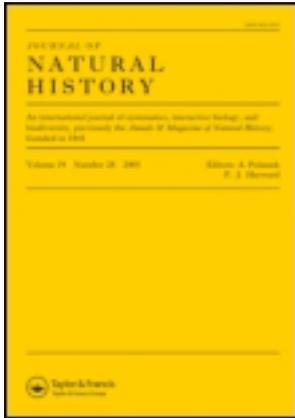


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A revision of *Micropodarke* (Psamathini, Hesionidae, Polychaeta)

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(Accepted 18 October 2004)

Abstract

Micropodarke Okuda, 1938 (Psamathini, Hesionidae, Polychaeta) is revised based on examination of all available types, other museum specimens, and a large number of newly collected specimens from Japan, Hong Kong, Papua New Guinea, Australia, New Caledonia, California, the west coast of Canada, and the Red Sea. The previous synonymy of *Micropodarke amemiyai* Okuda, 1938 with *M. dubia* (Hessle, 1925) is substantiated, and *M. trilobata* Hartmann-Schröder, 1983 is newly synonymized with *M. dubia*, leaving *Micropodarke* monotypic. A lectotype is selected for *M. dubia*. *Micropodarke dubia* is identified by the apomorphies of a proboscis diaphragm, segmental ventral adhesive papillae, distally nobby and slightly curved neuroaciculae, and median neurochaetae with few, basally situated prolonged teeth (“spurs”), with abrupt transition to the following, much shorter teeth. *Micropodarke dubia* has a main distribution in the tropical and warm temperate Indo-Pacific region, and appears to be absent from the Atlantic Ocean.

Keywords: *Hesionidae*, *Micropodarke*, *Micropodarke trilobata*, *new synonymy*, *Polychaeta*, *revision*, *taxonomy*

Introduction

We present a taxonomic revision of *Micropodarke*, based on examination of newly collected specimens of *Micropodarke* from southern and eastern Japan, Hong Kong, the Great Barrier Reef, New South Wales, South Australia, New Caledonia, western Canada, California, and the Red Sea, together with all available types and other deposited museum specimens. *Micropodarke* was erected by Okuda (1938) for a new hesionid from Japan, *M. amemiyai* Okuda, 1938. At present it includes three nominal species: *M. dubia* (Hessle, 1925) and *M. amemiyai* from Japan, and *M. trilobata* Hartmann-Schröder, 1983 from Australia. Okuda, in his original description of *M. amemiyai*, had clearly overlooked Hessle's earlier study on hesionids from Japan, including the description of *Kefersteinia dubia* from the same locality where he found *M. amemiyai*, and his species *M. amemiyai* was synonymized with

M. dubia by Imajima and Hartman (1964). The generic name *Micropodarke*, in contrast, has generally been considered valid by later authors. *Micropodarke trilobata* was described from an anterior fragment only, although Hartmann-Schröder in two later studies (1986, 1989) recorded further specimens from southern and south-western Australia. Several attempts to recollect specimens from the type locality in Dunsborough, Western Australia, unfortunately proved unsuccessful, although other specimens from elsewhere in Australia have been collected for comparison.

Material and methods

Specimens were extracted from scuba or intertidally collected sand samples by decantation through a 250 µm sieve, relaxed in a mixture of 7% magnesium chloride (in distilled water) and filtered sea-water (see Rouse and Pleijel 2001 for details). Relaxed specimens were studied alive, processed for long-term storage, light microscopy, and scanning electron microscopy (SEM). For long-term storage specimens were preserved in 10% formaldehyde (i.e. 25% formalin) in filtered seawater for one or a few days, rinsed in distilled water and transferred to 70–80% alcohol (all newly collected specimens were fixed in this way unless otherwise noted in the “Material examined” sections). Live, relaxed specimens were also mounted for light microscopy (LM) in BDH Gurr Aquamount® on slides for chaetal studies. Specimens for SEM were similarly relaxed, fixed in 1% osmium tetroxide (diluted in the MgCl₂ solution or in filtered sea-water) for 1 h, rinsed in distilled water, dehydrated in a graded ethanol series, critical point dried, and sputter-coated. Specimens preserved for DNA sequencing were fixed and stored in 70 or 95% ethanol.

Institutions and museums are indicated by the following abbreviations: MNHN (Muséum national d’Histoire naturelle, Paris), NMCA (Canadian Museum of Nature, Ottawa), NMW (National Museum of Wales, Cardiff), UHM (University of Hawaii at Manoa), USNM (United States National Museum, Smithsonian Institution, Washington, DC), and UUZM (Uppsala University, Zoological Museum, Sweden). Collectors are indicated by the following abbreviations: CHOT (City of Honolulu’s Oceanographic Team), TD (Thomas Dahlgren), LH (Leslie Harris), GHS (Gesa Hartmann-Schröder), FP (Fredrik Pleijel), and GWR (Greg W. Rouse). Specimens labelled FP are currently in Fredrik Pleijel’s personal collection for further studies, but will eventually be deposited at MNHN.

Micropodarke Okuda, 1938

Micropodarke Okuda 1938, p 90 (type species *Micropodarke amemiyai* Okuda, 1938, by monotypy); Fauchald 1977, p 76; Hartmann-Schröder 1983, p 125–126; Pleijel 1998, p 115–117.

Apomorphies

Monotypic, see *M. dubia*.

Description

Monotypic, see *M. dubia*.

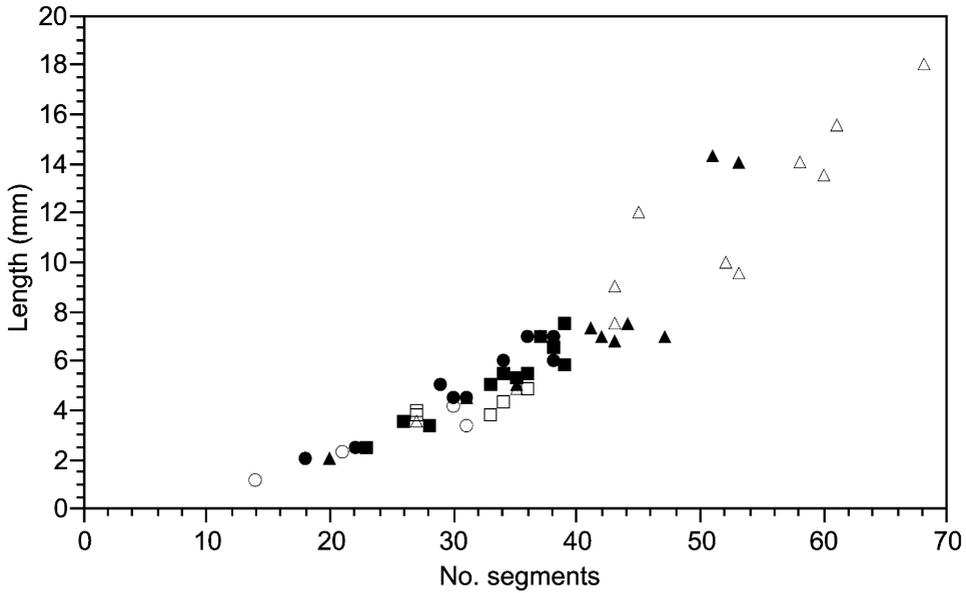


Figure 1. Relationships between number of segments and length in *Micropodarke dubia*. Specimens from (●) the Great Barrier Reef; (□) Papua New Guinea; (○) California; (■) western Canada; (▲) Hong Kong; (△) Japan.

Micropodarke dubia (Hessle, 1925)

(Figures 1–6)

Kefersteinia dubia Hessle 1925, p 32–34, Figure 11 (lectotype UUZM 674a1; this study).

Micropodarke amemiyai Okuda 1938, p 89–90, Figure 10A–E (type material appears to be absent); Uschakov and Wu 1965, p 71, figure 19.

Micropodarke dubia: Imajima and Hartman 1964, p 83; Banse and Hobson 1968, p 13–14, Figure 11.

Micropodarke trilobata Hartmann-Schröder 1983, p 125–126, Figures 1–3 (holotype HZM P-17394); 1986, p 36; 1989, p 17.

Micropodarke A Pleijel 1998, Figure 13A–F.

Micropodarke sp. Mackie et al. in press.

Material examined

Japan: lectotype (UUZM 674a1), paralectotype (UUZM 674a2), paralectotype (UUZM 674b), two or three paralectotypes (UUZM 674c; see Remarks), east Honshu, Sagami Bay, Misaki, 450 m, collector S. Bock, 29 June 1914; one specimen (FP), west Kyushu, Isahaya Bay, Konagai-cho, Isaki, collector H. Yamashita, 27 April 1995; seven specimens plus three mounted for SEM (FP), east Honshu, south-west Miura Peninsula, near Misaki Marine Biological Station, 35°09.3'N, 139°36.8'E, intertidal, sand, collectors FP and GWR, 14 May 1998; one specimen plus two mounted for SEM (FP), east Honshu, south-west Miura Peninsula, near Misaki Marine Biological Station, 35°09.6'N, 139°36.8'E, 10 m, sand among rocks, scuba, collector FP and GWR, 15 May 1998; hundreds of specimens, ca 15 mounted for SEM, three fixed for DNA analyses (two used) (FP), east Honshu, south-west Miura Peninsula, near Misaki Marine Biological Station, 35°09.3'N,

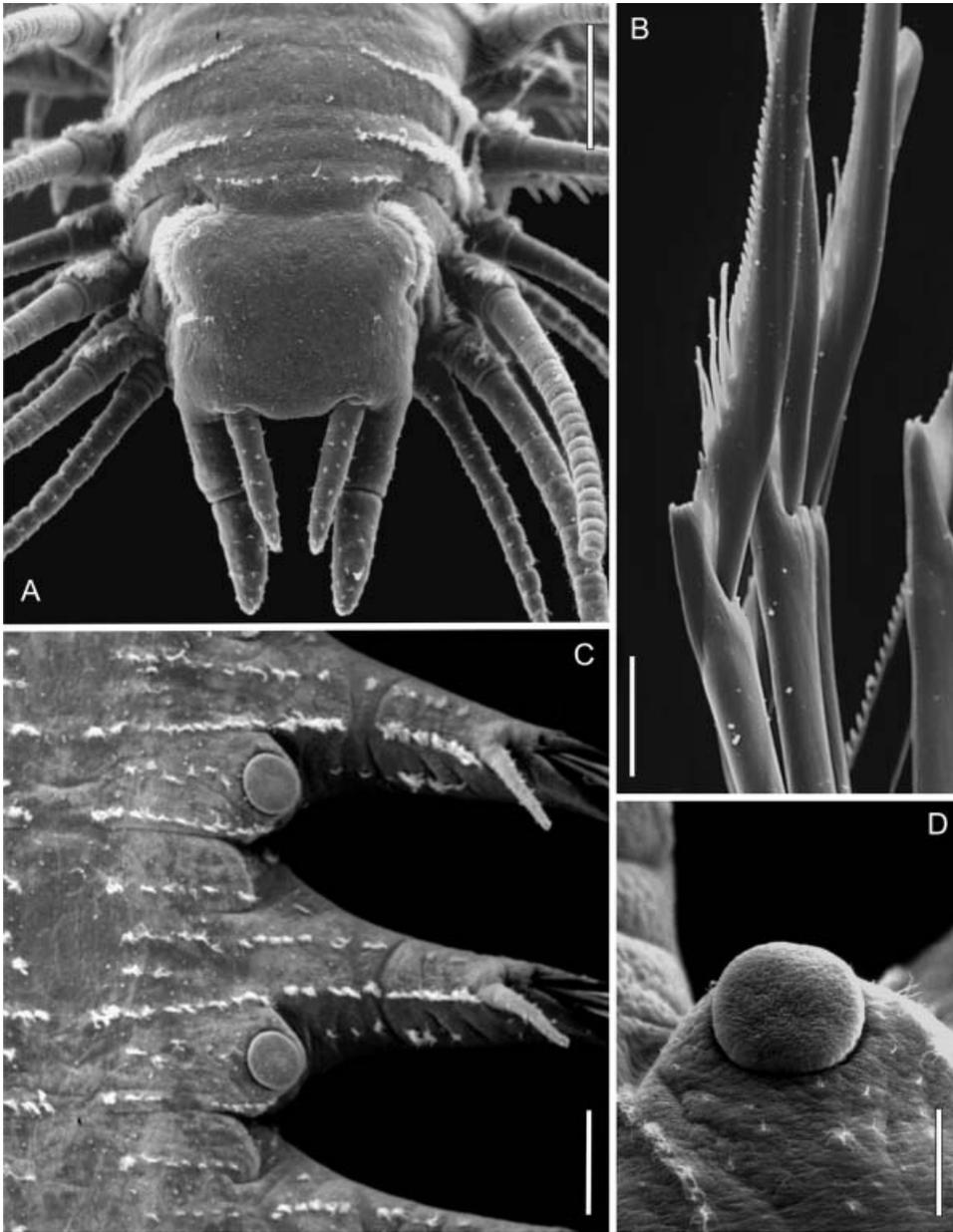


Figure 2. SEM pictures of *Micropodarke dubia* from Sagami Bay, Japan. (A) Anterior end, dorsal view; (B) median neurochaetae, showing blade with prolonged basal teeth; (C) adhesive papillae, left side, ventral view; (D) close-up of adhesive papilla. Scale bars: 0.1 mm (A, C); 10 μ m (B); 50 μ m (D).

139°36.8'E, intertidal, coarse sand with some detritus, collectors FP and GWR, 16 May 1998; three specimens, east Honshu, Sagami Bay, 35°07.9'N, 139°36.2'E, 44 m, fine shell sand, dredge, collector FP, 19 May 1998; 10 specimens (FP), east Honshu, Tanabe Bay, 33°41'N, 135°20'E, collectors FP and GWR, 26–30 May 1998; two specimens (FP), east Honshu, Kanagawa, Odawa Bay, seagrass bed, 12 October 2001. **China, Hong Kong:**

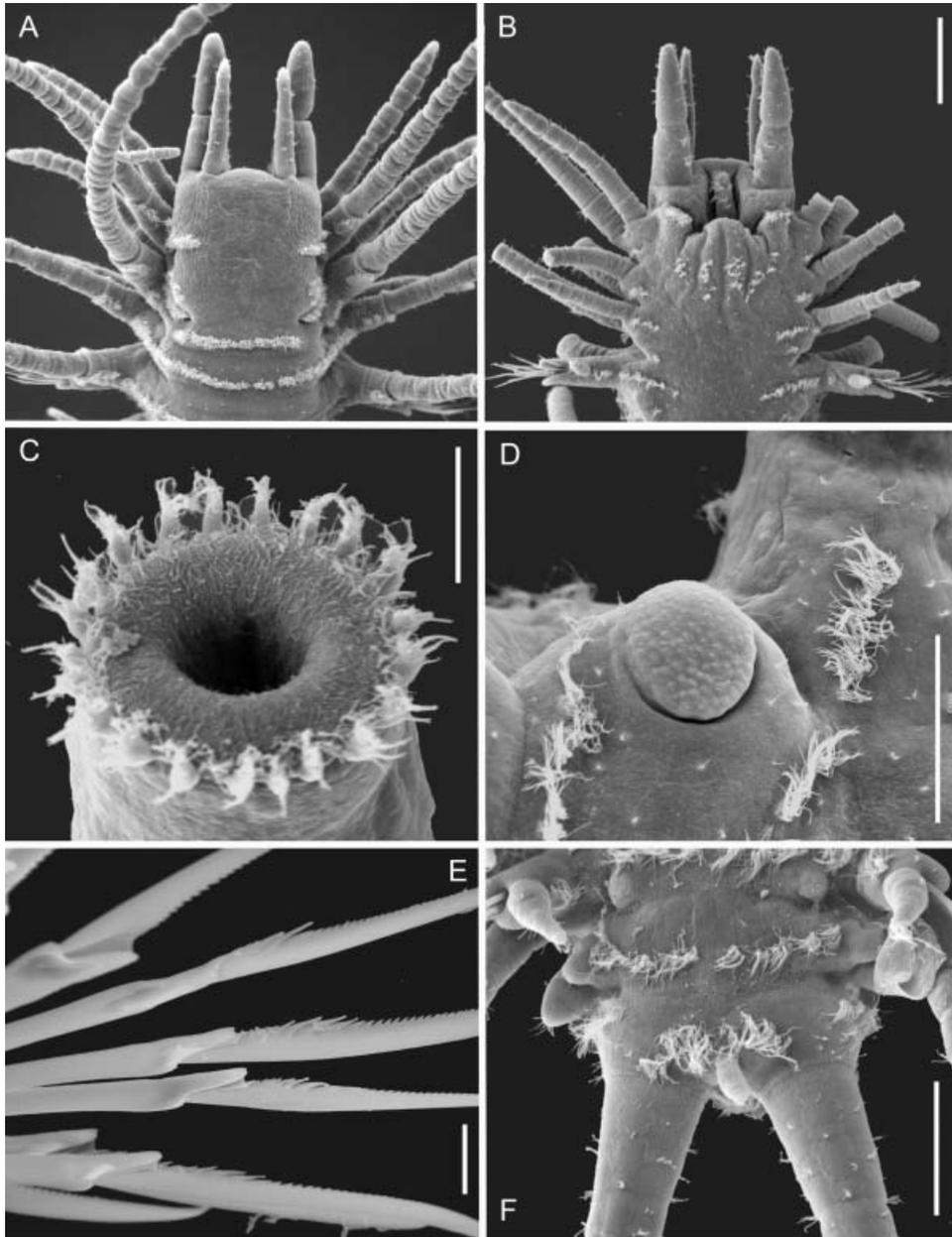


Figure 3. SEM pictures of *Micropodarke dubia* from Hong Kong. (A) Anterior end, dorsal view; (B) anterior end, ventral view; (C) terminal part of everted proboscis; (D) adhesive papilla; (E) chaetae from median parapodium, blades with prolonged teeth in the middle; (F) posterior end, ventral view. Scale bars: 0.1 mm (B, A same scale); 0.05 mm (C, D, F); 10 μ m (E).

several hundreds of specimens, four specimens fixed for DNA analyses, ca 10 specimens mounted for SEM, eight specimens mounted on slides (FP), Lobster Bay, Cape D'Aquilar, 22°12.4'N, 114°15.5'E, low tide, sand, collectors FP and TD, 10–15 July 1995. **Papua New Guinea, Madang:** one specimen (FP), south-west Wongat Island, 05°08.7'S,

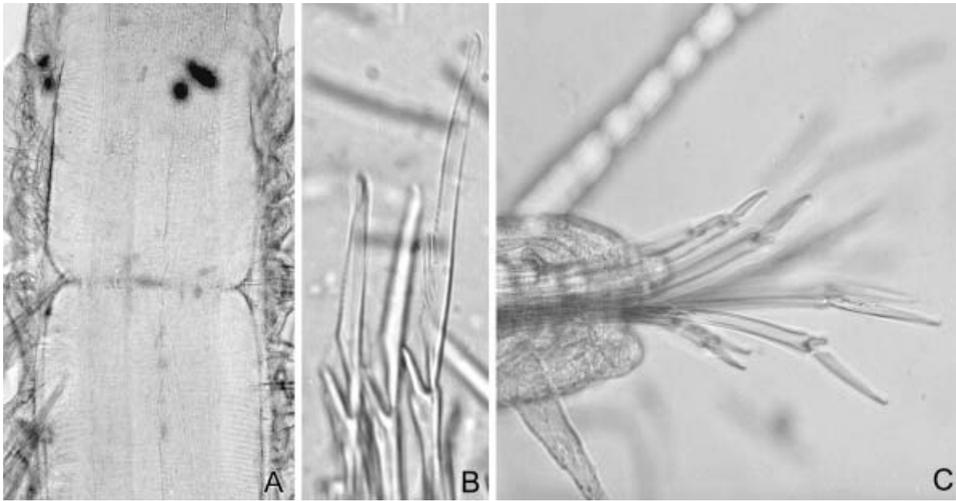


Figure 4. LM pictures of *Micropodarke dubia* from Hong Kong. (A) Anterior end, showing proboscis diaphragm, eyes visible as dark spots on top of picture; (B) Chaetae, median parapodium; (C) median parapodium, ventro-lateral view. Scales unknown.

145°49.6'E, 7 m, scuba, collector FP, 18 December 1994; ca 40 specimens, three specimens mounted on slides, ca 10 specimens mounted for SEM (FP), west Tab Island, 05°10.5'S, 145°50.10'E, 11 m, coral sand, scuba, collector FP, 18 December 1994 to 6 January 1995. **Australia, Great Barrier Reef, Lizard Island:** ca 25 specimens (FP), North Point, 14°38.78'S, 145°27.21'E, 5–9 m, coral sand, scuba, collectors FP and GWR, 17–23 March, 2000; eight specimens (FP), Entrance Lagoon, 14°41.32'S, 145°28.06'E, 5–7 m, coral sand, scuba, collectors FP and GWR, 18 March 2000; eight specimens, 11 specimens mounted on slides (FP), Loomis Beach, 14°40.88'S, 145°26.89'E, 1 m, coarse sand, scuba, collectors FP and GWR, 19–20 March 2000; ca 35 specimens, one specimen mounted on slide, 13 specimens mounted for SEM (FP), north Palfrey Island, 14°41.28'S, 145°26.64'E, 3–4 m, sand, scuba, collectors FP and GWR, 22 March 2000; ca 25 specimens (FP), Bommie Bay, 14°39.13'S, 145°28.03'E, 10–18 m, coral sand, scuba, collectors FP and GWR, 25 March 2000; ca 50 specimens, 13 specimens mounted for SEM, five specimens fixed for DNA analyses (FP), between Palfrey Island and South Island, 14°42.0'S, 145°26.3E, 6 m, coral sand, scuba, collectors FP and GWR, 27 March 2000. **Australia, New South Wales, Sydney:** one specimen (FP), Bondi Beach, north side, low tide, sand and gravel, collector FP, 5 December 1996. **Western Australia:** two specimens (HZM P-18727), Adelaide, Hallett Cove, intertidally, rock-pool, collector GHS, 13 December 1975; four specimens (FP), one preserved for DNA analyses, Gulf of St. Vincent, Yorke Peninsula, Edithburg jetty, 35°05'10.172'S, 137°44.825'E, 3–6 m, mixed sand and gravel, scuba, collector GWR, 20 July 2003; five specimens, three preserved for DNA analyses (FP), same locality and substratum, scuba, collectors FP and GWR, 28 February to 8 March 2004. **South-west Australia, Dunsborough:** holotype of *M. trilobata*, anterior fragment of 17 segments (HZM P-17394), upper sublittoral, among *Posidonia* and *Halophila*, collector GHS, 9 November 1975. **Loyalty Islands, Lifou:** ca 60 specimens, seven specimens mounted on slides, three fixed for DNA analyses (used) (FP), west Xépénéhé, 20°46.83'S, 167°08.20'E, 2–3 m, sand and rubble, scuba, collector FP, 5–27 November 2000. **USA, Hawaii Islands, Oahu:** five specimens (UHM), south-west

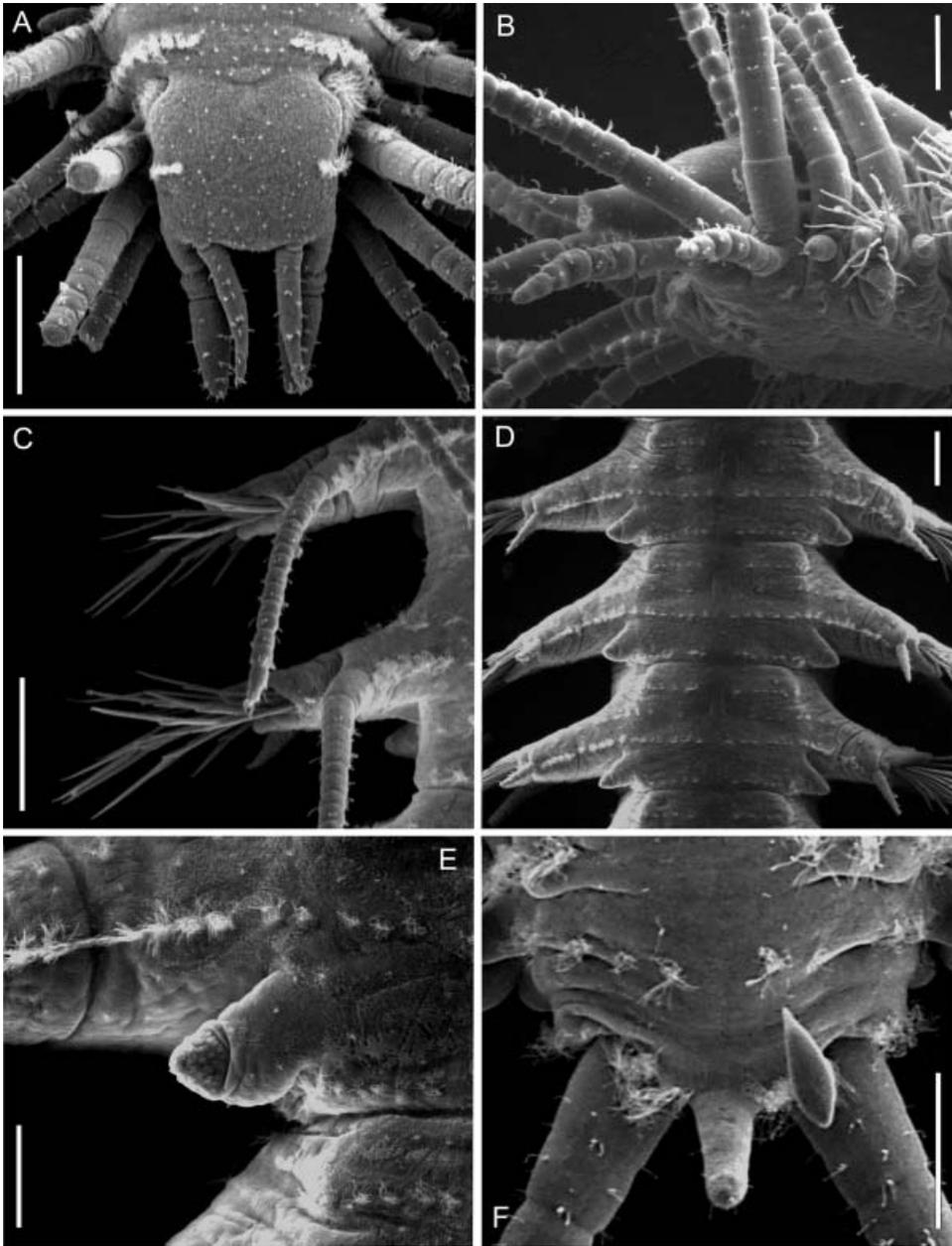


Figure 5. SEM pictures of *Micropodarke dubia* from California. (A) Anterior end, dorsal view; (B) anterior end, left side; (C) median parapodia, left side, dorsal view; ventral cirri segment 3 is regenerating; first adhesive papilla visible behind neuropodium segment 3; (D) median parapodia, ventral view; (E) adhesive papilla; (F) posterior end, ventral view; the elongated, attached object on the right side is an unknown commensal. Scale bars: 100 μm (A, C, D); 50 μm (B, E, F).

Oahu, Barber's Point outfall, 21°15.49'N, 158°03.255'W, 61 m, collectors CHOT; two specimens (UHM), Sand Island outfall, 21°17.01'N, 157°54.40'W, 70 m, collectors CHOT; ca 25 specimens (UHM), west Oahu, Waianae sewage outfall, 21°23.305'N,

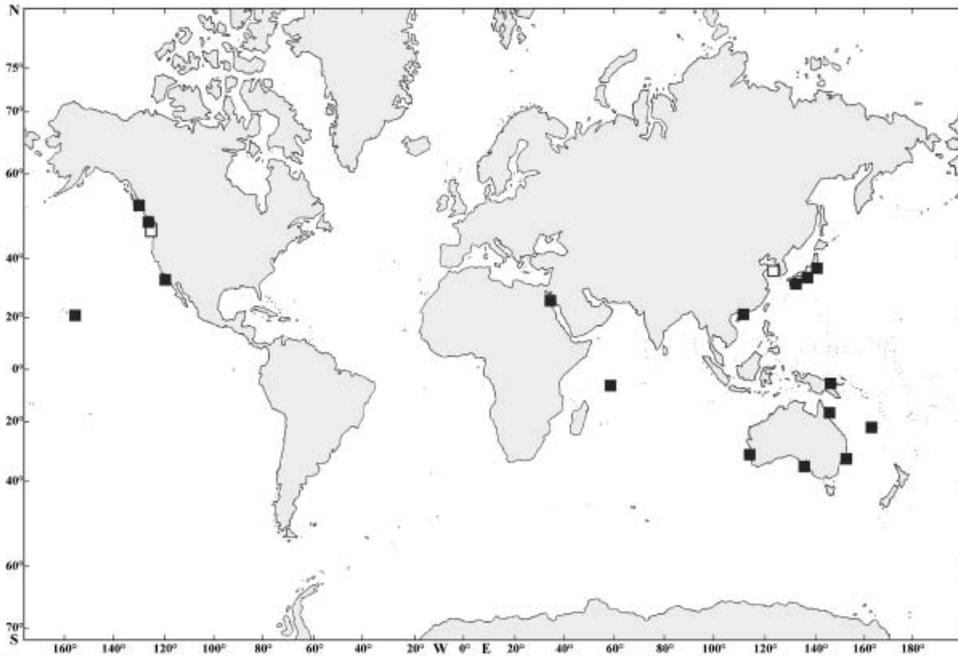


Figure 6. Geographical distribution of *Micropodarke dubia*. (■) Represents records based on examined specimens and (□) records from the literature.

158°11.277'W, 33 m, collector CHOT; six specimens (UHM), west Oahu, Waianae sewage outfall, 21°25.224'N, 158°11.52'W, 33 m, collectors CHOT. **USA, California:** ca 25 specimens, including one specimen mounted for SEM (FP), Santa Monica Bay, Palos Verdes shelf, 33°44.4720'N, 118°25.2780'W, 30 m, coarse sand, grab, collector FP, 16 January 1997; ca 25 specimens, one specimen mounted on slide, four mounted for SEM (FP), Santa Monica Bay, Palos Verdes shelf, 33°45.9000'N, 118°26.1180'W, 31 m, coarse sand, grab, collector FP and LH, 17 January 1997; seven specimens (FP), Los Angeles, Torrance, 33°48.588'N, 118°24.599'W, 20 m, sand, scuba, collector FP, 18 January 1997; two specimens mounted for SEM (FP), La Jolla, off Scripps Institution of Oceanography, ca 10 m, *Macrocystis* holdfasts, scuba, 10 January, 1997. **Canada, British Columbia:** ca 50 specimens (FP), west of Dundas Island, 54°33'N, 130°57.50'W, collector D. E. McAllister, 15 June 1965; ca 50 specimens (FP), Saanich Inlet, Mill Bay, collector K. E. Conlan, 28 April to 1 May 1975; one specimen (NMCA NMCIC 1983-0272), Hecata Strait, 53°25.0'N, 131°12.1'W, 29 m, collector J. Madill, 19 June 1983; hundreds of specimens, 10 mounted on slides (FP), outside Vancouver Island, Piper's Lagoon, 49°13.12'N, 123°57.2'W, 3 m, shell sand and gravel, scuba, collectors FP and LH, 28 January 1997. **Egypt, Hurghada:** seven specimens (FP), off Phenon Island, 8 m, coral sand, scuba, collector FP, 10 October 1990. **Seychelles Islands:** two anterior ends and three fragments (NMW.Z.2000.020.0168), south-east Mahé, east of Anse aux Pins, 4°41.20'S, 55°32.17'E, 20 m, fine and medium sand and coral, van Veen grab, collector NMW, 7 March 2000; two anterior ends and one fragment (NMW.Z.2000.020.169), north-east Mahé, 4°32.34'S, 55°34.08'E, 35 m, silty coarse sand, van Veen grab, collector NMW, 8 March 2000; one anterior end (NMW.Z.2000.020.170), north-east Mahé, 4°32.33'S, 55°34.14'E, 35 m, silty coarse sand, van Veen grab, collector NMW, 8 March

2000; one anterior end and one fragment (NMW.Z.2000.020.171), north-east Mahé, 4°36.97'S, 55°32.22'E, 25 m, medium coarse calcareous sand, van Veen grab, collector NMW, 8 March 2000; one anterior end (NMW.Z.2000.020.172), north-west Mahé, Baie Beau Vallon, 4°36.33'S, 55°24.98'E, 27 m, sand, van Veen grab, collector NMW, 9 March 2000; one anterior end and two posterior fragments (NMW.Z.2000.020.173), west Mahé, Anse à la Mouche, 4°44.16'S, 55°28.32'E, 27 m, muddy sand, van Veen grab, collector NMW, 9 March 2000; one anterior end and one median fragment (NMW.Z.2000.020.174), between Cerf and Mahé, 14 m, coarse coral sand and fine sand, van Veen grab, collector NMW, 20 March 2000.

Apomorphies

Presence of proboscis diaphragm, segmental ventral adhesive papillae, distally knobbed and slightly curved neuroaciculae, and three to six median neurochaetae with few, basally situated prolonged teeth ("spurs"), with abrupt transition to following, much shorter teeth.

Description

Longest, complete specimens observed 20 mm long for 66 segments; for further measurements, see Figure 1. Body outline long and thin, anteriorly truncate, posteriorly evenly tapered. Prostomium rounded quadrangular (Figures 2A, 3A, 5A) posteriorly without distinct incision, poorly delineated towards following segment. Palpophores cylindrical, slightly tapered, as long as palpostyles (Figures 2A, 3A, B, 5A). Palpostyles tapered to rounded tips. Paired antennae thinner and slightly shorter than palps, evenly tapered to rounded tips. Eyes medium-sized with lenses, anterior pair much larger than posterior pair, kidney-shaped, posterior pair rounded. Nuchal organs short, lateral (Figures 2A, 3A, 5A). Peristomium only visible ventrally as lips. Distinct facial tubercle absent, although small ciliated fold may be present (Figure 3B). Proboscis smooth and unarmed, divided into proximal and distal part by concentric groove, anteriorly ending in ring of 20–25 elongated ciliated papillae (Figure 3C). Proboscis diaphragm situated between segments 6 and 7 (Figure 4A) and proboscis posteriorly extending to segments 9 to 10, in non-everted condition. Segment 1 not visible dorsally, segment 2 narrower than following segments. Dorsal cirri segments 1–5 enlarged and prolonged compared to following segments, reaching ca segments 5–6, 7–9, 6–7, 8, and 7–10, respectively. Ventral cirri segments 1–3 thin, similar in size to each other, much longer than on following segments, with well-developed cirrophores, reaching ca segments 4–6 (Figures 3B, 5B). Ventral cirri segment 4 similar to following ones (Figure 3B). Cirrophores of all cirri segments 1–3 with several aciculae. Neuropodia and neurochaetae from segment 4 (Figures 3B, 5B). Dorsal cirri on segments 5, 8, 10, 12, 15, 17, 20, (22), 23, (25), 26, 28, 30, 32, 34, and 36 dorsally orientated and elongated (intermediate conditions within parentheses), dorsal cirri of other segments shorter and more laterally orientated. All dorsal cirri distinctly annulated, proximal rings about as long as wide or wider, distal rings relatively longer. Notopodia without notochaetae, with one or two notoaciculae with blunt tips. Neuropodia with ventrally positioned small rounded triangular pre- and postchaetal lobes, prechaetal lobe larger than postchaetal. Neuroaciculae one or two, tips rounded, slightly knobbed and bent (see Figure 2 in Hartmann-Schröder 1983). Neurochaetae 12–30 (Figures 3E, 4B, C). Median neurochaetae with longer blades than dorsal and ventral ones; ventralmost ones shortest, length less than half of longest median ones. Three to six median

neurochaetae with few, basally situated prolonged teeth (“spurs”), with abrupt transition to following, much shorter teeth (Figures 2B, 3E, 4B). Chaetal shafts and aciculae internally chambered. Ventral cirri evenly tapered without distinct annulation, inserted subdistally on neuropodium, without cirrophores (Figures 2C, 5D). Paired ventral adhesive papillae from segment 4 and backwards (Figure 5B), situated postero-laterally on each segment (Figures 2C, D, 3D, 5D, E). Papillophores and papillostyles distinct, papillostyles with large number of small glandular pores. Shape of papillae varying from low pads to elongated cirri-form (Figures 2E, 3D, 5F; see Remarks). Pygidium with pair of cirri, similar to dorsal cirri, median papilla present (Figures 3F, 5F).

Reproduction

Banse and Hobson (1968) reported a mature female in May from Washington, with egg size up to 60 µm. We have collected specimens approaching maturity in July in Hong Kong and in November in New Caledonia. The eggs are transparent to faint rose, and the egg size agrees with Banse and Hobson’s observation. Males from Hong Kong had spermatids in large clusters, though no mature sperm were present.

Colour

Live specimens transparent, without pigmentation. Posteriormost part of gut with white pigmentation. Eyes light red to orange. Preserved specimens more opaque, eyes darker red.

Distribution and habitat

Micropodarke dubia is mainly distributed in warm-temperate and tropical regions (Figure 6). Notably there are no current records from the whole Atlantic, the Pacific coast of South America, the Arctic, and the Antarctic. As presently known it is vertically distributed from the intertidal down to 450 m, and occurs in well-sorted sand and muddy sand; it may occur in high densities on sandy beaches.

Remarks

Hessle’s syntypes were originally separated in four tubes, UUZM 674a–d. Of these, 674a contains two specimens in good condition, tube 674b a specimen without head or posterior end, tube 674c an anterior end, but also two nereidid pieces, and tube 674d is empty. One of the specimens from UUZM 674a is here selected as lectotype, and obtains the new museum number UUZM 674a1.

There appears to be no type material of *M. amemiyai*. Nevertheless, a neotype designation would serve little purpose, since at present there are no doubts regarding the identity of *M. amemiyai* and its synonymy with *M. dubia*. The type localities are virtually the same, both being located in Sagami Bay on east Honshu in Japan, and examination of a large number of specimens from this area provided no evidence that several *Micropodarke* species may be involved.

Banse and Hobson (1968) included a description of *M. dubia*, which clearly agrees with the description above, as well as with specimens collected from the same area. Their remarks on *M. amemiyai*, however, appear confused. They interpreted the statement “uniramous parapodia” in Okuda’s (1938) original description to mean lack of

notoaciculæ, but this is likely to be incorrect, since Okuda made no explicit mention or drawing of either noto- or neuroaciculæ. Furthermore, Banse and Hobson argued that lack of notoaciculæ and presence of additional parapodial lobes (=ventral adhesive papillæ) would indicate a close relationship to *Nereimyra*, but none of these features are present in this taxon. In fact, notoaciculæ are present in all hesionids described to date.

Hartmann-Schröder (1983) described *M. trilobata* from Dunsborough, south-west Australia, based on an anterior fragment in poor condition. The new species was justified by differences in the shapes of the neuropodia, the prostomium, and the adhesive papilla. Although it is unclear on what descriptions or specimens she based her comparisons, none of these differences could be corroborated from examinations of the type and her additional specimens (see Hartmann-Schröder 1986, 1989), other Australian specimens, and topotypes of *M. dubia*. Contrary to her description, the parapodia have one pre- and one postchaetal lobe, the prostomium lacks a distinct posterior incision, and the ventral part of the neuropodium has the same form as other *M. dubia*. Since no other consistent differences were observed, *M. trilobata* is here treated as a junior synonym of *M. dubia*.

Populations from the west coast of North America differ from other *M. dubia* in having much longer adhesive papillæ (Figure 5D, E) and a slightly larger number of chaetae (often 20–28).

Live specimens of *M. dubia* can often be distinguished from other hesionids in samples by their habit of coiling up when disturbed. This may be related to the fact that they often live in unstable sediments that are exposed to waves and currents, and coiling up around sand grains or larger particles and attaching to them by means of the adhesive glands prevents them from being swept away.

Discussion

Following Pleijel (1998), *Micropodarke* belongs to Psamathini, which includes also *Hesiospina* Imajima and Hartman, 1965, *Psamathe* Johnston, 1836, *Bonuania* Pillai, 1965, *Nereimyra* Blainville, 1828, *Sirsoe* Pleijel, 1998, and *Syllidia* Quatrefages, 1866, and where it is sister to the latter four. The relationships within Psamathini are currently not well supported and require further studies. Although it was based on erroneous observations (see above), the suggestion by Banse and Hobson (1968) that *Micropodarke* and *Nereimyra* may be closely related can therefore not be excluded at present.

The monophyly of *Micropodarke*, as noted above, is supported by four apomorphies: the proboscis diaphragm, segmental ventral adhesive papillæ, distally knobbed and slightly curved neuroaciculæ, and median neurochaetae with few, basally situated prolonged teeth (“spurs”), which have an abrupt transition to the following and much shorter teeth, even though several of these features may be homoplastic. For instance, a similar proboscis diaphragm may also be present within *Podarkeopsis* Laubier, 1961 (although this warrants further investigation), segmental ventral adhesive papillæ are present also in *Simoehesione genitaliphora* Westheide, Purschke and Mangerich, 1994, and distally truncated aciculæ are present also in *Heteropodarke* (Pleijel, 1999). In spite of these homoplastic occurrences, we consider *M. dubia* well supported, since none of the other taxa where these features occur are closely related (see Pleijel 1998). The fourth apomorphy, the prolonged teeth (“spurs”), is highly characteristic and members of *M. dubia* can readily be identified from this feature. Nevertheless, prolonged teeth do occur also within other Psamathini, such as *Psamathe* (Pleijel 1998, Figure 17F) and *Hesiospina* (Pleijel 2004), and, although absent in many other hesionids, also in the more distant groups Chrysopetalidae (personal

observation) and Nereididae (Glasby 1999). In all these taxa, however, the blades differ in that the length of the teeth is less extreme, and in that they lack the abrupt transition to shorter teeth.

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