one equally long and about twice as long as medial element; leg 6 complex closing wide (single) transverse atrium in which both functional vasa differentia enter independently (dotted fields in Fig. 10B).

Variability. Ornamentation of the body somites is basically similar in all specimens examined, but the spinular ornament on the surface is often hardy discernable because of the detritus cover. The posteroventral margin of the genital double-somite and urosomites 4 and 5 is in some specimens furnished with a supplementary row of slim and widely spaced spinules, either located only midventrally or spanning the entire posteroventral margin. The number of long spinules at either side of the anal sinus closure is variable (3–5). Absence of this row appears to be rare and has been observed only once.

The globular inflation near the insertion of the median terminal seta of the caudal rami is characteristic but the extent of the setular encircling appears to be variable. Some specimens have a complete set of setules around the stem (Figs. 2A, 3A, B, D), when other have only a partial setule cluster on the outer margin of the stem (Fig. 3C and D). The setules are often difficult to see because a clear vision of the caudal ramus and its armature is in many instances obscured by clogged detritus.

Deviation of the typical armature formula (see table) of the natatorial legs is rare. Only one specimen was encountered with the terminal exopodite segment of leg 3 possessing 2 instead of 3 outer spines (male: Fig. 3D). Variability of leg 5 armature is more explicit. Although most specimens have 4 endopodal elements, specimens with only 3 elements are not rare. Reduction of the number occurs in females (Fig. 9A and C) as well as in males (Fig. 9E). Besides reduction of the armature number, their proportional lengths and ornamentation is rather variable as is visualized in Fig. 9A–F. The presence and number of spinular ornamentation on the leg 5 is difficult to estimate. In all cases filamentous detritus stuck on the frontal surface obscures the pattern.

Copepodids (only certain aspects emphasized)

Copepodid V

Body resembling adult in general but composed of cephalothorax, 3 metasomites and 5 urosomites; podoplean flexure indistinct; anal somite twice as long as penultimate one, laterally constricted in caudal third; urosomites 3 and 4 with midventral transverse row of slim spinules near posteroventral border, the latter straight; anal somite with additional transverse spinular irregular row in middle of ventral surface and row of widely spaced spinules along posteroventral margin on either side of anal sinus closure; caudal rami and armature as in adult; body length appr. 535 µm (females), 480 µm (males).

Antennule 5-segmented in male and female; mouthparts as in adult. Legs 1–4 with 3-segmented exopodites, 2-segmented endopodites in legs 1–3 and one-segmented endopodite in leg 4; leg armature and distribution as in adult; subdistal medial element on

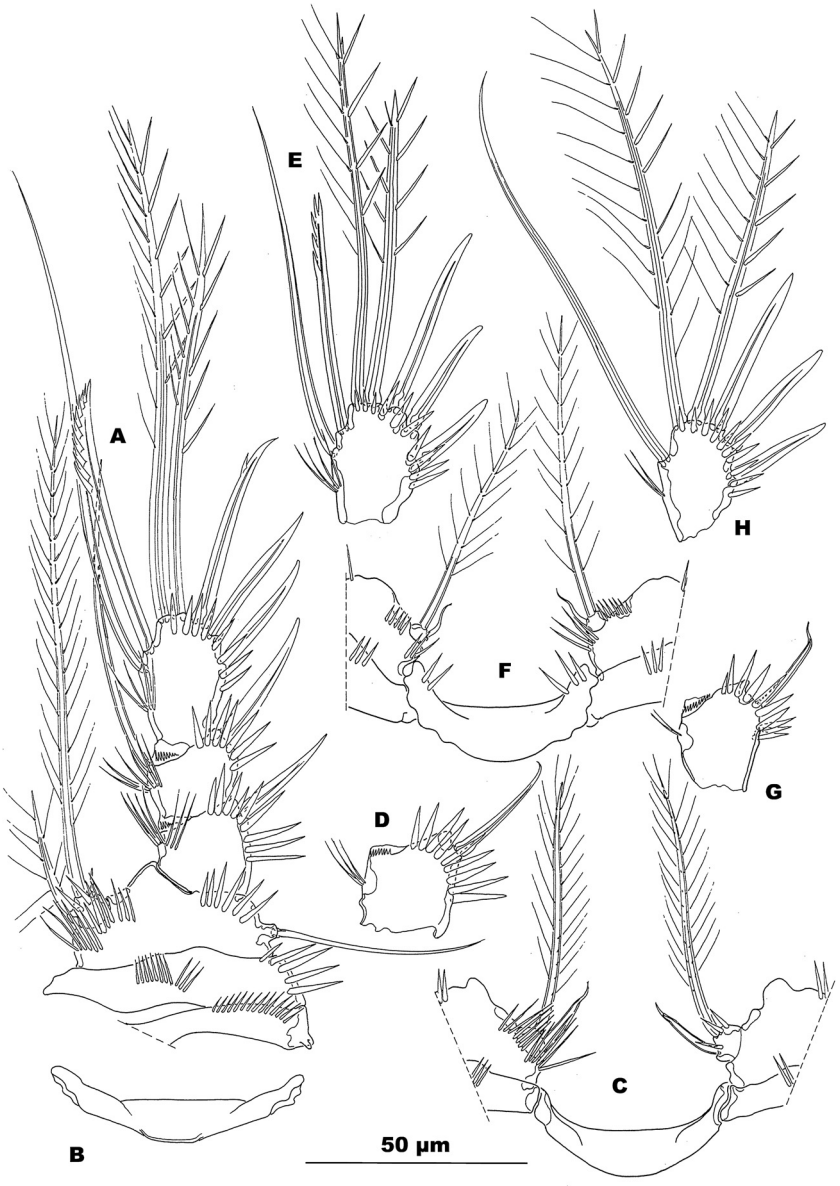

Fig. 8. *Nannopus didelphis* spec. nov., female (A–B), male (C). (A) Leg 4, frontal. (B) Leg 4 intercoxal sclerite, frontal (C) Leg 4 endopodites and intercoxal sclerite, frontal (ornament on basis of right leg not shown). (D) First exopodite segment of leg 4, frontal. (E) Terminal exopodite segment of leg 4, frontal. *Nannopus scaldicola* spec. nov., male (F–H). (F) Leg 4 endopodites and intercoxal sclerite, frontal. (G) First exopodite segment of leg 4, frontal. (H) Terminal exopodite segment of leg 4, frontal.

third exopodite segment of leg 4 as long as segment, with inflated and smooth proximal half, slender and serrate distal half (Fig. 11F).

Leg 5 with adult shape and complement: *i.e.* exopodite lobe with 5, endopodite region each with 4 armature elements; all setiform and shorter than in adult; distal margin of leg furnished with slender spinules; surface ornamentation unclear.

Leg 6 (Fig. 2B) similar in male and female, represented as large rectangular plate with 3 elements on outer distal edge: outer one long, middle one considerably shorter, and medial represented as a dwarfed hyaline, hardly visible, notch; opposite legs distinctly separated with deep midventral suture in female, not present in male; distal margin of leg 6 structure in both sexes with rigid spinules in middle half and slim spinules in outer half.

Copepodid IV

Body composed of cephalothorax, 3 metasomal somites and 3 urosomites and the anal somite; podoplean flexure indistinct; posteriodorsal margins of somites serrate, posteroventral margins of urosomites straight with spinules lined up parallel to margin: slender ones in female (Fig. 11A), coarse (midventrally) and slender (lateral) ones in male (Fig. 11B); anal somite with transverse row of spinules in middle of ventral surface; posteroventral margin with few long spinules on either side of anal sinus closure; caudal rami only 1.5 times longer than wide with 7 elements; spinular ornament limited to posteroventral margin and posteromedian edge only; median principal caudal seta slightly globular near insertion; setule cluster near insertion present in male and female; body length appr. 390 µm (female), 345 µm (male).

Rami of legs 1–3 and exopodite of leg 4 2-segmented; endopodite of leg 4 present as small elevation of, but confluent with, distal margin of basis; complement of legs 1–3 as in adult, of leg 4 (Fig. 11E) with one short outer spine (on second exopodite segment); armature far less rigid than in adult and ornamentation of segments far less dense; leg 3 endopodite similar in male and female with outer subdistal element slender and articulating with segment but inner subdistal element shorter in male (Fig. 11D) than in female (Fig. 11C).

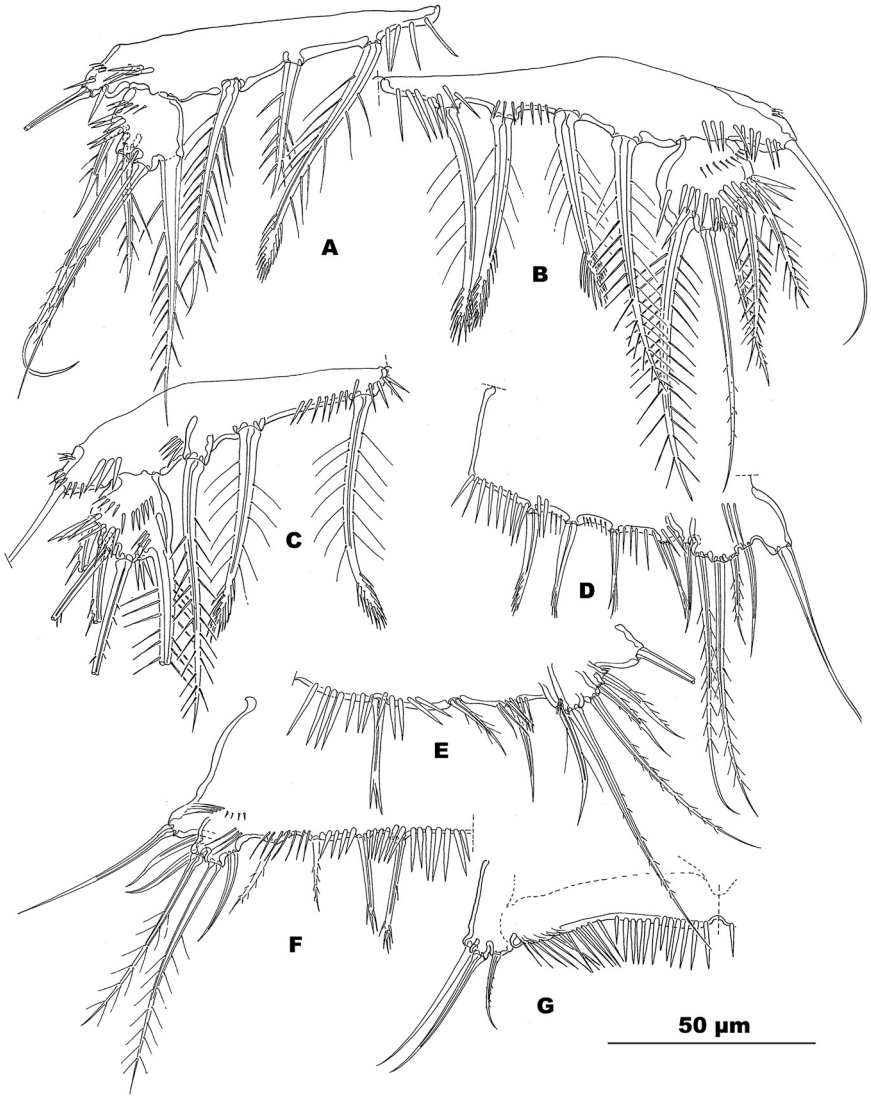

Fig. 9. *Nannopus didelphis* spec. nov., female (A–C), male (D–G). (A–C) Leg 5 variability. (D–F) Leg 5 variability. (G) Male leg 6.

Leg 5 (Fig. 11A and B) confluent with pediger with opposite legs separated by medial suture in female, not clearly defined in male; exopodite and baseoendopodite discernable, the former confluent with the latter; outer seta of basis present; endopodal region with 4 elements: medial one and both outermost rather short and setiform, next to medial element minute; exopodite subdivided with invagination between medialmost element and outer ones; future medial exopodal element short with lanceolate appearance (in female) or setiform and pinnate (male); medial part of endopodal margin with spinules.

Leg 6 (Fig. 11A and B) represented as crescent ridge with spinular margin; outer edge slightly elevated, bearing 2 elements: outer one long, inner one short.

Comparison. Mielke's (1974) *N. palustris* from the littoral zone near Longyearbyen is most likely to be considered as conspecific with *N. didelphis* spec. nov. The setae on the female leg 4 endopodite are significantly longer than described for *N. didelphis* spec. nov. They show dimorphism as described above with the inner shorter element terminating with a hook-shaped tip. The dimorphic aspect of the inner seta appears thus far to be a unique feature among the members of *Nannopus*.

The identifications by Wojtasik and Kur (2007) of specimens as *N. palustris* and obtained at two distant locations on Spitsbergen (Petunia Bay, Isfjorden and Nottingham Bay, near Hornsundfjord) were not supported by structural data. Their identities have to be reconfirmed when material becomes available. The animals from Petunia bay, with the compact body, are likely conspecific with *N. didelphis* spec. nov. The more slender animals from Nottingham Bay are clearly different.

Nannopus scaldicola spec. nov.
(Figs. 8–16(F–H))

Type locality. Belgium, Kallo: close to the Kallo Sluice on the left bank of the river Scheldt, known as "Keetenisse Schor" (appr. 51°16′60″ N and 4°18′0″ E): mud sample between dense reed vegetation near highest level of intertidal zone. Leg. Dr. J. Soors, 26 May 2005.

Type series. Female (holotype) dissected on 3 slides, registered RBINSc COP 9890A-C, male (allotype) dissected on 3 slides, registered RBINSc COP 9891A-C, 1 paratype female dissected (RBINSc COP 9892A-C) and 2 paratype females preserved (RBINSc COP 5382).

Etymology. The specific epithet is a conjunction of the Latin word *Scaldis* (the river Scheldt) and the Latin suffix cola (inhabitant of).

Description. Female. Habitus (Fig. 12A and B) depressed dorsoventrally, ovate in dorsal view, widest along caudal margin of

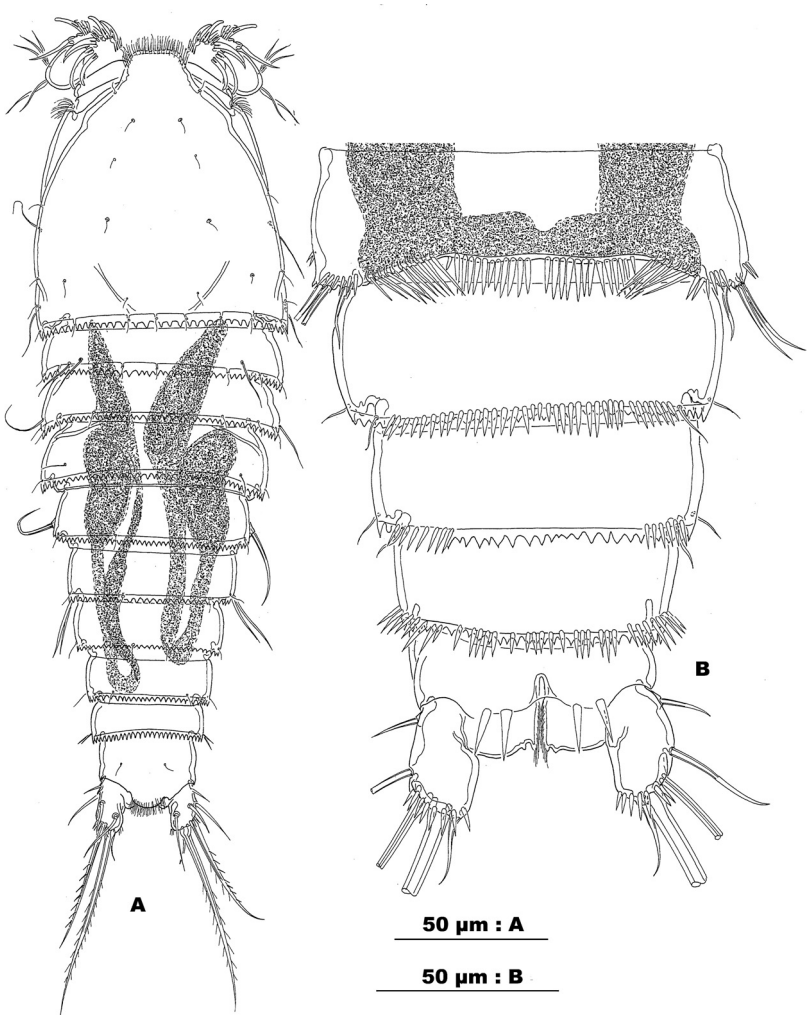

Fig. 10. *Nannopus didelphis* spec. nov., male (A–B). (A) Habitus, dorsal. (B) Urosomites 2–6, ventral.

cephalothorax; postcephalic somites narrowing caudally lacking distinct demarcation of podoplean flexure; cephalothorax prominent, longer than 2/5 of entire body length; prosome equal to 2/3 of entire body length; genital somite completely fused with succeeding somite forming genital double-somite but with posterior margin of genital somite (urosomite 2) discernable dorsally and laterally; genital double-somite (Fig. 14A) distinctly wider than long (ratio: 3/1), with flat ventral surface; anterior half of genital double-somite only faintly wider than posterior half; succeeding urosomites ovate in cross-section; presence of integumental window unclear, possibly present on cephalothorax, located middorsally in caudal half (drawn in Fig. 12A, but uncertain); presence of lateral (metasomal) windows unclear; body length 460–515 µm.

Body ornament: integument of cephalothorax smooth, hirsute on metasomites and urosomites (not illustrated); ventral surface of urosomites naked, except for transverse spinular row in anterior half of anal somite; posterodorsal margins of cephalothorax and postcephalic somites coarsely serrate; pleural region of pedigers with short setules and ventral margin of cephalothorax with long and coarse setules; posteroventral border of genital double-somite and urosomites 4 and 5 straight and set with spinules arranged in discrete groups; posterolateral edge of genital double-somite with cluster of setules, of urosomites 4 and 5 with spinules.

Anal somite (Figs. 13A, C–E and 14A) with row of coarse spinules along dorsal half of posterolateral border and 1 or 2 sets of coarse spinules between lateral group and anal operculum; posteroventral margin spinular row on either side of anal sinus closure; anal operculum crescent, densely covered with stiff (Fig. 14A and C) setules; dorsal sensillar pair located close to anterodorsal margin; pair of wide pore orifices located halfway between sensilla pair and anal operculum edge.

Caudal rami (Figs. 13A–F and 14A) basically as in former species, cylindrical, with 7 elements; anterolateral accessory seta short, shorter than ramal width, inserted near to ramal articulation with somite; anterolateral seta inserted at same distance, above accessory one, slightly longer than the latter; posterolateral seta inserted halfway lateral margin, longer than ramus; outer terminal seta near to 4 times longer than ramus, wide at insertion, without breaking plain and ornamented with long widely spaced and strong setules; median terminal seta twice as long as outer one with anterior half wide and naked, lacking breaking plain (Fig. 13B); posterior half slender, cylindrical and pinnate; inner terminal seta located medially at same level of both principal elements, and half as long as ramus; proximal half rather voluminous and ornamented with circlet of setules; distal part slender and naked; dorsal seta located in anterior half of ramus, articulating on 2 basal parts; surface of ramus, dorsally and laterally, with minute spinules (not illustrated); lateral and ventral spinular rows reduced to few spinules (1 or 2 spinules each); medial margin with row (5–6 spinules) of caudally directed coarse spinules extending dorsoventrally; posterodorsal and posterolateral margin set with numerous spinules; posteroventral margin with few but long spinules along inner half.

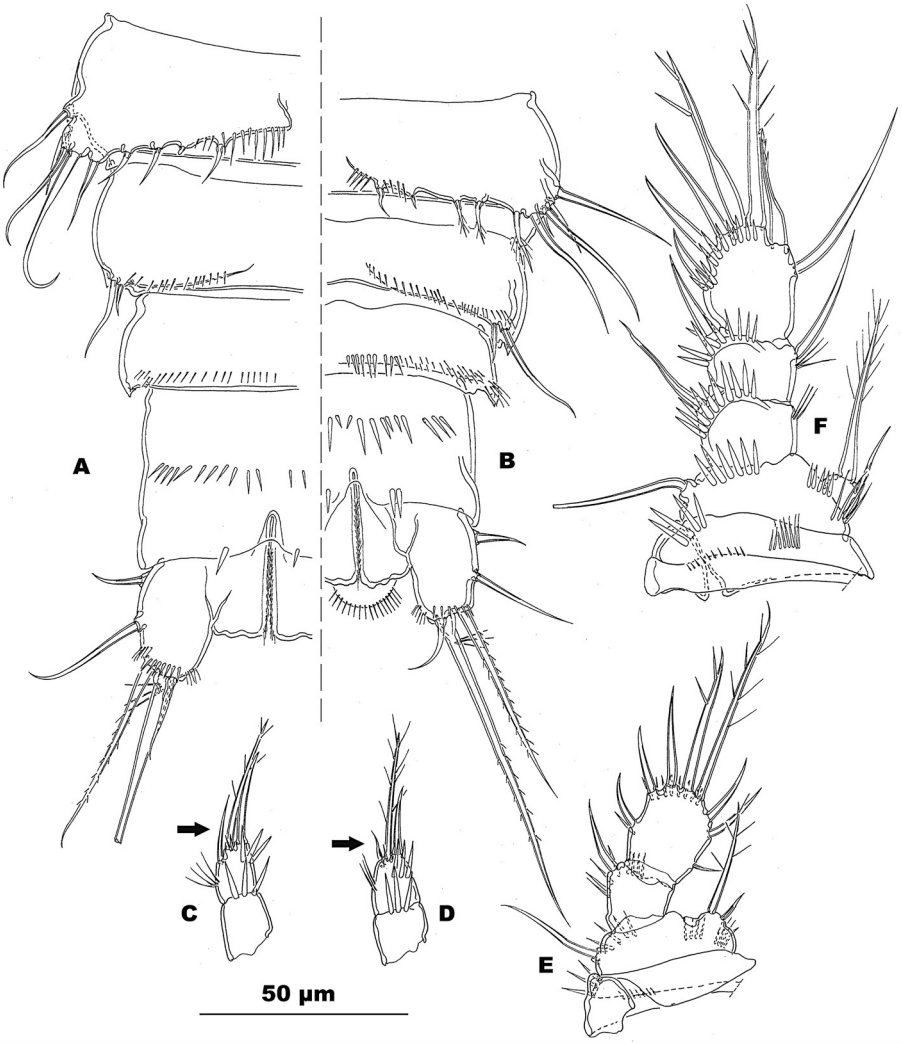

Fig. 11. *Nannopus didelphis* spec. nov., copepodid IV (A–E), copepodid V (F). (A) Urosome of female copepodid IV, ventral. (B) Idem of male copepod IV. (C) Leg 3 endopodite of female copepodid IV. (D) Idem of male copepodid IV. (E) Leg 4 of female copepodid IV, caudal. (F) Leg 4 of female copepodid V, frontal.

Rostrum, antennule and mouthparts as in *N. didelphis* spec. nov. described above.

Leg 1–4 basically as in *N. didelphis* spec.nov. with armature distribution in Table 2; intercoxal sclerite of legs 1–3 (Fig. 15C, E and H) wide, with deep concave distal margin and ornamented with spinular cluster on lateral corners; leg 1 with 2 transverse spinular rows on frontal surface of sclerite, absent in legs 2 and 3; intercoxal sclerite of leg 4 (Fig. 8F) considerably wider and narrower with surface smooth except for 2 or 3 long spinules on lateral edge; spinular ornament on prea-coxa, coxa and basis of legs 1–4 as in *N. didelphis* spec. nov. but medial spinular armature on leg 4 basis stout and less dense.

Leg 1 (Fig. 15A) with outer armature on exopodite segments short and robust, all smooth; outer terminal element stout robust, recurved medially, smooth, hook-shaped at tip; inner terminal element setiform, naked in proximal and distal third, with rigid spinules in middle third; ornament of segments as in *N. didelphis* spec. nov., except for additional medial setule cluster on second segment and absence of setule cluster on proximal segment; endopodite reaching halfway along second exopodite segment, at most, composed by two equally long segments; distal corner of proximal endopodite segment produced in obvious blunt expansion; spinular ornament of both segments as in *N. didelphis* spec. nov.; medial subapical element of leg 1 endopodite sigmoid (Fig. 15B), as long as outer spine, at most; apical (median) element robust and blunt, not reaching beyond distal margin of exopodite, armed with stiff and widely spaced setules.

Leg 2 (Fig. 15D) with short and more compact outer exopodite armature than in *N. didelpis* spec. nov., distalmost outer spine coarsely serrate along medial directed margin, all other outer armature elements naked; both terminal elements longer than ramus, rigid, ornamented with rigid setules along outer margin; ornamentation of exopodite segments as in *N. didelphis* spec. nov. except for presence of additional setule cluster along median margins; endopodite reaching just beyond first exopodite segment, composed by 2 equally long segments; proximal segment with small triangular expansion of outer distal corner; outer subdistal element, nearly twice as long as segment, coarsely serrate medially; terminal and inner subdistal element long, reaching far beyond

Table 2
Leg armature distribution in *N. scaldicola* spec. nov.

		EXO	END
Leg 1	Fig. 15A	I,0-I,1-II,I+1,0	0,0-I,1,1
Leg 2	Fig. 15D	I,0-I,1-III,I+1,1	0,0-I,1,1
Leg 3	Fig. 16A	I,0-I,1-III,I+1,2	0,0-I,1,1
Leg 4	Fig. 16B	I,0-I,1-III,I+1,1	020

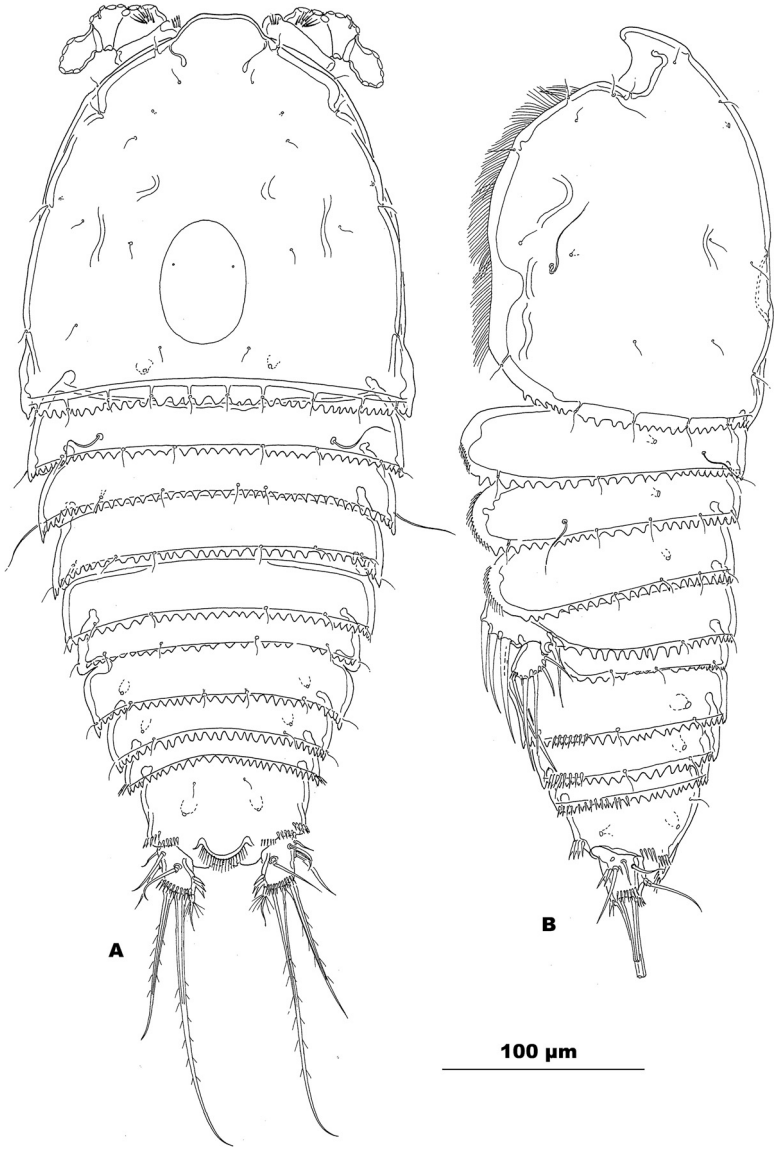

Fig. 12. *Nannopus scaldicola* spec. nov., female (A–B). (A) Habitus, dorsal. (B) Idem, lateral.

exopodite and pinnate; ornament of endopodite segments as in *N. didelphis* spec. nov., except for additional median setule cluster on proximal segment.

Leg 3 (Fig. 16A) as in *N. didelphis* spec. nov. but with shorter outer exopodite armature elements; outer terminal and subterminal elements of exopodite and endopodite coarsely serrate medially; additional setule clusters along the medial margin of exopodite and endopodite segments.

Leg 4 (Fig. 16B) as in *N. didelphis* spec. nov. except for the serrate nature of the 3 outer armature elements on distal exopodite segment and delicate pinnate (not illustrated) ornament of the medial setae on the terminal exopodite segment (pectinate element absent); medial seta on the endopodite segment short, as long as segment; additional setule clusters along the medial margin of proximal and median exopodite segment.

Leg 5 (Fig. 14B and C) basically as in *N. didelphis* spec. nov. with 4 elements on endopodite expansion, 5 on exopodite, but differing as follows: (1) medial element on exopodite articulating with segment and shorter (3 times longer than exopodite segment *versus* 4 times longer than segment) and (2) spinular ornament on endopodite expansion more dense, on exopodite less dense.

Leg 6 (Fig. 14A) represented as narrow plate with single pinnate seta on outer margin; opposite legs confluent midventrally with square caudally directed expansion; receptacles separated with thick walled medial margin (located below caudal expansion of legs) with copulatory pores located near transition between outer part of leg vestiges and medial squar expansion.

Male

Habitus as in female, but urosome less wide with pediger 6 and urosomite 3 separated; length 460 µm ($n = 1$); posteroventral margin of urosomites 3–5 with uninterrupted transverse row spinules arranged in discrete groups according to length of spinules; anteroventral transverse spinular row composed by longer spinules than in female; caudal rami and armature as in female, but medial terminal element without circlet of setules.

Antennule as in *N. didelphis* spec. nov., mouthparts and leg 1 as in female.

Leg 2 as in female except for the terminal armature of the distal exopodite segment: (1) the slightly more robust, non-serrate, shape of the distalmost outer spine and (2) the stout spiniform aspect, medially pinnate, of the outer terminal element (Fig. 15G).

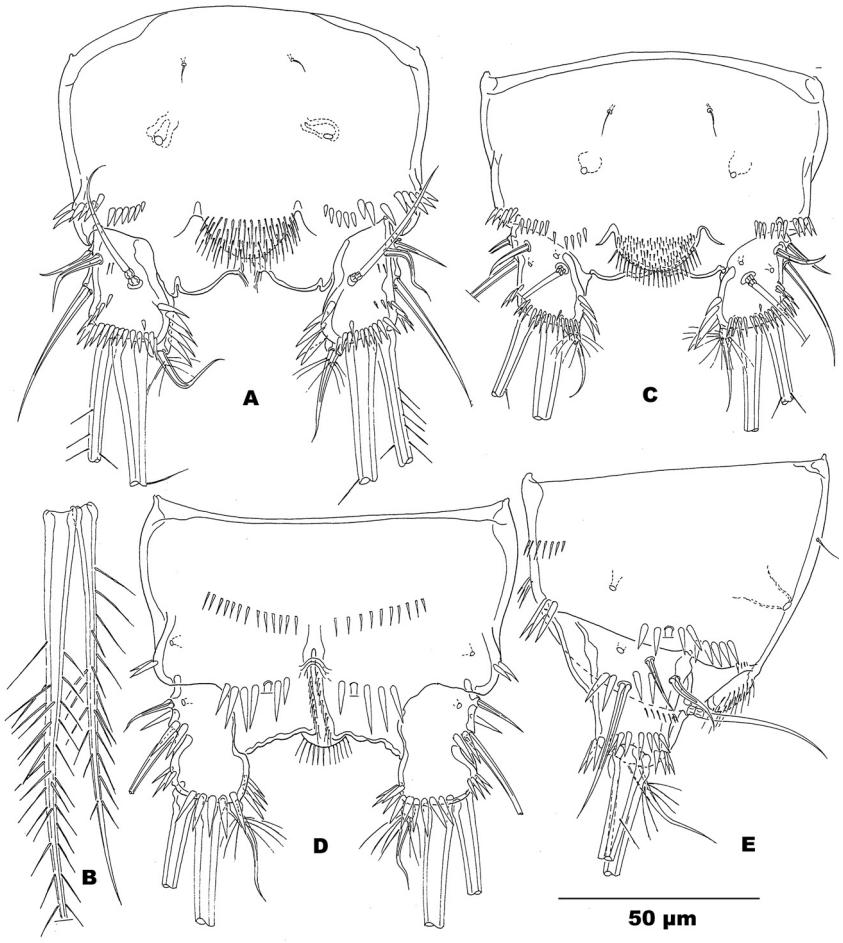

Fig. 13. *Nannopus scaldicola* spec. nov., female (A–E). (A) Anal somite, dorsal view. (B) Principal caudal setae, right pair. (C) Anal somite of paratype specimen, dorsal view. (D) Idem, ventral view. (E) Idem, lateral view.

Leg 3 (Fig. 16C) with smooth and longer outer exopodite armature than in female; outer terminal element of exopodite spiniform and pinnate medially; medial element on second segment as long as segment and naked; terminal element setiform and pinnate; subdistal outer apophysis confluent with segment, as long as segment, and sigmoidally recurved in front of terminal element; apex of apophysis sharp.

Leg 4 as in the female, except for the narrow shape of the outer element on the proximal exopodite segment (Fig. 8G) and the non-serrate aspect of the outer spines of the third exopodite segment (Fig. 8H).

Leg 5 (Fig. 14E) represented as rectangular plate with 4 short endopodite, 5 exopodite elements; exopodite confluent with baseoendopodite, represented as narrow elevation; opposite legs separated by deep midventral invagination; two medial endopodite elements serrate distally, two outermost ones pinnate; exopodite armature as in *N. didelphis* spec. nov.; distal margin of leg with numerous spinules.

Leg 6 pair assymetrical with right leg operational and distinctly larger than left one (Fig. 14D); the latter apparently confluent with somite; leg vestiges represented by 3 elements: outer and median one pinnate and long, inner one half as long and serrate; posterior margin of both leg vestiges with uninterrupted row of stout spinules.

Comparison: *Nannopus scaldicola* spec. nov. is unique because of the absence, in both genders, of a pectinate medial element on the third exopodite segment of leg 4. In this respect, *N. scaldicola* spec. nov. resembles most the original description of *N. palustris* and Canu's specimens (see general discussion below for further comments). In the three other species described here, and in all the other morphs of which the leg 4 has been described in detail (Scott, 1902; Lilljeborg, 1902; Sars, 1909a; Gurney, 1932; Coull and Fleeger, 1977; Tai and Song, 1979; Jakobi, 1956) the subdistal element (the sole inner element in *N. palustris* sensu Sars) is represented as a robust pectinate element.

Nannopus scaldicola spec. nov. is most reminiscent of *N. palustris* s. str. as both share, in addition to the leg 4 armature morphology, the flattened body shape. However, the former lacks the inflated median terminal seta on the caudal rami and possess two long setiform elements on the leg 2 endopodite instead of 2 short ones and has only one medial element on the third exopodite segment of leg 4.

Nannopus procerus spec. nov.
(Figs. 17–26A)

Nannopus palustris Brady, 1880 – Sars, 1909a,b: 307–309, pl. CCIX.
Nannopus palustris Brady, 1880 – Pesta, 1932: 150, Fig. 81.
Nannopus palustris Brady, 1880 – Lang, 1936a: 46, Figs. 147, 148.
Nannopus palustris Brady, 1880 – Lang, 1948: 1291 [partim], figs. 514(4), 517(1).
? *Nannopus palustris* Brady, 1880 – Klie, 1929: 377 [partim]; Chislenko, 1967: 173–174, fig. 68; Letova, 1982: 63, fig. 14; Gárlitska et al., 2012: tbl. 1.

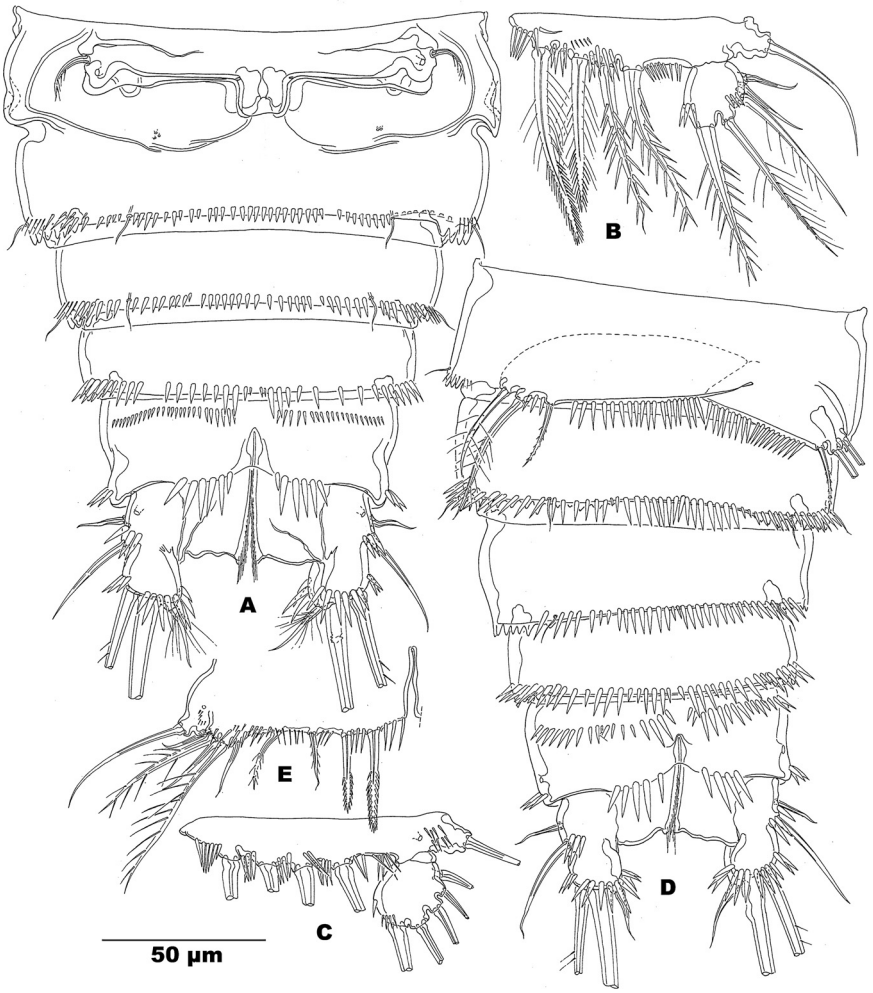

Fig. 14. *Nannopus scaldicola* spec. nov., female (A–C), male (D–E). (A) Genital double-somite and urosomites 4–6, ventral. (B) Leg 5, frontal. (C) Leg 5, frontal, armature partially illustrated (paratype). (D) Urosomites 2–6, ventral; (E) leg 5, frontal.

Type locality. The Netherlands, Oosterschelde (=Eastern Scheldt), "*Slikke*" of Bergen-op-Zoom ("slikke", Dutch for the bi-diurnal flooded part of the litoral zone), east of Oesterdam, among the angiosperm *Zostera* (Zosteraceae). Fine to very fine sand (mean grain size 75–145 µm) with silt contents between 4.5 and 16.2%. Leg. K. Willems, March 1980.

Type material. Female (holotype) dissected, registered RBINSc COP 9912A-C, male (allotype), dissected, registered RBINSc COP 9914A-C, paratypes, dissected 2 females and 1 male, registered RBINSc COP 9915A-C, COP 10081A-C-COP 10082A-C; paratypes, preserved: 8 females, 1 male and 1 CV female registered RBINSc COP 9894.

Additional material. Norway, Oslofjord, intertidal mud flat at Bestumkilem, Oslofjord: 6 females, preserved in alcohol. G.O. Sars Collection at Zoological Museum, Oslo, reg. F.20375

Etymology. *Procerus* (Latin meaning slim, svelte) referencing to the slender and elegant body shape (noun in apposition).

Description. Female. Habitus (Fig. 17A and B) fusiform, narrow, with nearly parallel sided metasome and tapering urosome; cephalothorax and metasome, and prosome and urosome equally long; podoplean flexure indistinct; genital double-somite with distinct remnant of fusion line on dorsal and lateral sides; anterior somite of genital double-somite (urosomite 2) slightly wider than caudal one; integument of cephalothorax smooth, densely hirsute (partially illustrated for ventral margin of pediger 5: Fig. 21B) on pedigerous somites and on dorsal and lateral surface of urosomites; ventral surface of genital double-somite and urosomites 4–5 smooth (Fig. 19A); posterodorsal margin of prosomal somites and posterodorsal and posteroventral margin of genital double-somite and abdominal somites coarsely serrate; posteroventral margin of genital double-somite with complete additional spinular row parallel to margin, of urosomite 4 and 5 limited to mid section of margin; posterolateral edges of genital double-somite and urosomites 4 and 5 without spinule or setule cluster; no integumental window observed on cephalothorax; lateral windows discernable on pedigers 2 and 3; body length: 615–635 µm.

Anal somite about as long as wide with small crescent anal operculum; integument of somite furnished partially with spinules (not illustrated); anal operculum hirsute; posterodorsal and posterolateral margin unadorned except for some minute spinules along part of lateral margin; posteroventral margin with row of slender and short spinules on either side of anal sinus closure (Figs. 18B and 19A); dorsal pair of sensilla in middle between anterior margin and anal operculum with pore orifices at same level, located between sensillum and outer margin (Fig. 18A and C).

Caudal rami (Fig. 18A–C) cylindric, 1.5 times as long as wide in dorsal view, 2.5 times in ventral view; accessory seta inserted close to anterior edge, shorter than ramal width; lateral setae located in middle of margin, anterolateral one positioned near dorsal surface, posterolateral one near ventral surface (Fig. 18C); former as long as ramal width, latter one twice as long; outer terminal element

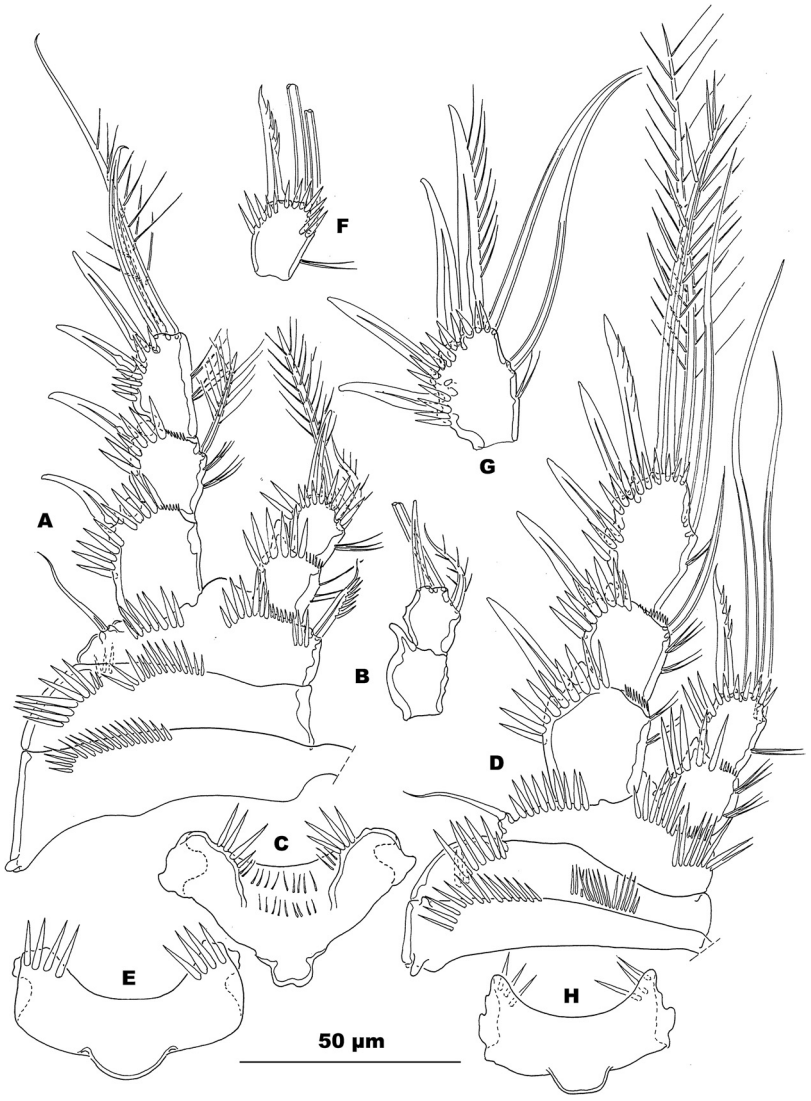

Fig. 15. *Nannopus scaldicola* spec. nov., female (A–E, H), male (F–G). (A) Leg 1, frontal. (B), Leg 1 endopodite, spine ornament omitted. (C) Leg 1 intercoxal sclerite. (D) Leg 2, frontal. (E) Leg 2 intercoxal sclerite, frontal. (F) Terminal endopodite segment of leg 2, frontal; (G) terminal exopodite segment of leg 2, frontal; (H) leg 3 intercoxal sclerite, caudal.

short, 1.5 times longer than ramus, sturdy, and furnished with minute stout setules; median terminal element with anterior third swollen and naked, terminating in sharp dorsally directed triangular process; distal 2/3 of seta slim and densely furnished with short spinules (more than illustrated in Fig. 18A); outer and median terminal elements without breaking plain; medial terminal element dwarfed, located, ventrally below median terminal seta; dorsal element articulating on two basal parts and inserted, medially, halfway ramus; dorsal and lateral surface covered with minute spinules (see example in Fig. 18E); outer margin without additional spinules; medial margin with spinular row close to dorsal surface; spinules along posterodorsal and medial margin slim and short.

Rostrum linguiform, confluent with cephalic shield, recurved ventrally and hirsute in anterior third (Fig. 17A and B); antennule and mouthparts as in *N. didelphis* spec. nov.

Legs 1–4 basically as in *N. didelphis* but with armature distribution in Table 3; intercoxal sclerites (Fig. 20D–E) wide with concave distal margin, devoid of ornament; spinular and setular ornament patterns on protopodites and rami as in preceding species; outer terminal spine of leg 1 exopodite straight, twice as long as subdistal one, half as long as inner terminal seta, and coarsely serrate in distally; medial element on second exopodite segment short, as long as segment, at most; terminal elements on endopodite short with inner subdistal one as long as spinule ornament, median seta and subdistal outer spine equally long, and only slightly longer than segment; leg 2 and leg 3 exopodite with terminal outer element spiniform bearing single subdistal tooth; outer exopodite spines stout and smooth; medial elements on middle and terminal segment shorter than segments and stout; terminal elements on leg 2 second endopodite segment short as in leg 1; leg 3 endopodite with medial subdistal seta and outer subdistal spine short as in leg 1 and median element twice as long as outer spine; outer spine on proximal segment of leg 4 narrow, sparsely serrate; outer spines on median and terminal exopodite segment smooth, except for

Table 3
Leg armature distribution in *N. procerus* spec. nov.

		EXO	END
Leg 1	Fig. 20A, B	I,0-I,1-II,I+1,0	0,0-I,1,1
Leg 2	Fig. 20C	I,0-I,1-III,I+1,1	0,0-I,1,1
Leg 3	Fig. 20F	I,0-I,1-III,I+1,1	0,0-I,1,1
Leg 4	Fig. 20G	I,0-I,1-III,I+1,1	020

Fig. 16. *Nannopus scaldicola* spec. nov., female (A–B), male (C). (A) Leg 3, frontal. (B) Leg 4 frontal. (C) Leg 3, caudal.

single subdistal tooth on outer subdistal spine; distal elements on terminal segment equally long and sturdy; inner element robust and pectinate; endopodite with outer seta less long than exopodite.

Leg 5 (Fig. 21B) with endopodite armature consisting of 4 equally long stout elements: two innermost serrate distally, two outermost pinnate; exopodite articulating with baseoendopodite, bearing 5 elements; medialmost element confluent with segment, half pinnate, half sparsely serrate; apical pair of setae smooth, outer pair pinnate; surface and distal margin of baseoendopodite and surface of exopodite with spinular rows of slender and robust spinules.

Leg 6 (Fig. 19A) represented as semi-triangular plate with three elements on caudal outer edge: outer one long and pinnate (not illustrated), middle and medial one dwarfed with hyaline appearance; opposite leg vestiges not interconnected midventrally; pair of copulatory pores located midventrally surrounded with reinforced tissue of medial margin of receptacles.

Male

Habitus (Fig. 17C) fusiform with urosome slimmer than prosome; podoplean flexure indistinct; cephalothorax and metasome, and prosome and urosome equally long; integument and posterior margins of body somites as in female, except for posteroventral margins of urosomites 4–5 being furnished with complete and uninterrupted spinular row parallel to posterior margin; anal somite with set of long spinules on either side of anal sinus closure (Fig. 19B); length 510–525 µm ($n = 3$).

Caudal rami (Figs. 18D, E and 19B) as in female; outer terminal element 1.5–2 times longer than ramus; median terminal element less wide proximally and lacking dorsal triangular process; smooth in anterior third.

Rostrum, cephalic appendages and leg 1 as in the female; antennule as in *N. didelphis* spec. nov. but not observed in detail because of clustered dirt; protopodite and intercoxal sclerite in legs 2–4 as in female; exopodite armature as in female but outer spines stouter and outer element on proximal exopodite segment of leg 4 densely serrate; terminal element of leg 2 endopodite and inner subdistal element of leg 2, 3 and 4 endopodite longer than in female (Fig. 21C, D, G); outer element on distal endopodite segment of leg 3 confluent with segment, smooth, longer than endopodite, and sharp (Fig. 21D–F); median terminal seta slightly longer than in female and sparsely pinnate.

Leg 5 (Fig. 21A) with baseoendopodite narrow and confluent with pediger; exopodite obsolete, represented by narrow elevation; separation between opposite legs indistinct; endopodite regio with 4 setae: both medial ones thick and serrate distally, both outer ones slender and pinnate; medialmost exopodite element short, articulating, and serrate; median setae smooth, outer ones serrate; distal margin of endopodite region furnished with coarse spinules; surface of leg apparently smooth.

Leg 6 vestiges (Fig. 19B) fused midventrally forming undulating complete lamellar structure with 3 elements on either side and furnished, along the caudal border, with slender (outer part) and coarse (medial part) spinules; spinule row interrupted midventrally; outer and middle seta long and sparsely pinnate (not illustrated); medial element less than half as long as outer elements, spiniform and sparsely serrate.

Comparison: The resemblance between the Oosterschelde specimens and the specimens from Bestumkilem (Oslofjord,

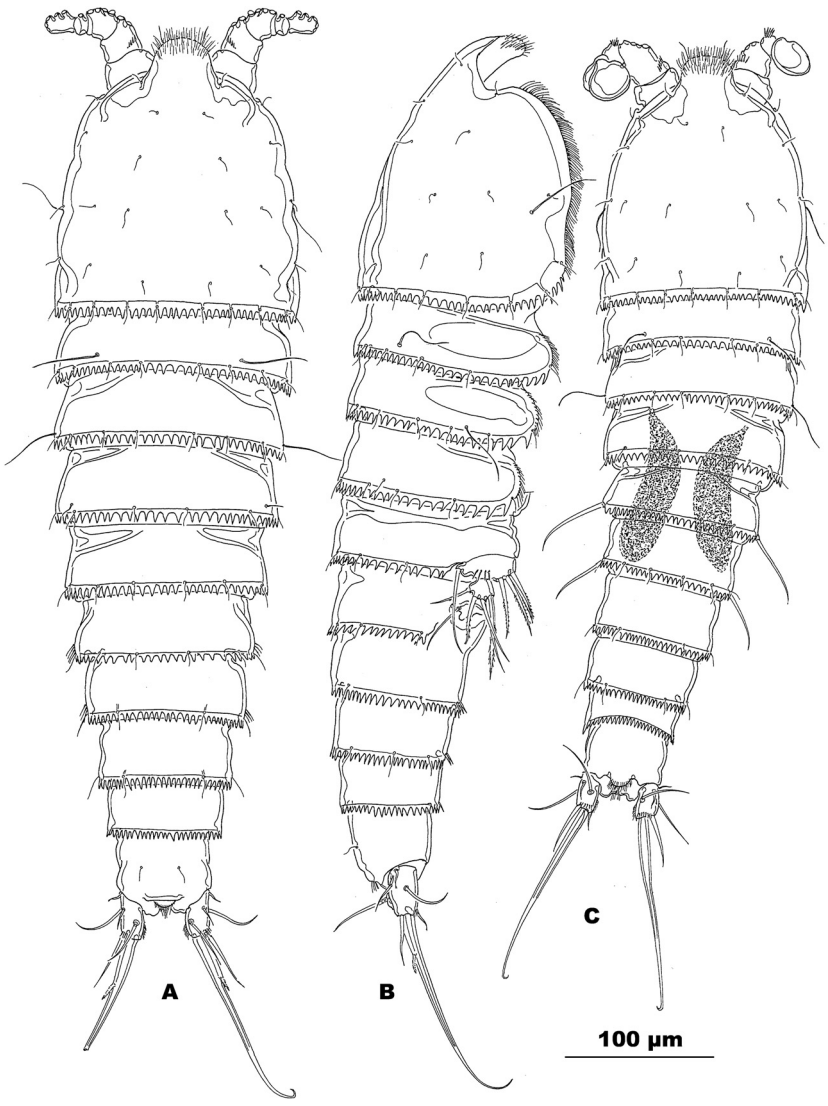

Fig. 17. *Nannopus procerus* spec. nov., female (A–B), male (C). (A) Habitus, dorsal. (B) Idem, lateral. (C) Idem, dorsal.

Norway) and named *N. palustris* by Sars (1909a) is striking although differences are noticeable when referring to Sars' description only. Re-examination of the Norwegian material clearly revealed the conspecificity between both populations.

As in the Oosterschelde specimens, none of the Norwegian specimens possess more than a single (short) medial seta on the terminal exopodite segment of legs 2 and 3. Each of them has a cluster of long setules located proximally which Sars interpreted as an additional short seta. Leg 1 endopodite, illustrated by Sars with a single terminal element on its distal segment, bears 3 elements instead. The distal and medial ones, absent in Sars' illustration, must have been detached. Leg 3 possesses the inner subdistal setiform slender element, hidden behind the spinular ornamentation.

The Norwegian specimens possess a midventral spinule row on urosomite 5 composed of spinules comparable with those along the margin of the preceding somite (minute spinules in the Eastern Scheldt population) and the proximal part of the median terminal seta on the caudal rami has a more cylindrical appearance (Fig. 26A). Leg 5 of a Norwegian specimen possesses only 3 elements on the endopodal expansion lobe. Body length of the Norwegian specimens ranges between 610 and 665 µm.

The presence of a spur on the principal terminal seta of the caudal rami was mentioned by Klie (1929) in a specimen from Kiel Harbor (Germany) co-occurring with specimens without such spur. Lang (1936a,b) clearly noted the presence of a spur in the material from Öresund. Likely, both records refer to *N. procerus* spec. nov.

The female specimen from the Karelian coast, reported as *N. palustris* by Chislenko (1967) is assumed to be attributable to *N. procerus* spec. nov. The short length of the medial seta on the leg 1 exopodite and the slender aspect of the medial element on the leg 4 endopodite are indications which support this assumption. Unfortunately, the absence of information on the other appendages and the caudal rami makes a definite statement about the Karelian material impossible. The same applies to the material from the White Sea for which some morphological data is available (Letova, 1982; Gárlitska et al., 2012) and appears to be conform to *N. procerus* spec. nov.

The records in Borutzky (1952) are ambiguous and confusing and are to be cited with caution. The description is a translation of Sars's description (incl. illustrations: Figs. 105 (10–19), 108 in Borutzky, 1952). In the absence of morphological information, the identity of the specimens referred to by Borutzky (*i.e.*: Volga estuary; the Caspian Sea drainage: Amu-Darya and Syr-Darya; the Black Sea drainage at Kuban' limans) remains to be verified.

The "notched" morph from South Carolina (Coull and Fleeger, 1977; Staton et al., 2005) and Louisiana (Fiers and Rutledge, 1990) is clearly not assignable to the present species as the characteristic flattened body shape of these specimens is significantly different.

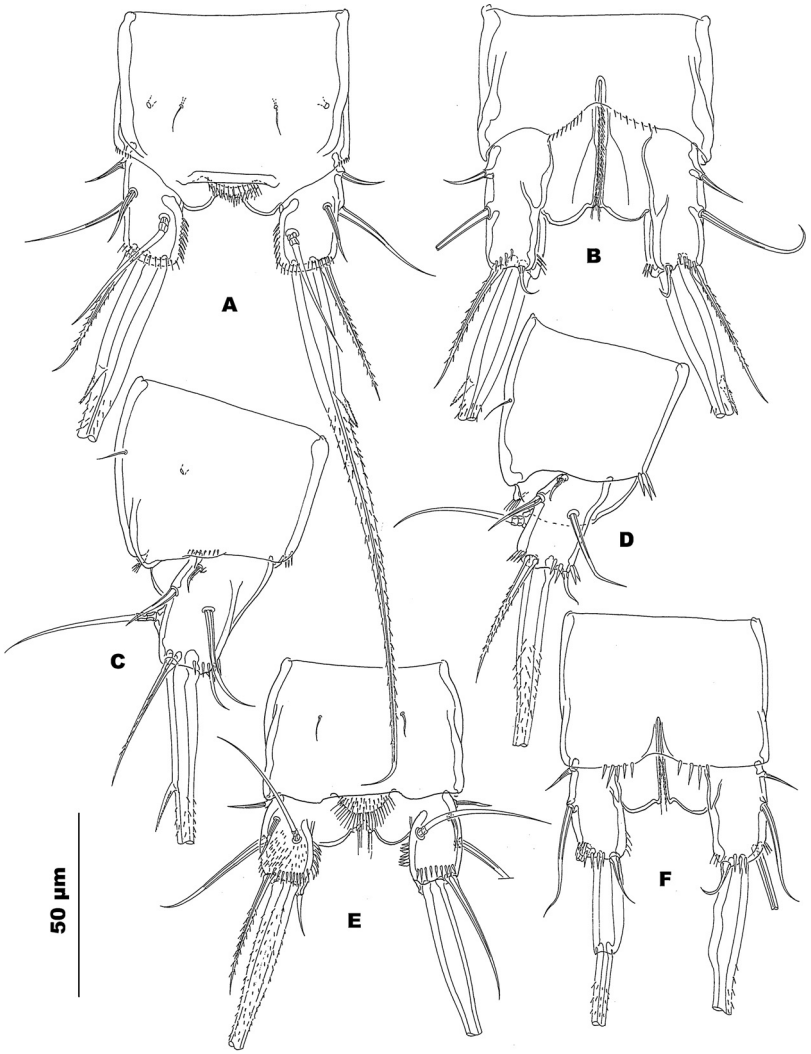

Fig. 18. *Nannopus procerus* spec. nov., female (A–C, F), male (D–E). (A) Anal somite, dorsal. (B) Idem, ventral. (C) Idem, lateral. (D) Idem, lateral. (E) Dorsal. (F) Anal somite with aberrant armature, ventral.

Nannopus hirsutus spec. nov.
(Figs. 22–25)

Type locality. The Netherlands, Oosterschelde (=Eastern Scheldt), "*Slikke*" of Bergen-op-Zoom ("slikke", Dutch for the bi-diurnal flooded part of the litoral zone), east of Oesterdam, among the angiosperm *Zostera* (Zosteraceae). Fine to very fine sand (mean grain size 75–145 μm) with silt contents between 4.5 and 16.2%. Leg. K. Willems, March 1980.
Type material. Female (holotype) dissected, registered RBINSc COP 9911A-C, female (paratype), dissected, registered RBINSc COP 9913 A-C.
Etymology. *Hirsutus* (Latin adjective for hairy, bristly) referring to the stiff dense clusters of bristles on the lateral edges of the urosomites and the principal terminal seta of the caudal rami.

Description. Female. Habitus (Fig. 22A and B) fusiform, widest along posterior margin of cephalothorax and first two free pedigers; transition between prosome and urosome faintly distinct, the former nearly as long as the latter; podoplean flexure indistinct; cephalothorax with symmetrical pattern of ridges dorsally; integumental window on cephalothorax apparently absent, probably present laterally on metasomites (area between curved lines in Fig. 22B); genital double-somite wider than long (ratio: 1.9/1) with deep invagination between anterior and posterior half; anal somite rather as long as wide with large produced rounded operculum; body length: 425–465 μm ($n = 2$).

Integument of cephalothorax smooth, of metasomites and urosomites with rows of minute spinules arranged either in transverse rows or undulating patterns (partially illustrated); posterodorsal and posterolateral margin of cephalothorax and succeeding somites coarsely serrate; ventral margin of cephalothorax and pleural region of metasomites with slender setules; lateral edges of urosomites 2–4 with dense cluster of long and stiff bristles; posteroventral margin of genital double-somite and urosomites 4–5 coarsely serrate with uninterrupted row of spinules parallel to margin; ventral surface of genital double somite and urosomites 4–5 smooth; dorsal surface of anal somite (Fig. 25A–C) with dense pattern of minute spinules; sensilla pair located in anterior half of somite with pore orifices situated between sensilla and posterior margin; lateral margin and posterodorsal margin of anal somite with rows of stiff bristles; posteroventral margin with row of long spinules on either side of anal sinus closure; anterior half of anal operculum with short transverse row of setules, caudal margin completely hirsute; anal sinus furnished with minute spinules (Fig. 23A).

Caudal rami (Fig. 25A–C) 1.5 times longer than wide in dorsal view, 2 times in ventral view; accessory element (seta I), as long as

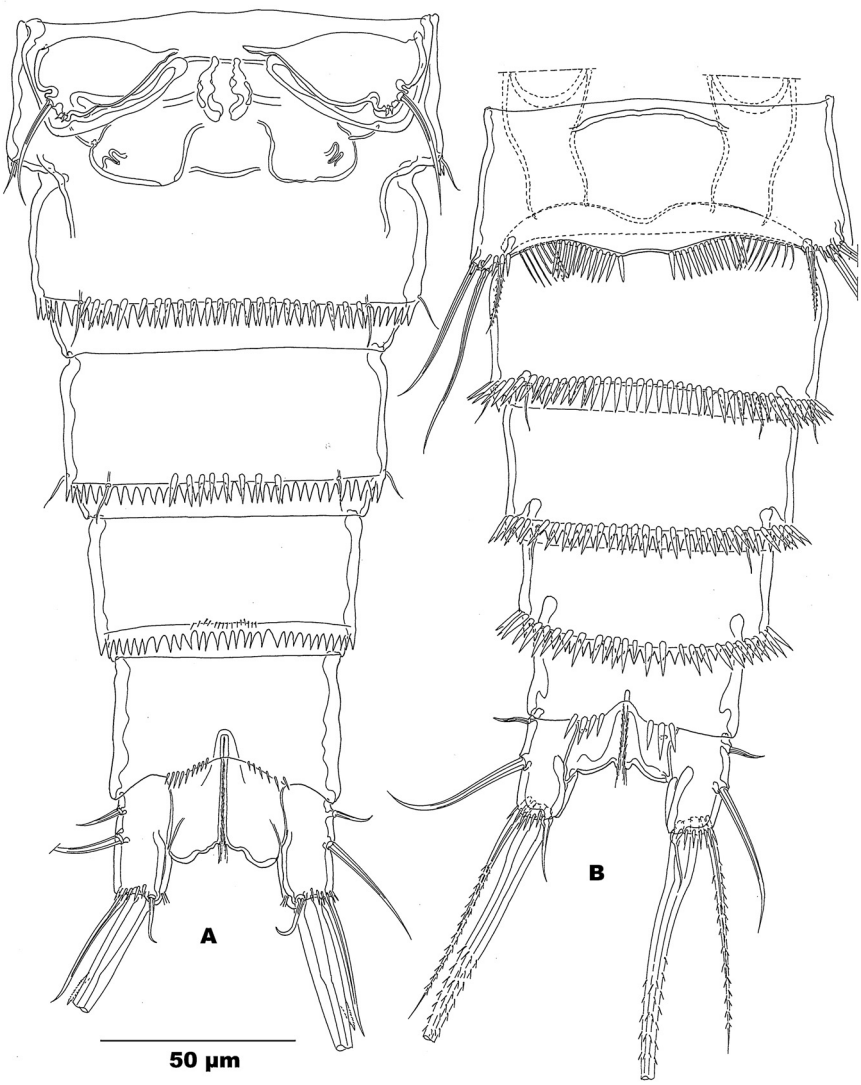

Fig. 19. *Nannopus procerus* spec. nov., female (A), male (B). (A) Genital double-somite and urosomites 4–6, ventral. (B) Urosomites 2–6, ventral.

ramal width, located near anterior margin of ramus; anterolateral and posterolateral elements located halfway margin, the former inserted in dorsal plane, slightly in a more frontal position than the latter; both equally long; dorsal seta, articulating on two basal parts, inserted halfway, close to medial margin; outer terminal seta stout, twice as long as ramus, sparsely pinnate and globular at insertion; anterior part of median terminal seta inflated, semi-cylindrical with circlets of slender bristles in anterior half and combs of slender spinules along outer side in distal half; caudal part of stem slender, furnished with widely spaced stout setules; medial terminal element short, less than half ramal length, located at lower caudal edge of ramus; rami with dense rows of long slender setules along outer margin and in anterior half of ventral surface; medial margin set with robust spinules along dorsal border; posterior margin with row of slender (dorsal) and robust (ventral) spinules.

Antennule, mouthparts and legs 1–4 as in *N. didelphis* spec. nov. except for: (1) outer spines on exopodite segments more stout, robustly armed in leg 1, (2) outer distal corner of proximal segment of leg 1endopodite with large blunt expansion and (3) the considerable more robust and stouter aspect of the pectinate medial element on leg 4 exopodite.

Leg 5 (Fig. 25D and E) typical, with 5 elements on exopodite, 3 or 4 elements on endopodal lobe of baseoendopodite; alle setae densely pinnate with serrate apical part on innermost and next to innermost (if present); medial exopodite element robust and diferrentiated from segment; frontal surface of rami with rows of slender spinules.

Leg 6 (Fig. 23A) represented as a compact linguiform plate, bearing 1 outer long setiform element and 2 min hyaline blunt inner elements; opposite legs widely separated; surface smooth; copulatory pores separated, each one located medially at some distance from ovipore, and sunk in shallow irregular depression.

Male. unknown

Comparison: *N. hirsutus* spec. nov. most resembles *N. didelphis* spec. nov. Both display a similar body shape and leg armature with a pectinate subdistal medial element on the distal segment of the leg 4 exopodite. Differences between both species are mainly related to the body ornamentation and the aspect of the caudal rami. In *N. hirsutus* spec. nov. body ornamentation is far more dense and expressed along the lateral margins of the urosomites and the caudal rami than in *N. didelphis* spec. nov. The posteroventral margin of the genital double-somite and the following ones are furnished with an uninterrupted row of stout spinules which are either absent or less numerous and much weaker in some specimens of *N. didelphis* spec. nov. The most obvious difference between the two species is the structure of the median principal seta on the caudal rami with, in *N. hirsutus* spec. nov. having a long cylindrical and heavily

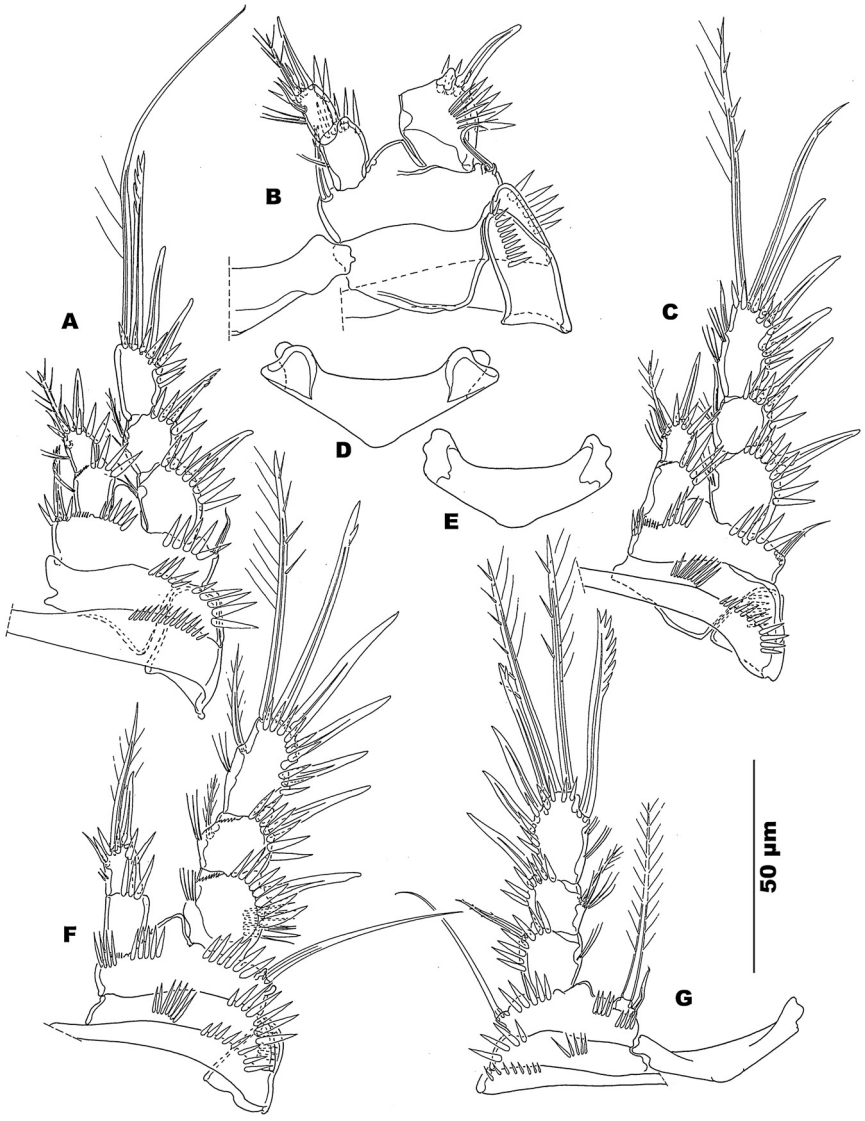

Fig. 20. *Nannopus procerus* spec. nov., female (A–G). (A) Leg 1, frontal. (B) Leg 1 protopodite and endopodite, caudal. (C) Leg 2, frontal. (D) Leg 2 intercoxal sclerite, frontal. (E) Leg 3 intercoxal sclerite, frontal. (F) Leg 3, frontal. (G) Leg 4, frontal.

ornamented proximal region, which is significantly different from the limited globular modification of the seta in *N. didelphis* spec. nov.

N. hirsutus spec. nov. co-occurred with *N. procerus* spec. nov. but was represented in the sample with only two female specimens.

3.2. Discussion

Nannopus palustris is, in the way it was introduced by Brady (1880), hardly recognizable today. Neither the text nor the accompanying illustrations (Pl. 77: Figs. 18–20) are exemplary in detail and are in fact confusing. The statement that the endopodite of leg 3 as well as leg 4 is reduced to a "setiferous tubercle" must now be considered as unjustified, as has been noticed first by Canu (1892) and confirmed by subsequent authors. The leg identified as leg 1 (Brady, 1880: pl. 77, Fig. 19) is either leg 2 or leg 3, most probably the former. Canu (1892) noticed the absence of the medial spine on the basis in Brady's illustration but expressed no doubts about the identification of it as leg 1. Sars (1909a), Lang (1948) as well as Por (1968) referred to it as leg 1.

The fact that certain morphological features appear to be species specific as indicated by the initial genetic work (Staton et al., 2005; Gárlitska et al., 2012) and on morphological grounds detailed herein, demands a reinterpretation of the original description of *N. palustris* for which we only can rely on the published data since no type material nor additional material studied by Brady could be located. The following features may be of primary importance in the recognition of the species:

(1) Body shape dorsoventrally flattened. Canu (1892), dealing with specimens with a much more slender body, interpreted the broad body form depicted by Brady as a result of pressure of the cover glass. Sars (1909a) was of the same opinion. However, a flattened body, nearly ovate in appearance, is characteristic for *N. scaldicola* spec. nov. and the "notched" morph in Staton et al. (2005). A fusiform flattened body shape as illustrated by Brady appears to be characteristic for *N. palustris* sensu Scott, 1902, *N. palustris* sensu Gurney, 1932, *N. palustris* sensu Tai and Song, 1979, *N. brasiliensis* Jakobi, 1956, the "fat" morph in Staton et al., 2005 and *N. hirsutus* spec. nov.. The body is far less flattened in *N. palustris* sensu Canu, 1892, *N. flexibilis* (Lilljeborg, 1902) but nearly fusiform cylindric in *N. procerus* spec. nov. and the "thin" morph in Staton et al., 2005.

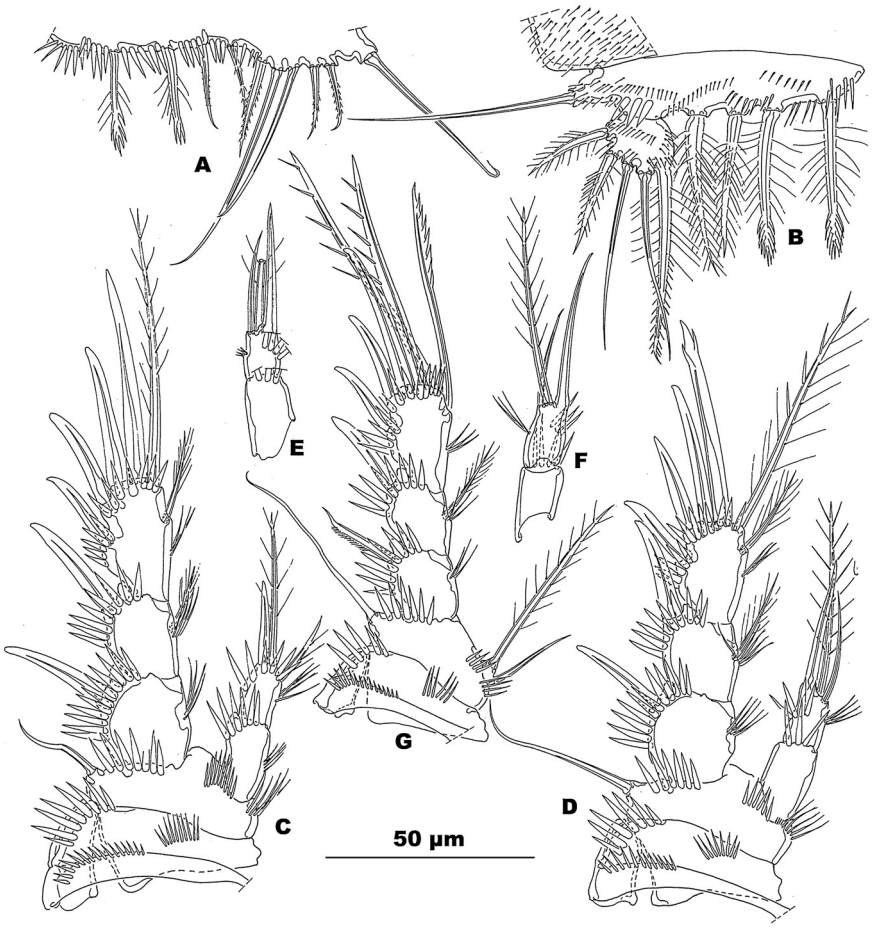

Fig. 21. *Nannopus procerus* spec. nov., female (B), male (A, C–G). (A) Leg 5, frontal. (B) Leg 5 with part of pleurotergite attached. (C) Leg 2, frontal. (D) Leg 3, frontal. (E) Leg 3 endopodite, frontal, ornament partially illustrated. (F) Leg 3 endopodite, caudal. (G) Leg 4, frontal.

(2) The caudal rami are characterized by the presence of an inflated principal median caudal seta. The outer margin is shown to bear 3 elements. A dorsal element was not illustrated (as in most of Brady's descriptions), and either the accessory or one antero-lateral element has been overlooked. The medial terminal seta is obvious and located on the inner distal corner.

An inflated principal caudal seta is present in *N. palustris* sensu Canu (1892), *N. p. tiberiadis* Por, 1968, *N. flexibilis* Lilljeborg (1902), *N. hirsutus* spec. nov. and the "thin" and "fat" morphs in Staton et al. (2005). *N. procerus* spec. nov. (incl. *N. palustris* sensu Sars) and the "notched" morph in Staton et al. (2005) possess in addition a spur at the caudal end of the inflated region. *N. didelphis* spec. nov. and *N. palustris* sensu Tai and Song, 1979 have a restricted globular expansion of the seta at its insertion on the ramus. The principal terminal seta in *N. palustris* by Scott (1902), Gurney (1932), Schäfer (1936), Kunz (1935) and *N. brasiliensis* Jakobi, 1956 appear to be a normal unmodified setal element similar to the one in *N. scaldicola* spec. nov.

(3) The outer terminal seta on the caudal rami is remarkably short, even slightly shorter than the median terminal one, but is well presented. A comparable short outer terminal element was depicted in *N. palustris* sensu Tai and Song, 1979, *N. palustris* sensu Damian-Georgescu (1970) and *Nannopus* spec. of Hemsen (1952). It is reduced to a knob in *N. p. tiberiadis* and appears to be absent in *N. flexibilis*.

(4) Leg 2 endopodite (referred to as leg 1 by Brady) is characteristic by the presence of three equally long terminal armature elements. The shortness of the apical seta of the leg 2 endopodite is remarkable as it is commonly a long setiform element whereas the median element on the leg 1 endopodite is far more shorter being, at the most, twice as long as the outer subdistal spine. The only exception is exhibited in leg 2 of *N. procerus* spec. nov. in which the median and the subdistal outer elements are equally long (in the female). A short subdistal inner seta on the leg 2 endopodite is common. Only *N. nannopus* sensu Canu and *N. scaldicola* spec. nov. deviate from this scheme as they have a long setiform subdistal inner element.

(5) Leg 4 in *N. palustris* was described (but captioned as leg 3 in Brady, 1880) with only 2 outer spines on the terminal exopodite segment. Whether this is typical for the species has to be confirmed. Variation of the number of the outer spine armature occurs occasionally (example leg 3 in Fig. 7D of *N. didelphis* spec. nov.). Most noticeable is the absence of a subdistal inner pectinate element on the third exopodite segment. Brady's illustration clearly depicts two long inner elements of which the subdistal one is a long slender and pinnate seta. In so far leg 4 has been illustrated in subsequent descriptions (Lilljeborg, 1902; Scott, 1902; Sars, 1909a,b; Gurney, 1932; Jakobi, 1956; Tai and Song, 1979; Coull and Fleeger, 1977) this armature element is a noticeable rigid and pectinate appendage distinctly shorter than the proximal element (when the latter is present). In *N. palustris* sensu Canu and *N. scaldicola* spec. nov. the subdistal element is a long untransformed pinnate seta (note: the interpretation of Wells (1971) that the normal number of setae on the inner margin of the distal segment is 3 is incorrect).

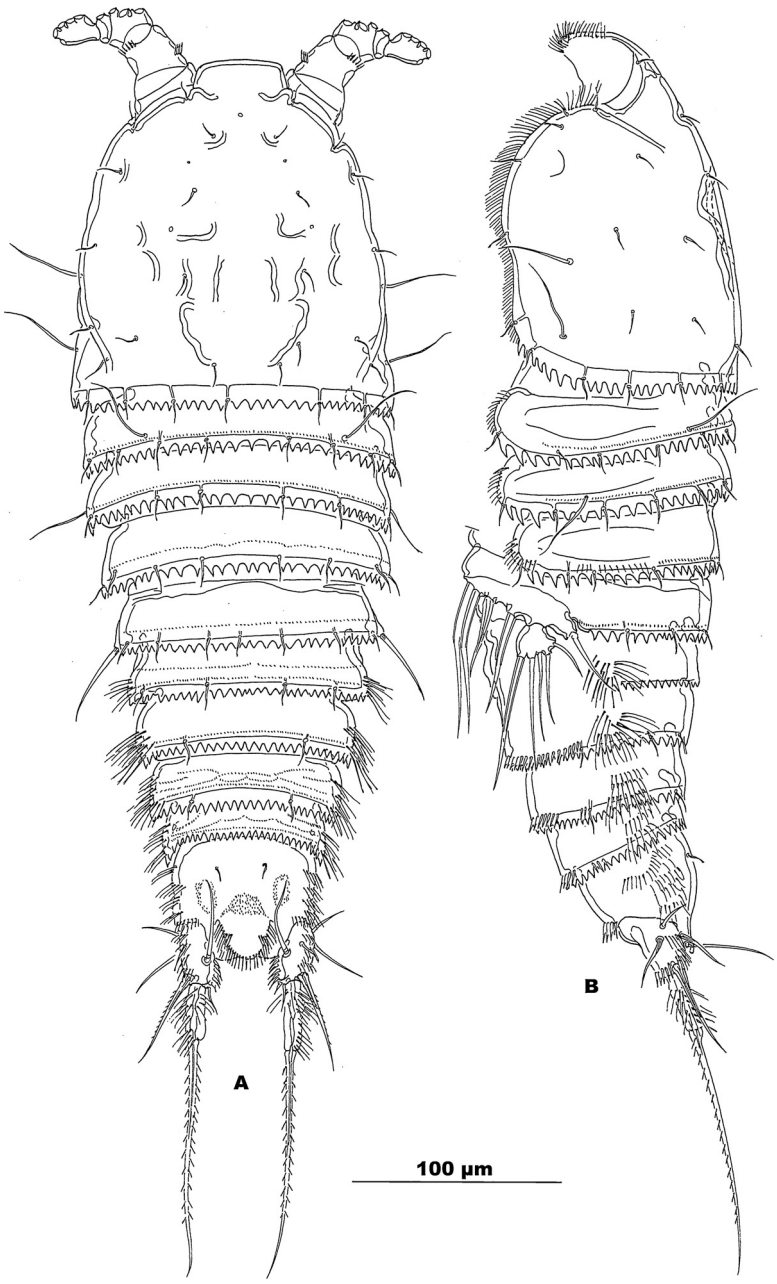

Fig. 22. *Nannopus hirsutus* spec. nov., female (A–B). (A) Habitus, dorsal. (B) Idem, lateral.

The most recent updates (Bodin, 1997; Wells, 2007) recognize only 3 valid species in the genus *Nannopus*: *N. palustris* Brady, 1880, *N. perplexus* Sars, 1909b and *N. unisegmentatus* Shen and Tai, 1964. *Ilyophilus flexilibis* Lilljeborg, 1902, currently *Nannopus flexilibis* (Lilljeborg, 1902), and *N. littoralis* Willey, 1923 have been sunk in synonymy with *N. palustris* by Sars (1909a,b) and Lang (1936b), respectively; *Nannopus* spec. of Hemsen, 1952, *N. brasiliensis* Jakobi, 1956 and *N. palustris tiberiadis* Por, 1968 by Wells (1971). Complete or partial descriptions of specimens identified as *N. palustris* have been provided by Canu (1892), Scott (1902), Sars (1909a), Gurney (1932), Lang (1936a,b), Klie (1929), Willey (1929), Kunz (1935), Schäfer (1936), Chislenko (1967), Damian-Georgescu (1970), Wells (1971), Coull and Fleeger (1977), Tai and Song (1979), Letova (1982), Kikuchi and Yokota (1984), Yoo and Lee (1995) and Kornev and Chertoprud (2008).

In the previous section, *N. palustris* reported by Sars (1909a) from Oslofjord and those examined by Lang (1936) from Öresund are referred to *N. procerus* spec. nov. One specimen reported from Kiel Harbor and mentioned by Klie (1929) is probably referable to *N. procerus* spec. nov. as well. Chislenko's (1967) report of *N. palustris* from the White Sea is assumed to be conspecific with *N. didelphis* spec. nov. which, however, needs to be confirmed.

With considerable insight, Canu (1892) recognized the animals he collected along the mud flats in Wimereux (France) as a member of *Nannopus* and was the first who introduced a detailed account on the morphology of all appendages, males were not found. Canu identified his specimens with *N. palustris*.

These French specimens resemble the original description more closely than any subsequent one. The absence of a pectinate subdistal medial element on the terminal exopodite segment of leg 4 and the inflated proximal region of the principal caudal seta appear to be similar in the French and English morphs. However, the presence of 3 medial setae on the terminal exopodite segment of leg 4 is odd. The position of the middle one, squeezed between the

Fig. 23. *Nannopus hirsutus* spec. nov., female (A–D). (A) Genital double-somite and urosomites 4–6, ventral. (B) Leg 4, frontal. (C) Leg 4 endopodite. (D) Leg 4 intercoxal sclerite.

subdistal and the proximal one, allows us to assume that the presence of it is an aberrancy of the normal pair. The slender fusiform body shape, the length of the outer principal seta on the caudal rami (twice as long as the ramus), and the position of the lateral setae on the caudal rami are different and may indicate that Canu's specimens represent a different species, not conspecific with *N. palustris* s. str.

Nannopus scaldicola spec. nov. is the only other species known thus far in which leg 4 exopodite lacks a pectinate medial element but cannot be confused with *N. palustris* sensu Canu. The strongly flattened and ovate body shape, the presence of long setae on the leg 2 endopodite, and the unmodified principal setae on the caudal rami of *N. scaldicola* spec. nov. are significant differences supporting the differentiation of the Scheldt material as a distinct species.

Scott's (1902) description of *N. palustris* from brackish water pools near Newburgh on the Ythan (East Scotland) is the first contribution in which males were reported and partially described. That the caudal rami bear only 6 elements has to be confirmed but most probably the accessory or the anterolateral element has been overlooked. Scott's illustration enumerated 20 on Plate 23, claimed to be the representation of the female leg 2, depicts in fact the female leg 3 (2 long inner setae on the terminal exopodite segment, 2 long setae on the endopodite). The leg 4 exopodite is armed with a complete set of elements and has the long subapical pectinate element on the exopodite. The apophysis on the leg 3 endopodite is sigmoid and bifid at the apex (Scott, 1902: "hooked at the end").

The animals examined by Scott and by Gurney (1932) from Norfolk resemble in almost all detail the description by Brady, but Gurney (1932: figs. 1178 and 1179) does depict the caudal rami with seven setae in which the anterolateral and the posterolateral elements are positioned at the same level, the former above the latter. Both authors claim that, with the exception of the modified leg 3 endopodite, the rami are identical in both genders. However, Scott's illustration of the male leg 3 shows that the outer terminal element of the exopodite has a spiniform appearance which contrasts with the setiform morphology of this element in the female. Gurney's illustrations of legs 2 and 3 are from the male and demonstrate the spiniform nature of this element.

Neither Scott, nor Gurney mention a particular modification of the median principal seta of the caudal rami. Instead, both authors depicted this element without any particular inflation in the proximal part of the stem. Scott's illustrations (1902: pl. XXIII: 13–14) are rather undetailed, but Gurney (1932: figs. 1178–1180) observed the caudal rami and its armature in close detail and it is assumable that when present any modification of the principal seta would be documented. In addition, the outer principal seta on the caudal rami in Scott's and Gurney's specimens is considerably longer than the ramus which contrasts with the shortness of it in Brady's type description of *N. palustris*. The presence of a pectinate medial element on the leg 4 exopodite and the different structure of the caudal rami armature are clear indications to suppose that the specimens studied by Scott and Gurney are not conspecific with *N. nannopus*.

Lilljeborg (1902) introduced the genus *Iliophilus* for *I. flexibilis* Lilljeborg, 1902 obtained from the freshwater Lake Malaren near Stockholm. *Iliophilus* was absorbed into *Nannopus* by Sars (1909a) who, for mysterious reasons and contrary to the obvious

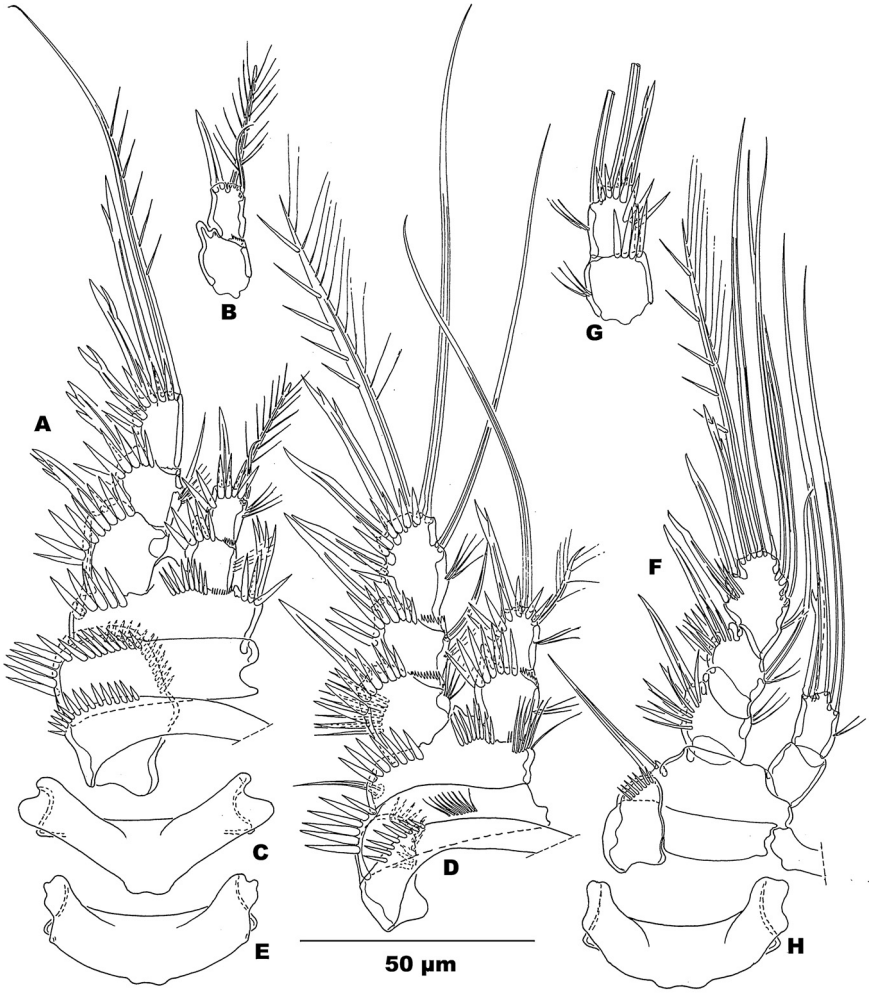

Fig. 24. *Nannopus hirsutus* spec. nov., female (A–H). (A) Leg 1, frontal. (B) Leg 1 endopodite, spinular ornament omitted. (C) Leg 1 intercoxal sclerite, frontal. (D) Leg 2, frontal. (E) Leg 2 intercoxal sclerite, frontal. (F) Leg 3, caudal. (G) Leg 3 endopodite, frontal. (H) Leg 3 intercoxal sclerite, frontal.

differences with his specimens, relegated *I. flexibilis* to the synonymy of *N. palustris*. Both actions have been generally accepted by subsequent scholars (Lang, 1936b, 1948; Borutzky, 1952; Wells, 1971).

However, the conspecificity of *I. flexilibis* with *N. palustris* is doubtful as the former displays significant dimorphism of the caudal rami armature (absence of the outer principal seta in female, present in male) and possesses a wide straight triangular apophysis on the outer distal corner of the male leg 3 endopodite. Although the male of *N. palustris* sensu Brady is still unknown, the female has caudal rami with a distinct outer principal element. For males of *N. palustris* auct. dealt with herein, the outer terminal setae on the caudal rami are present and quite similar in both genders (in males commonly slightly longer; without spur in "notched" morphs), *N. palustris* sensu Kikuchi and Yokota excepted (see below). Furthermore, since the presence of a medial subdistal pectinate element on the leg 4 exopodite in *N. flexilibis* (absent in *N. palustris*) and the narrow body shape (flattened in *N. palustris* s. str.) are considered here as relevant features in species discrimination, the Malaren morph is reassessed herein as a distinct species, *Nannopus flexibilis* (Lilljeborg, 1902).

Brief, *N. flexibilis* (Lilljeborg, 1902) is a *Nannopus* with fusiform body shape and characterized by the dimorphic appearance of the terminal caudal rami armature in which the outer one (III) is absent or dwarfed in the females, but well developed in the male; 2-segmented endopodites in legs 1–3; and the presence of a pectinate subdistal medial element on the terminal exopodite segment of leg 4 exopodite.

Por (1968) differentiated *N. palustris tiberiadis* from the nominal form on the basis of the particular dimorphism of the terminal armature on the caudal rami and the short straight and sharp triangular apophysis on the male leg 3 endopodite. The description is not complete and the illustration (Por, 1968: plate IV, Fig. 3) does not depicts leg 1 but leg 2 (terminal exopodite segment with formula III.2.1). Differentiation was based comparing the Lake Tiberias (Israel) material with Gurney's 1932 description of *N. palustris*.

Sars (1927) reported *N. palustris* from the Caspian Sea (exact locality unknown) but did not support the identification by morphological data. One slide (acc. #F6287 Mp337) with the dissected parts of a male specimen, is present in the collection of the Oslo Museum and is referable to the Caspian Sea collection. In addition, two slides containing the dissected parts of a male and a female, respectively are present in the collection at Oslo (acc. # F7279 Mp 385, F7278 Mp 385). The labels bear the indication *Nannopus* and the number 390 as a reference to the sample number. Amongst Sars notes, archived at the National Library at Oslo, a handwritten list of the species encountered in Birket Qarun (Egypt) is present, although this collection obtained by Sars and identified by him has never been published upon. Unfortunately, the archives do not hold specific indications on the location of the sample site (loc. 390 on the list and on both slides: pers. obs. F. Fiers, spring 2012). The entry of *N. palustris* is annotated by Sars: "*2 specimens only*" and

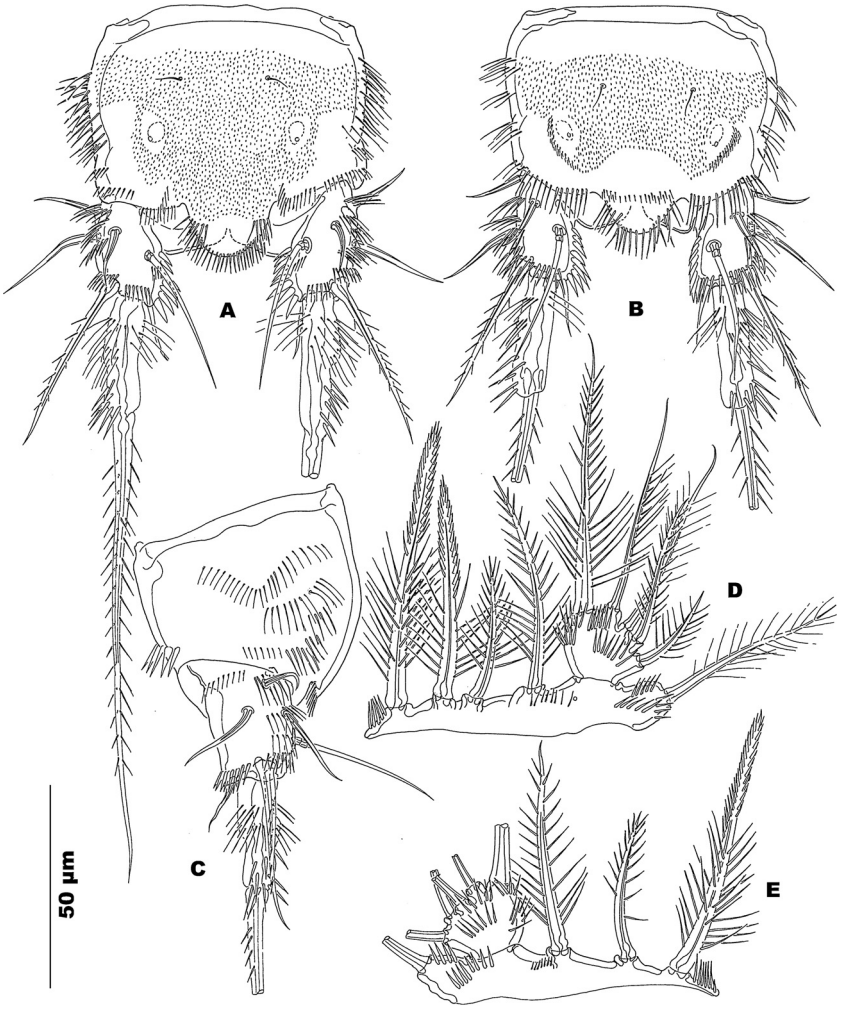

Fig. 25. *Nannopus hirsutus* spec. nov., female (A–E). (A) Anal somite and caudal rami, dorsal. (B) Idem, dorsal (paratype specimen). (C) Idem, lateral. (D) Leg 5, frontal. (E) Idem, frontal (paratype specimen).

"*differ a little from the form seen to my account of the Crustacea of Norway*". Re-examination revealed that the morphology of the terminal armament on the caudal rami in both genders coincides completely with that of *N. p. tiberiadis*, except for the fact that the outer terminal element, distinctly globular at its insertion, still has a short setiform apical outgrowth (indicated by arrow in Fig. 26B and C for the female, Fig. 26D). The Caspian Sea and Egyptian males possess a leg 3 (Fig. 26E) with the heavy triangular apophysis on the endopodite. The male and female from Birket Qarun and the male from the Caspian Sea furthermore completely correspond to the description of *N. flexilibis*. *Nannopus.* spec. of Hemsen (1952) known from a freshwater pond in Iran and *N. palustris* reported by Damian-Georgescu (1970) from several localities along the Romanian Black Sea coast, display similar modifications of the caudal rami armature. Males were not observed by Hemsen, but Damian-Georgescu reported the dimorphic character of the caudal setae (*i.e.* the absence of the outer principal one in the female) and the triangular appearance of the leg 3 apophysis. Based on these similarities, *N. palustris tiberiadis*, the specimens obtained in and near the Caspian Sea by Sars (1927) and Hemsen (1952), those from the Black Sea (Damian-Georgescu, 1970) and the material from Birket Qarun are considered here as junior synonyms of *Nannopus flexibilis* (Lilljeborg, 1902). The identity of the specimens from the Caspian Sea and the Black Sea referred to as *N. palustris* by Borutzky (1952) remains unclear as these identifications are not supported by morphological data.

The introduction of *Nannopus littoralis* by Willey (1923) is rather confusing. The subsequent amendments (Willey, 1929) and his comparisons with *N. palustris* auct. do not enhance the original description, but rather add to the confusion. In as far as can be deduced Willey's 1929, *N. palustris* is similar to *N. palustris* sensu Sars, 1909a,b, herein referred to as *N. procerus* spec. nov., whereas *N. littoralis* has more in common with *N. palustris* s. str. However, these are assumptions only. The truth remains that the identity of the morphs reported by Willey will forever be difficult to establish without direct examination of his specimens.

The description of *N. brasiliensis* by Jakobi (1956) is puzzling. The species was discriminated from "*N. palustris*" collected among the mangals of Rio Nanáu and Baía de Guaratuba (Cananéia), although morphological details of those specimens were not given. The most intriguing feature of *N. brasiliensis* is the unmodified structure of the outer apical element on the third exopodite segments of leg 3. Instead of being spiniform and robust, it appears to be long and pinnate and is as such reminiscent of its homologue in the females described above. Dimorphic modification of the leg 3 endopodite seems to be limited to the medial subdistal element only, which is represented as a short sigmoid and slender element. The outer element does not look as it is modified. The Brazilian morphs ("*N. palustris*" and *N. brasiliensis*) are currently considered as conspecific with *N. palustris* (see Reid, 1998 and references therein) but material should be re-examined in order to elucidate their status.

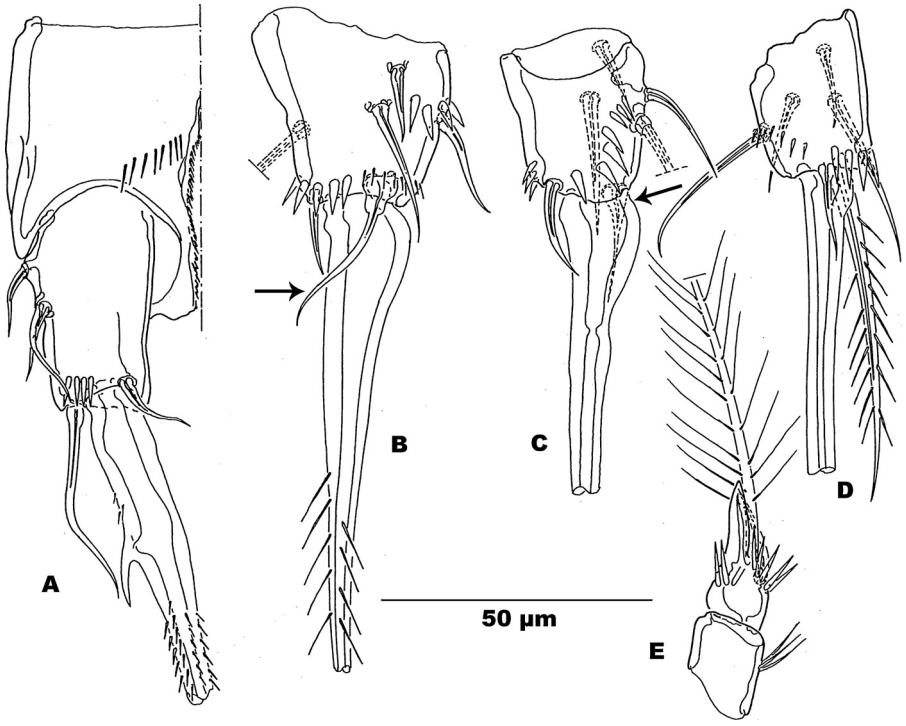

Fig. 26. *Nannopus procerus* spec. nov., female (A). (A) Right half of anal somite and caudal ramus, ventral. *Nannopus flexibilis* (Lilljeborg, 1902), female (B–C), male (D–E). (B) Caudal ramus, outer view. (C) Idem, medial view. (D) Idem, medial view. (E) Leg 3 endopodite, frontal (A: specimen from Bestumkilem, G.O. Sars collection, Oslo; B–E: specimens from Caspian Sea, G.O. Sars collection, Oslo).

N. palustris sensu Tai and Song, 1979 from China, is recognizable by the structure of the outer and median principal setae on the caudal rami. The globular expansion near the insertion of the median element and the shorter length (barely extended beyond the expansion) of the outer principal seta are particular to this form. Unfortunately, the armature of the male caudal rami nor the structure of the legs has been documented (only leg 5 and 6). With only the female characteristics depicted, the Chinese freshwater morphs resemble *N. palustris* described by Kikuchi and Yokota (1984) from Lake Hinuma (Japan). Males of the latter have the outer principal element on the caudal rami well developed. As such they are reminiscent of *N. flexibilis*, but differ from the latter by the normal setiform appearance of the outer principal seta and the unmodified proximal part of the median principal element on the female caudal rami. The modification of the median element in *N. didelphis* spec. nov., is much more restricted in diameter and dimension, whereas the outer element is considerable much longer than in the Chinese and Japanese morphs. The presence of only 2 outer spines on the terminal exopodite segment of leg 2 in *N. palustris* sensu Tai and Song may be an additional specific feature.

Scattered across the literature, details of specimens attributed to *N. palustris* have been published by Schäfer (1936: Hiddensee Island, Germany), Kunz (1935: Schleswig-Holstein, Germany), Wells (1971: from Madras, India), Letova (1982: from Murmansk, Russia), Yoo and Lee (1995: Korea, Yellow Sea coast) and Kornev and Chertoprud (2008: White Sea) but none of them provide decisive information. Until those specimens are re-examined and compared with the other descriptions they are preferentially to be treated as doubtful identifications.

N. palustris from South Carolina reported by Coull and Fleeger (1977) is now known to be a complex of at least two different species (Staton et al., 2005). Besides an obvious "notched" morph (*i.e.* with a spur on the principal caudal ramus seta), two morphs with simple inflated principal median setae on the caudal rami occur ("thin" and "fat" morphotypes). The genetic signal separates the "notched" one significantly from the other morphs, but the applied methodology failed so far to distinguish the latter two.

N. palustris sensu Sars, 1909a (= *N. procerus* spec. nov.) is the only other "notched" morphotype known thus far (except for a "notched" morph mentioned in Gárlitska et al. (2012), see below). The differences between the South Carolina and the North Atlantic representative are obvious. When the former has a slender nearly cylindrical body, the latter is characterized by its strongly flattened semi-ovate habitus, as in *N. scaldicola* spec. nov. Furthermore, the additional ornamentation with the obvious barbed region behind the spur contrasts significantly from the moderate spinular ornamentation found on the seta in *N. procerus* spec. nov. The single female specimen from Louisiana, reported as *N. palustris* by Fiers and Rutledge (1990) is reminiscent of the "notched" morph occurring in South Carolina. Their conspecificity is highly probable, but cannot be ascertained now in the absence of sufficient material and a detailed description of the South Carolina morph.

The two "un-notched" morphs are both marked by their inflated principal median seta on the caudal rami. Although they did not differentiate as two distinct branches in the genetic analysis (mitochondrial Cyt b and nuclear 28S rDNA) they are morphological different as demonstrated by their body shape. Closer examination of the caudal rami armature and ornamentation, amongst other structures will undoubtedly reveal significant, as yet undocumented, structural differences of which the significance will have to be tested by analyses of other genetic markers.

Morphological comparison analyzed by Gárlitska et al. (2012) is mainly an elaboration of the tabulated data in Wells (1971) expanded with observations on material from the North Sea, Black and White Sea. Just as in Wells (1971) the descriptions by Canu (1892) and Scott (1902) are considered the standard reference to *N. palustris sensu stricto* and are as such of limited relevance. Apparently no attempt has been made to critically evaluate the original description by Brady. Moreover, the use of over-simplified tabulated character states (*e.g.* male P3 with "sharp" spine; exopodite

leg 4 with 2 "setae" on the terminal segment; caudal rami armature specificities), the partially erroneous citations (*e.g.* leg 1 exopodite terminal segment with 1 seta; exopodite leg 3 with 3 setae), and the exclusion of certain relevant previously published data (Lilljeborg, 1902; Gurney, 1932, amongst others) is poised to be seen as uncritical, outdated and uninformative.

Beyond doubt, Staton et al. (2005) and Gárlitska et al. (2012) supply relevant information on genetic species divergence and co-occurrence, and add primary information to understand basic issues of meiofaunal colonization, differentiation and biogeography. Unfortunately, and to the contrary of their claims perhaps, the absence of detailed morphological data on each population hampers current diversity assessments as comparison on structural grounds is impossible. The complete absence of registered voucher specimens of each of their morphs is most unfortunate and will consequently severely hinder future faunistic and taxonomic analysis.

Whilst species specific character sets in *Nannopus* are being clarified, the question emerges if the genus should be considered as a single phylogenetic lineage. The here described *N. scaldicola* spec. nov., *N. nannopus* s. str. and *N. nannopus* sensu Canu are the 3 morphotypes known thus far in which the subdistal inner element on the leg 4 exopodite is either absent (*N. scaldicola* spec. nov.) or presented as a unmodified pinnate seta (both other morphs). In all other representatives (including *N. palustris* auct. for which leg 4 is described, *N. perplexus* and *N. unisegmentatus*) this element is a modified armature element (robust, largely smooth but pectinate along the distal part of the stem) and is the derived condition. In addition, the male leg 6 and the associated male genital apparatus in *Nannopus* is significantly different among the several species and is clearly divisible in two groups. In *N. scaldicola* spec. nov. the leg 6 complex is asymmetrical with one side present as a functional valve closing the spermaduct, the opposite leg is undifferentiated and apparently fixed to the somite. Only one spermaduct is developed and opens below the functional leg 6. In contrast, in *N. didelphis* spec. nov. and *N. procerus* spec. nov. the leg 6 vestiges from both sides are confluent with each other resulting in the formation of a single transverse and wide plate along the posteroventral margin of the genital somite. Both spermaducts are developed and open into a large transverse atrium closed by the leg 6-complex.

The groundpattern of the male genital apparatus and its associated structures is assumed to be paired, by which each leg 6 vestige individually closes a spermaduct. In *Nannopus* the male leg 6 deviates from this basic plan in two ways: assymetrical and unpair (*N. scaldicola* spec. nov.) or symmetrical and midventrally confluent (*N. didelphis* spec. nov. and *N. procerus* spec. nov.). Each represents an advanced derivation of the original morphology. The symmetrical configuration is probably the ancestral condition and is shared with *Huntemannia* Poppe, 1884 (see *Huntemannia doheoni* Song et al., 2007). Unfortunately, the morphology of the leg 6 and the male genital apparatus in *Nannopus* has received scant attention in previous reports. If the nature of the subdistal inner seta on the leg 4 exopodite would be confirmed as an apomorphy, *N. palustris* s. str., *N. palustris* sensu Canu, and *N. scaldicola* spec. nov. are to be considered as the only representatives thus far known of the genus *Nannopus*. Consequently, the genus *Ilyophilus* Lilljeborg, 1902 should be reinstated with *I. flexibilis* (as the type) and including *N. perplexus*, *N. procerus* spec. nov., *N. didelphis* spec. nov, *N. hirsutus* spec. nov. and those characterized with a pectinate armature element on the leg 4. The two different conditions of the male leg 6 may sustain this assumption.

It is a fact that detailed examination of specimens of *N. palustris* sens lat. is not tempting. In many cases, specimens are densely covered with detritus, sometimes filamentous, sometimes composed by particles, which was already used by Brady (1880) as an excuse for the vague description. However, the foreign matter appears to be located solely on the dorsal and lateral surfaces of the somites, clustered around the caudal rami and anal somite and in a lesser degree on the ventral surface of the urosome. Even densely detritus clogged animals have their buccal appendages and legs covered with far less, sometimes even completely devoid of, foreign material. In the majority of cases the cleanness of the appendages allows the examination of specimens in the required, level of detail.

Since we now know, based on genetic and morphological evidences, that *N. nannopus* auct. is a complex of pseudo-cryptic species, future references to their presence have to dealt with more caution. Until we can rely with confidence upon a redescription of *N. palustris* s. str. reports on the occurrence of populations resembling the species should refer to it in a more general way (ex.: *N. aff. palustris*, *N. palustris auct.*) to avoid any further taxonomic confusion.

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