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Revision of *Marenzelleria* Mesnil, 1896 (Spionidae, Polychaeta)

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SARSIA

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Marenzelleria is revised on the basis of material from the Arctic, North America, Europe and the Far East. Types of all species included in the genus are examined. Five species are registered. *Marenzelleria neglecta* sp. nov. is described from the coastal waters of the southern Baltic. Two species, *M. arctia* and *M. wireni*, occur in the Arctic, whereas *M. viridis* and *Marenzelleria* sp. A are found in coastal waters of the Atlantic. *Marenzelleria neglecta* occurs both in arctic and boreal estuaries. Complete description of *Marenzelleria* sp. A must await additional material. A generic diagnosis and a key to the species are given.

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INTRODUCTION

The classification within the genus *Marenzelleria* presents many difficulties as there are only a few external characters suitable for classification. In general, three to four extremely variable numerical characters are used and these overlap in different species, thus making correct identification nearly impossible. However, the invasive nature of some members of the genus has made it increasingly important to identify the different species of this group, particularly in environmental assessment studies. Seven valid species names actually belonging to the genus are known (see "Historical review"). The names are often used incorrectly (see the lists of synonyms below). Many papers have been published over the past two decades on the genus *Marenzelleria* [Leling 1986; Bick & Zettler 1997; Sikorski & Buzhinskaya 1998; see list in Zettler (1997) for more], particularly in Europe. This interest arises mainly from the detailed investigations of problems stemming from the invasion of North American *Marenzelleria* spp. into the North Sea and Baltic Sea in the late 1970s and early 1980s. The introduced species have become an important faunistic element. Therefore, most studies have concentrated on their distribution in the North Sea and Baltic Sea, as well as on the Atlantic coast of North America. *Marenzelleria* has also been recorded after introduction by man, from the San Joaquin Delta, California, the Pacific coast of North America (identified as *M. viridis* by Cohen & Carlton 1995). The need to identify *Marenzelleria* correctly has prompted a revision of the genus based on a morphological examination of all *Marenzelleria* types and material available to us. The investigation presented here attempts to resolve the taxonomic problems as far as practicable, to provide clear descriptions of all species to facilitate future investigations and to clarify the area of distribution of these species.

MATERIAL AND METHODS

All available European and North American material of *Marenzelleria* has been examined, consisting of, in total, 180 samples and ~3000 specimens from the following sources: Zoological Museum, Rostock University, Germany (ZSRO): 22 samples, 402 specimens; Zoological Museum, Moscow State University, Russia (ZMUM): 90 samples, ~1430 specimens; Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia (ZISP): 48 samples, ~880 specimens; National Museum of Natural History, Washington DC, USA (USNM): three samples, 100+ specimens; Swedish Museum of Natural History, Stockholm, Sweden (SMNH): three samples, 12 specimens; Zoological Museum of the Hamburg University, Germany (ZMH): five samples, 15 specimens; Peabody Museum, Yale University, New Haven, Connecticut, USA (PYM): five samples, 33 specimens; Zoological Museum,

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University of Copenhagen, Denmark (ZMUC): one sample, one specimen; Museum of Comparative Zoology, Harvard University, Boston, New England, USA (MCZ): two samples, one specimen; Scripps Institution of Oceanography, La Jolla, California, USA (SIO): one to 13. In addition, about 300 specimens from 15 sites were collected for this investigation from the Atlantic coast of North America and from the North, Baltic, Barents and White Seas.

The following abbreviations are used for the numerical characters examined: VHH, first setiger with neuropodial/ventral hooded hooks; DHH, first setiger with notopodial/dorsal hooded hooks; Br, last setiger with branchiae; NO, last setiger with nuchal organs.

To obtain further diagnostic characters, arithmetical differences were calculated from the above-mentioned features: Br–VHH, Br–DHH and DHH–VHH. First setiger with ventral inferior tuft of neuropodium (according to the terminology given in Radashevsky & Fauchald 2000) bearing sabre setae is not a reliably distinguished character and thus not very useful in providing distinctions within the genus. All listed characters are size dependent. Width, length and number of setigers (in case of complete specimens) are used as parameters of size, but width is used in most cases as complete specimens are generally very rare in fixed material. We measured the width of the body (minus parapodia) at setiger 10.

Scanning electron microscopy (SEM) was used for detailed descriptions. For SEM studies, specimens were dehydrated in a critical point drier, attached to a stub and sputter-coated with gold palladium. SEM observations were made with a Zeiss DSM 960A.

HISTORICAL REVIEW

In 1873, A. E. Verrill described two species, *Scolecolepis viridis* and *Sc. tenuis*, from the Atlantic coast of North America between Rhode Island and New Jersey. They were found together and declared to be inhabitants of sandy bottoms at low water. According to the descriptions, they had hooded hooks in both rami of the parapodia and the notopodial post-setal lamellae of the anterior setigers were connected, for most of their length, with the branchiae (in *Sc. viridis* at least). Branchiae occurred only on anterior segments ("on about 100 segments" in *Sc. viridis*) and the shape of the prostomium was described in both species.

von Marenzeller (1892) described a specimen that, in his opinion, resembled *Sc. vulgaris* depicted by Cunningham & Ramage (1888), but did not give it a name. Mesnil (1896) erected the new genus *Marenzelleria*, characterized by the presence of anterolateral prostomial horns, notopodial hooks and branchiae starting from setiger 2. The new generic description was based on von Marenzeller's specimen only, but, like von Marenzeller, he did not name the species. He suggested that the arctic spionid worm, poorly described and named as *Nerine vulgaris* by Wirén (1883), might also belong to *Marenzelleria*. Thus, at that time, there was no described species belonging to the genus. Augener (1913) described a new species, *M. wireni*, based on new material from Franz Joseph Land (Flora Cap) obtained by the Scottish expedition of Professor W. S. Bruce in 1896–1897, on material from the Swedish "Vega" expedition in 1878 (Wirén 1883) and on one specimen from Spitsbergen (von Marenzeller 1892). In spite of the absence of anterolateral horns (he supposed they might have been lost) and branchiae starting from setiger 1, he placed the species in *Marenzelleria* and suggested (rather than specified) that *M. wireni* should be considered as the type species of the genus.

Chamberlin (1920) described a new species, *Sc. arctius*, from Colinson Point in Alaska, based on three specimens having branchiae on the anterior segments only, from setigers 1 to 29, basally fused to the notopodial post-setal lamellae and with hooks in both branches of the parapodia.

Zachs (1925) gave a very short description of a new species, *Laonice annenkovae*, from Kola Bay, in the mouth of the Tuloma River. He doubted that the species belonged to the genus *Laonice* due to the absence of such generic characteristics as the occipital tentacle, long nuchal ciliary tracts and genital pouches. It also had branchiae starting from setiger 1, prostomium widening frontally, and hooks present in both neuropodia and notopodia.

George (1966) published a description of *Sc. viridis* from intertidal mud–sand at Lawrencetown, Nova Scotia. No mention was made of other closely related species being in the samples or from the sampling area.

Holmquist (1967) examined the syntypes of *M. wireni* deposited in the Swedish Museum of Natural History and published figures of them. She supposed that her material from the freshwater Kotsebu Bay (Alaska) contained *M. wireni*. She maintained that *M. wireni* was the only species in the genus.

Foster (1971) examined the types of *Sc. arctius* and synonymized the species with *Sc. viridis*.

Fauchald (1977) mentioned *M. wireni* as the type species by monotypy.

Maciolek (1984) examined Augener's syntypes of *M. wireni* from the Hamburg Museum and published the first detailed description of the species, based also on material from the Beaufort Sea. She gave a

description of *M. viridis* and described a new species, *M. jonesi*, from Cape Henlopen on the Atlantic coast of North America. *Scolecolepis tenuis* was included in *M. viridis* as a junior synonym. She also mentioned that the type specimen of *Sc. viridis* had been lost. However, nothing was mentioned about the types of *Sc. tenuis*. She suggested that these three species belonged to *Marenzelleria*. *Scolecolepides arctius* and *L. annenkovae* were not mentioned in the paper.

Tzetlin (in Sikorski & al. 1988) moved *L. annenkovae* to *Marenzelleria* and synonymized it with *M. wireni*.

The European immigrant species was identified as *M. viridis* on the basis of Maciolek's revision (Atkins & al. 1987; Bick & Burckhardt 1989).

Rodi & Dauer (1996) synonymized *M. jonesi* with *M. viridis* sensu Maciolek (1984).

Several population genetic studies showing the presence of genetically distinct forms in the North and Baltic Seas as well as in different regions of the northeastern coast of America and at Tuktoyaktuk Harbor (Canadian Arctic), were carried out by Bastrop & al. (1995, 1997, 1998) and Röhner & al. (1996a, b). The investigations demonstrated the presence of three morphotypes on the Atlantic coast of North America: *Marenzelleria* types I, II and III (Bastrop & al. 1997). Types I and II were found together along the section of the American coast from Durham, Fox Point to Chester River including the type localities of *Sc. viridis* (from Rhode Island to New Jersey), *Sc. tenuis* (Great Egg Harbor, New Jersey) and *M. jonesi* (Cape Henlopen, Delaware). The morphological studies undertaken against this background allowed good discrimination between these species. The species were named as *Marenzelleria* cf. *wireni*, *Marenzelleria* cf. *viridis* and *Marenzelleria* sp. A, respectively (Bick & Zettler 1997). Bick & Zettler (1997) agreed with the opinion of Rodi & Dauer (1996) in treating *M. jonesi* as a junior synonym of *M. viridis* and also suggested that the syntypes of *M. wireni* might consist of two species.

Sikorski & Buzhinskaya (1998) examined the types of *Sc. arctius* and *L. annenkovae* and synonymized them with *M. arctia*, suggesting that this species was separate from *M. viridis*. They described *M. wireni* based on all the Russian arctic material and synonymized the poorly described *Spio gobunovi* Averintsev, 1990 with *M. wireni*. *Marenzelleria arctia* was also mentioned in Stoljarov 1994, Burkovsky & al. 1995 and Burkovsky & Stoljarov 1995. However, all those papers were ecological, not taxonomic (the identification of the material was done by A. Sikorski).

Thus, taking into account all the studies mentioned above, seven valid names are known to belong to the genus at present: *Scolecolepis viridis* Verrill, 1873; *Scolecolepis tenuis* Verrill, 1873; *Marenzelleria wireni* Augener, 1913; *Scolecolepides arctius* Chamberlin, 1920; *Laonice annenkovae* Zachs, 1925; *Marenzelleria jonesi* Maciolek, 1984; *Spio gorbunovi* Averintsev, 1990.

RESULTS

Marenzelleria Mesnil, 1896

Prostomium bell- or T-shaped, broadly rounded or incised anteriorly; occipital tentacle absent; two pairs of eyespots (sometimes invisible in adults). Peristomium well developed, distinctly separate from setiger 1, never forming lateral wings around prostomium. Branchiae from setiger 1, basally fused to notopodial post-setal lamellae, continuing for at least one quarter of body length. Nuchal organs comparatively short, resembling a pair of epaulettes bordered by ciliated bands, running posteriorly from bases of palps and caruncle. Anterior setae all limbate capillaries arranged in two parallel rows; neuro- and notopodial hooded hooks present posteriorly in a posterior row. Hooks in neuropodia without alternating (according to the terminology given in Radashevsky & Fauchald 2000) capillaries. Hooks bi- or tridentate; apical teeth never paired. Ventral sabre setae present but resemble long, stout capillaries; superior fascicles of long setae present in notopodia from setiger 1. Genital pouches absent. Pygidium circled by variable numbers of bilaterally symmetrical pairs of anal cirri.

Type species: *Marenzelleria wireni* Augener, 1913 (by monotypy).

Marenzelleria wireni Augener, 1913
Figs 1A–F, 2A, 3A

Marenzelleria wireni Augener, 1913:203, 267 (partim).
Spio gorbunovi Averintsev, 1990:165–166, fig. 13.
Nerine vulgaris – Wirén 1883:408 (partim).
Microspio wireni – Söderström 1920:249–250 (partim).
Marenzelleria wireni – Annenkova 1952:126; Maciolek 1984:49–51, figs 1A–G (?partim); Sikorski & al. 1988:835–837, fig. 4 (partim); Sikorski & Buzhinskaya 1998:1112–1115, fig. 1; non-Holmquist 1967:298–313; non-*Marenzelleria* cf. *wireni* – Bick & Zettler 1997: 138–141, figs 1–2.
Marenzelleria arctia – Sikorski & Buzhinskaya 1998 (partim):1115–1118.

Material examined

Thirty-seven samples including 252 specimens, and three slides.

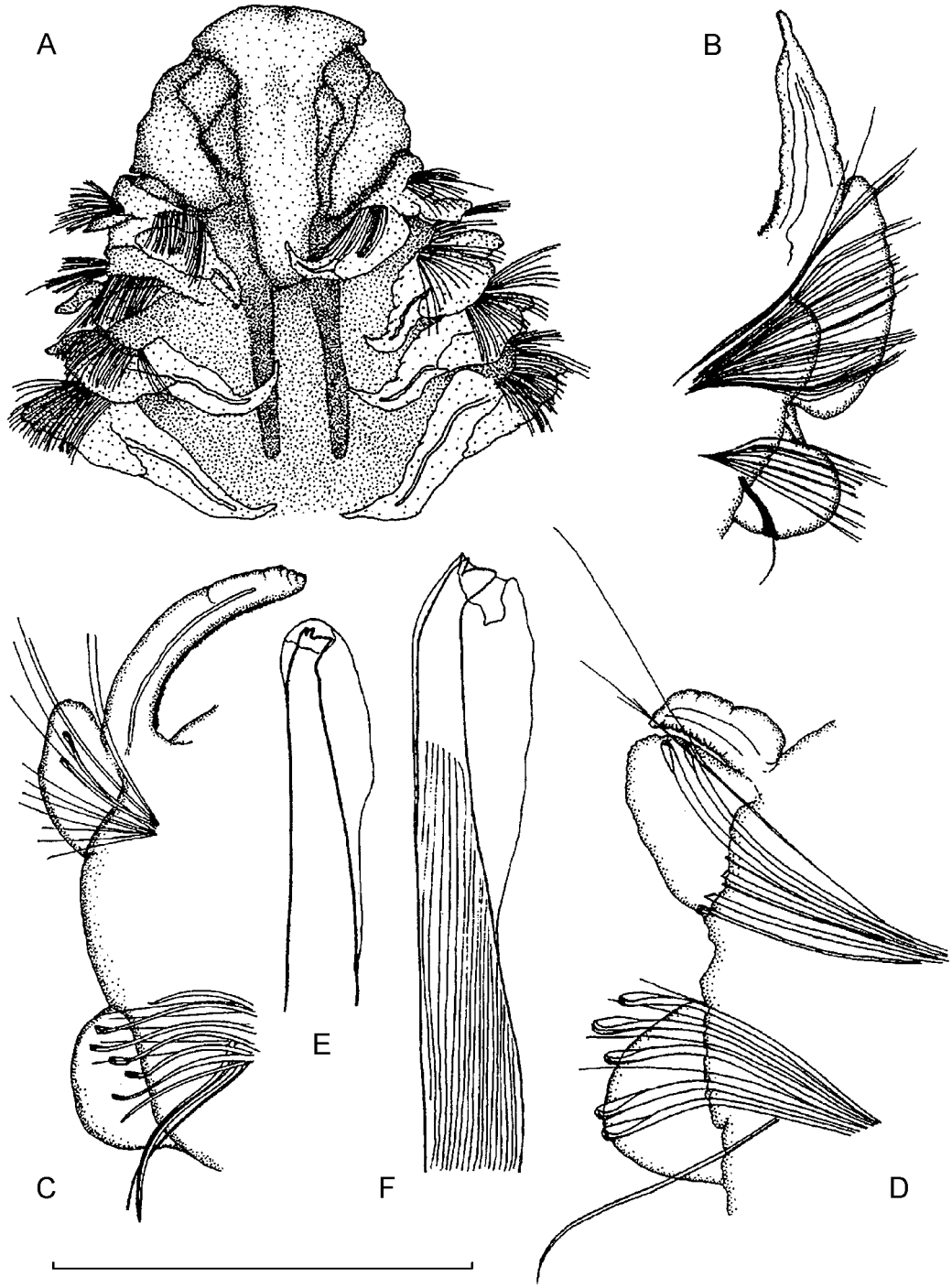

Fig. 1. *Marenzelleria wireni* Augener, 1913. A. Anterior end, dorsal view. B. Left parapodium of setiger 5, anterior view. C. Right parapodium of setiger 49, anterior view. D. Right parapodium of setiger 20 (counting from the pygidium), anterior view. E. Neuropodial hook, setiger 60. F. Neuropodial hook, setiger 20 (counting from the pygidium). Material: A – Syntype SMNH 2042; B – Syntype SMNH 4921; C – Syntype SMNH 4922; D, F – Syntype SMNH 4923; E – White Sea, 29 July 1974, ZISP, no no. Scale (mm): A = 1.2; B, C = 1; D = 0.2; E = 0.07; F = 0.06.

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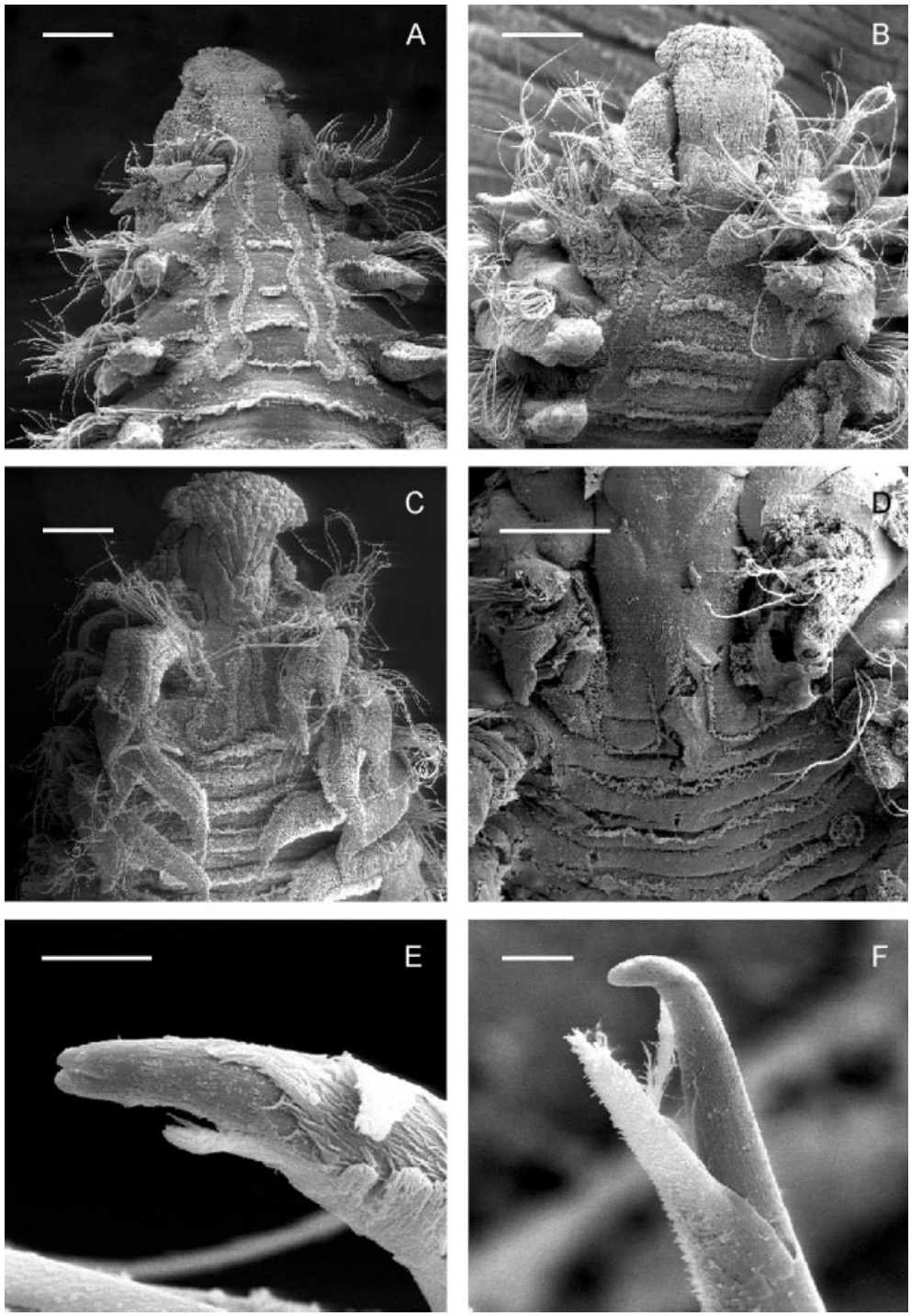

Fig. 2. Scanning electron micrographs. A. *Marenzelleria wireni*, nuchal organs. B. *Marenzelleria neglecta*, nuchal organs. C. *Marenzelleria viridis*, nuchal organs. D. *Marenzelleria arctia*, nuchal organs. E. *Marenzelleria wireni*, tip of hook. F. *Marenzelleria arctia* tip of posterior notopodial hook. Material: A, E – White Sea, "Prof. Zenkevich", Stn 113/2; B – ZSRO P-893; C – ZSRO P-33; D, F – ZSRO P-892. Scales (mm): A–D = 0.2; E, F = 0.005.

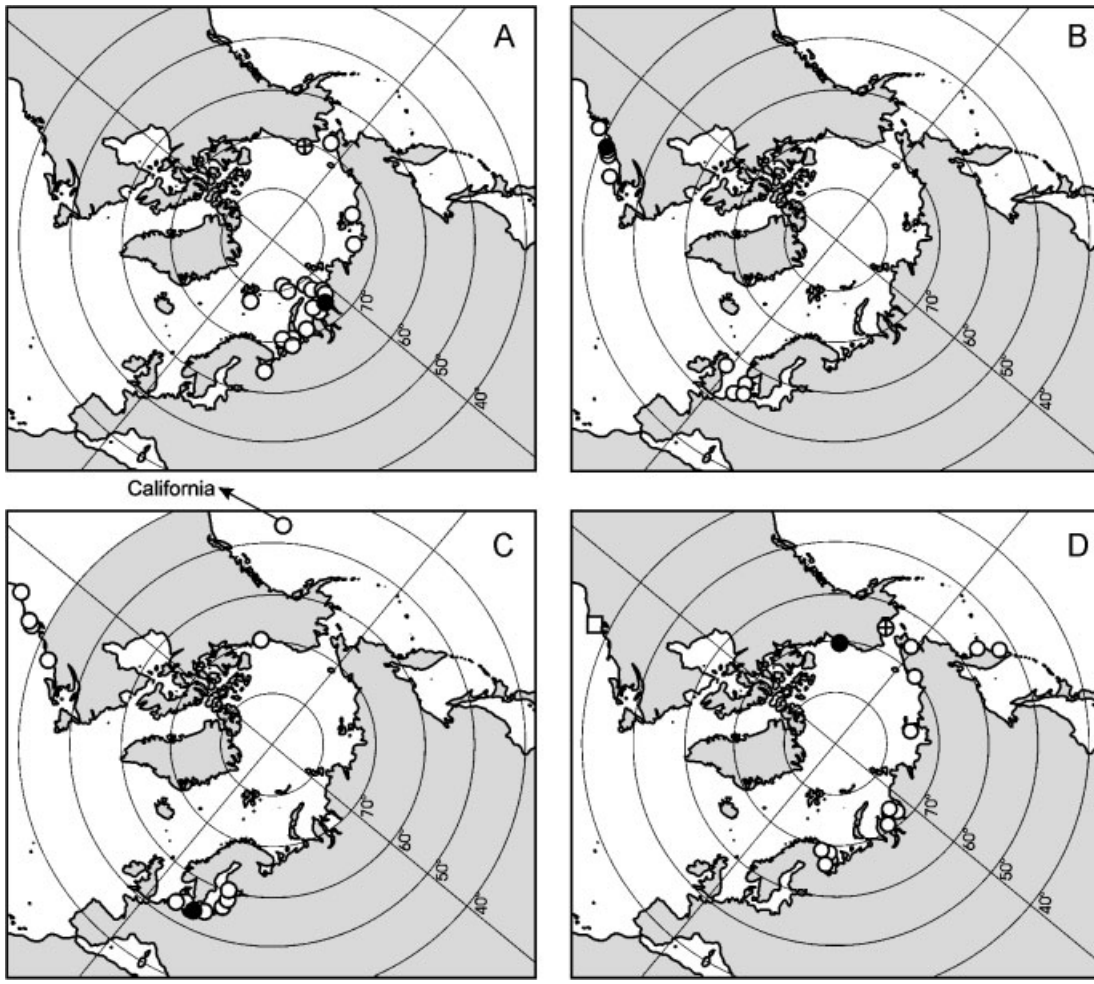

Fig. 3. Distribution of: A. *Marenzelleria wireni*; B. *M. viridis*; C. *M. neglecta*; D. *M. arctia* (circles) and *Marenzelleria* sp. A (open square). Filled circles – Type locality; Open circles – Material examined; Circle with cross inside – Literature data.

SYNTYPES: Kara Sea – "Vega" Expedition, Stn 7, 70°14′N 61°21′E, fine soft clay, 1878 (SMNH 2045, one specimen); Stn 25, anchorage of Pjasina, 74°52′N 85°08′E, 3–10 fathoms, sand with algae, 11 August 1878 (SMNH 2042, seven specimens; three slides – SMNH 4921–4923). Franz Joseph Land – Stn 3 (Cap Flora), Scottish expedition of Professor W. S. Bruce 1896–1897 [HZM PE-890, two specimens (three syntypes were in the collection, but one was lost)].

Syntype series contains also SMNH 2040 with one specimen of *Prionospio cirrifera* and one specimen of *Aricidea quadrilobata*; SMNH 2041 with four specimens of *M. arctia* and SMNH 2043 with one specimen of *L. cirrata*.

NON-TYPE MATERIAL: White Sea – Expedition of the Leningrad State University: Gridino, 65°54′N 34°40′E, 0.8 m, drag, 1946 (ZISP 13/8161, 1). – R/V *Prof. Zenkevich*: Stn 110, 5 m, 26.31‰; 96.2% sand, no pelite, 29 July 1974 (ZISP 22/49486, 1); Stn 111, 8 m, 27.11‰; 50.07% sand, 49.93% gravel, no pelite, 29 July 1974 (ZISP 23/49487, 1); Stn 113, 20 m, 27.55‰; 92% sand, 3% pelite, 5% alevrite, 29 July 1974, "Ocean-50" grab, replicants 1 and 2 (ZISP 24/49488 and 25/49489, 11 and 15); Stn 115, 8 m, 25.81‰; 76.6% sand, 23.4% alevrite, no pelite, 30 July 1974 (ZISP 25/49490, 1). Franz Joseph Land – 4.5–7 m, 8 August 1929, coll. Gorbunov (ZISP 2/25659, 1). Spitsbergen – Haketangen, Storfjorden,

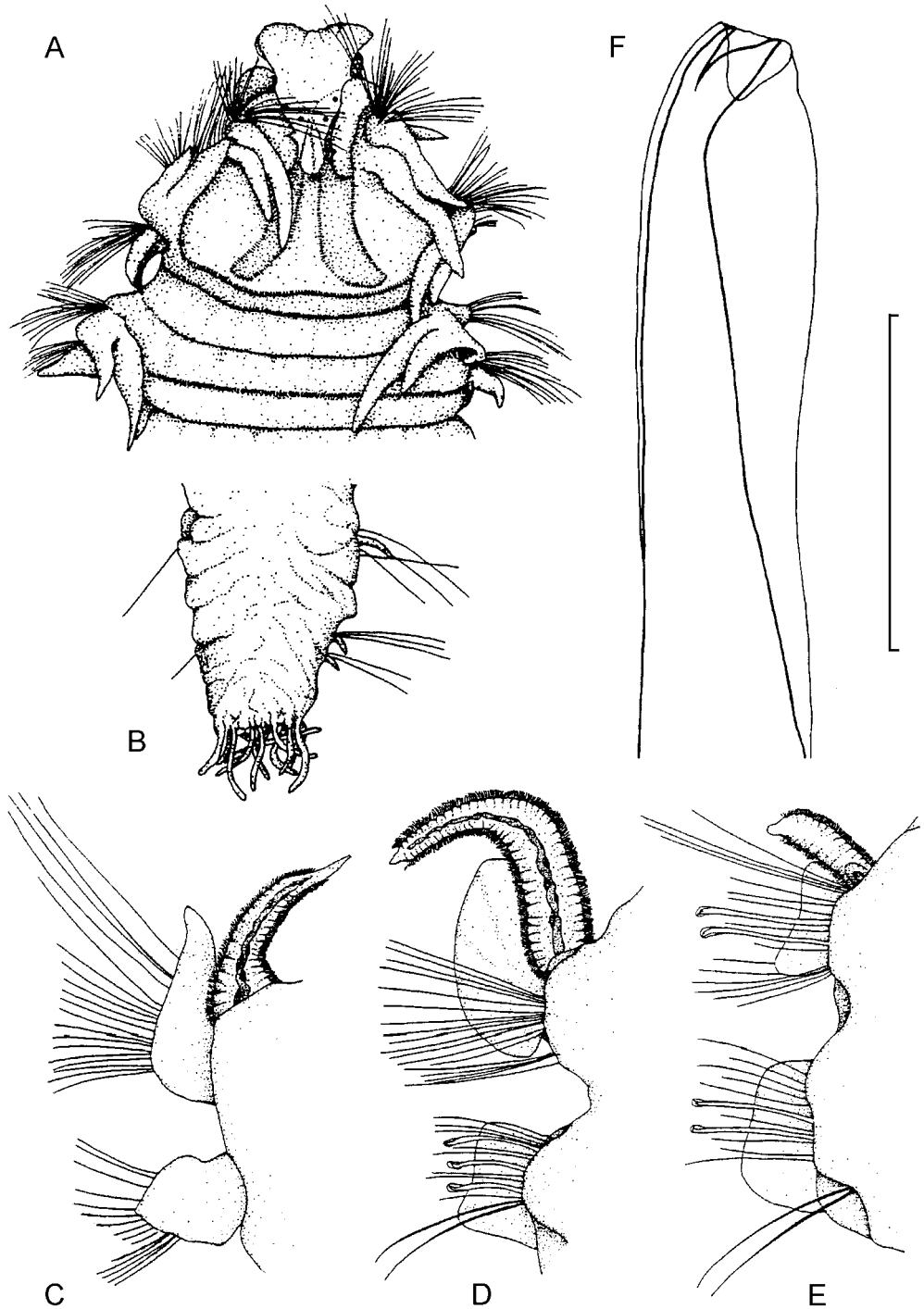

Fig. 4. *Marenzelleria viridis* (Verrill, 1873). A. Anterior end, dorsal view. B. Pygidium, dorsal view. C. Left parapodium of setiger 3, posterior view. D. Right parapodium of setiger 45, anterior view. E. Right parapodium of setiger 57, anterior view. F. Neuropodial hook, setiger 75. Material: Tay Estuary ZSRO P-33. Scale (mm): A, B = 0.9; C–E = 0.7; F = 0.026.

coll. E. Olafsson & T. Andersson (ZMUC-POL-1007, 1). Barents Sea – R/V *N. Maslov*, *Cr. 10*: Stn 8, 68°47′N 48°10′E, 14 m, 0.99 °C, coarse sand, "Ocean-50" grab, 11 August 1970 (ZMUM Pl-835, 1); Stn 50, 69°20′N 56°00′E, 18 m, 1.23 °C, sandy silt, Sigsbee trawl (ZMUM Pl-836, 1); Stn 53, 69°25′N 55°06′E, 30 m, 0.40 °C, sandy silt, "Ocean-50" grab, 18 August 1970 (ZMUM Pl-837, 5). – R/V *Pomor*, Cr. 17: Stn 4, 69°01′N 53°24′E, 25 m, clean coarse sand, −1.68 °C, 34.429‰, 15 July 1985, "Ocean-50" grab no. 1 (ZMUM Pl-825, 9; ZSRO P-328, 3); grab no. 2 (ZMUM Pl-826, 7), grab no. 3 (ZMUM Pl-827, 13); Stn 4a, 69°01′N 53°29′E, 24 m, grey silty sand with broken shells, −1.65 °C, 34.283‰, 15 July 1985, grab no. 3 (ZMUM Pl-828, 3); Stn 4b, 69°01′N 53°10′E, 26 m, clean sand, −1,24 °C, 34.363‰, 15 July 1985, grab no. 1 (ZMUM Pl-829, 14); grab no. 2 (ZMUM Pl-830, 16); grab no. 3 (ZMUM Pl-831, 9); Stn 5b, 68°08′N 50°22′E, 19 m, sand, 4.30 °C, 31.874‰, 16 July 1985, grab no. 1 (ZMUM Pl-832, 3); grab no. 2 (ZMUM Pl-833, 2); grab no. 3 (ZMUM Pl-834, 2). – R/V *GS-260*, 30 September 1998: Stn 1, 68°56′N 58°30′E, 10 m, sand (ZMUM Pl-2241, 34); Stn 2, 68°59′N 58°53′E, 6 m, sand (ZMUM Pl-2242, 7); Stn 3, 68°59′N 58°53′E, 6 m, sand (ZMUM Pl-2243, 8). Kara Sea – 74°50.8′N 86°34′E, 18 m, ooze with pebbles and coarse gravel, coll. Khmyznikov, 13 September 1930 (ZISP 7/25664, 3). – 73°36′N 78°22′E, 17 m, yellow sand with insignificant admixture of brown silt, ship trawl, coll. Gorbunov, 17 September 1931 (ZISP 6/25663, 1). – R/V *Sibirjakov*: Stn 2, 73°26.1′N 80°29.5′E, 55 m, grey sandy silt with small-sized gravel, boat drag, 3 August 1933 (ZISP no no., 7); Stn 14, 73°32′N 81°40′E, 23 m, brownish-grey silty sand, 16 August 1933 (ZISP 15/8663, 12); Stn 15, 73°32′N 81°40′E, 23 m, small-grained yellow sand with gravel, pebbles and black sandy clay, 16 August 1933 (ZISP 17/8665, 8; 21/49193, 1); Stn 17, 74°51′N 79°43′E, 11.7 m, sand with gravel and pebbles, boat grab, 18 August 1933 (ZISP 11/25668, 24). – R/V *Sedov*: Stn 43a, 78°27′N 82°23′E, 27 m, clean sand, 1934 (ZISP 18/8924, 1); Stn 43b, 78°27′N 82°23′E, 27 m, clean sand, 1934 (ZISP 19/8925, 1). Laptev Sea – Dunay Island, 3 m, silty sand, remarkable current, 20 August 1973 (ZISP 1/46765, 1 – holotype of *Spio gorbunovi* Averincev, 1990). East Siberian Sea – R/V *Temp*: Stn 20, 72°45′N 143°31′E, 6.5 m, 21 August 1934 (ZISP 12/8117, 1). Chukchi Sea – R/V *Krasin*: Stn 27, off Cap Gitletlen, 67°08′N 173°39′W, 19 m, sand, 27 August 1935 (ZISP 9/25666, 17).

Description

SYNTYPES: Ten incomplete specimens 0.9–1.9 mm wide. Two pairs of eyespots visible in five specimens. Nuchal organs extend to between anterior part of setiger 3 and middle of setiger 5. Neuropodial hooded hooks present from setigers 24 to 40; notopodial hooded hooks from setigers 30 to 53. Ventral inferior tuft of neuropodium bearing sabre setae visible from setiger 4.

All material examined

Maximum width 2.4 mm, maximum length 68 mm, maximum number of setigers 177.

Prostomium T-shaped (Fig. 1A); may be slightly bilobed in juveniles. Two pairs of eyespots on posterior part of prostomium, clearly visible in juveniles, may be obscured in adults. Eyespots larger and more widely spaced in anterior pair than in posterior one, bean-shaped. Eyespots circular in posterior pair. Caruncle short, extending posteriorly to between beginning of setiger 1 and middle of setiger 2.

Nuchal organs (Fig. 2A) extend to between anterior part of setiger 2 and middle of setiger 5 (e.g. middle of setiger 4, Fig. 1A); may not reach mid-dorsal ciliary band of setiger 2 in very small juveniles, but always cross border between setigers 1 and 2.

Branchiae basally fused to notopodial lamellae. Branchiae of setiger 1 longer (often twice as long) than notopodial lamellae; last visible branchiae between setigers 5 and 15 (counting from the pygidium) in large adults; last three to six pairs of branchiae rapidly decreasing in size (Fig. 1D). Specimens $\leq$0.8 mm wide have branchiae on one half to two thirds of total number of setigers only.

Notopodial post-setal lamellae reach over dorsum on anterior quarter of body (Fig. 1B), becoming low thereafter (Fig. 1D). Neuropodial post-setal lamellae of anterior-most setigers slightly extended, with triangular–rounded margins (Fig. 1B), becoming low and trapezoid thereafter (Fig. 1C) and triangular at end of body (Fig. 1D).

Dorsal superior tufts of numerous longer, thinner capillaries, pronounced in notopodia from setiger 1. Ventral inferior tufts in neuropodia bearing sabre setae from setigers 2 to 5 (commonly from setigers 3 to 4), resemble ordinary large capillaries, numbering two to five per fascicle (decreasing in number posteriorly). Neuropodial hooded hooks present from setigers 22 to 43 (Table 1), up to seven per neuropodium; notopodial hooded hooks from setigers 26 to 57 (Table 1), up to six per notopodium. Hooks bi- or trifid, with one or two unpaired apical teeth (Figs 1E, F, 2E).

Anus terminal, with a variable number of surrounding anal cirri developed to different degrees (may be branched), numbering seven to 19 (even less in juveniles).

Specimens mostly unpigmented. However, juveniles may have ventral pair of anal cirri darkly pigmented and dorsal side of prostomium with trace of pigment along anterior margin and main axis of body; lateral parts of pygidium sometimes show dark pigment.

Distribution

Arctic species. Spitsbergen, Franz Josef Land, Barents Sea (Pechora Sea and Kolguyev area), White Sea, Kara Sea, Laptev Sea, East Siberian Sea, Chukchi Sea and Beaufort Sea (Fig. 3A). Type locality: Kara Sea and Franz Josef Land.

Biology and ecology

From 1 to 55 m depth, on sandy or mixed bottoms; from –1.68 to 4.3°C; salinity sometimes lower than 34–35‰ but not less than 30‰.

Juveniles found at the end of September to the beginning of October 1998 in the southeast of the Barents Sea (Pechora Sea).

Remarks

Marenzelleria wireni can be identified by the combination of long nuchal organs and the presence of branchiae on nearly all setigers (excluding some posterior-most) in specimens >0.8 mm wide. Br–VHH and Br–DHH are also useful (Table 1). We cannot confidently give a list of distinctions for the identification of small specimens, but the following remarks might be helpful. Specimens of *M. wireni* under 0.4 mm wide may be distinguished quite distinctly from all other species by the late introduction of ventral (from setigers 22 to 24) and dorsal hooks (from setigers 26 to 29). Specimens between 0.4 and 1.0 mm wide may be distinguished from *M. arctia* by Br (Table 1); specimens of the other two species treated in this paper (*M. viridis* and *M. neglecta*) of similar size have clearly bilobed prostomia, which is never the case in *M. wireni*; a combination of characters, as for example long nuchal organs and Br–DHH, may be rather helpful for identification (Table 1).

All existing syntypes were examined, but the absence of complete specimens was a problem. Thus, there were no types demonstrating the distribution of branchiae along the body. Only anterior, middle and posterior fragments were found in the vials of syntypes, but it would be incorrect to reconstruct them into one specimen. Experience indicates that researchers working with the incomplete syntypes of *M. wireni* have been easily confused, especially if they examined them merely for comparison with material containing other species. Moreover, the syntypes of *M. wireni* from SMNH consist of several different species, including *M. wireni*, *M. arctia*, *L. cirrata*, *Prionospio cirrifera*, and *Aricidea quadrilobata*. Thus, considering the above speculations it might be useful from our point of view to designate a neotype for *M. wireni* following the recommendations of the International Code of Zoological Nomenclature (4th edition, Articles 75.3.2 and 75.3.6) in order to permit an objective definition, thus allowing more repeatable and reliable taxonomic results. This is particularly important as *M. wireni* is the type species of the genus.

Unfortunately, it was not possible to examine the arctic material mentioned in Maciolek (1984) from the Beaufort Sea. Maciolek (1984:51) wrote "nuchal organ, extending to base of setiger 2" for *M. wireni*. Taking into account the body width up to 2 mm reported by Maciolek, this character can only refer to *M. arctia* (see Table 1). She also says that branchiae were "absent from last few setigers", which clearly refers to *M. wireni*. In view of this confusion, it is possible that Maciolek's (1984) material might contain specimens of both *M. wireni* and *M. arctia*.

When analysing the correlation between the width of the body and the number of branchiae (see Table 1), parameters of specimens from the Kara Sea (ZISP 21/49193) and Franz Joseph Land are different from those seen in the material from the White Sea, the south of the Barents Sea and Spitsbergen. It would appear that mature animals grow only in width, not in length. Comparing the specimen from Franz Joseph Land (ZISP 2/25659) with the one from Spitsbergen (ZMUC-POL-1007) we can see that they both have 50 pairs of branchiae and very close values of VHH and DHH (30 and 35, 29 and 39, respectively), but the former has a width of 1.07 mm and the latter only 0.68 mm. Syntypes from the Kara Sea and Franz Joseph Land are incomplete but their values of VHH and DHH are also smaller than respective values in worms of the same size from the White Sea. We cannot explain this phenomenon. We can only state that Franz Joseph Land and the Kara Sea are certainly areas with harsher arctic conditions.

Marenzelleria viridis (Verrill, 1873)
Figs 2C, 3B, 4A–F

Scolecolepis viridis Verrill, 1873:345, 600–601.
Scolecolepis tenuis Verrill, 1873:345, 601.
Marenzelleria jonesi Maciolek, 1984:55–58, figs 3–4.
Marenzelleria viridis – Maciolek 1984 (partim):51–55, fig. 2; non-*Marenzelleria viridis* – Sikorski & Buzhinskaya 1998:1118–1119, fig. 4 (= *M. neglecta* sp. nov.);

Table 1. Ranges of numerical characters for different size classes (the number of specimens in parentheses).

		Width (mm)						
	Species	≤0.4	0.5–0.7	0.8–1.0	1.1–1.3	1.4–1.6	1.7–1.9	≥2.0
Set.	*M. viridis*	28–41 (12)	87–130 (4)	163–221 (8)	172–243 (7)	215–232 (2)	–	–
	M. neglecta	15–57 (3)	52–122 (13)	79–181 (4)	160–210 (9)	194–203 (4)	–	205–209 (2)
	M. wireni	48–53 (2)	87–96 (2)	115–175 (7)	–	–	–	174 (1)
	M. arctia	25–51 (5)	–	54–83 (2)	–	67 (1)	83–89 (3)	91 (1)
VHH	*M. viridis*	16–19 (12)	25–36 (28)	31–44 (19)	33–48 (19)	41–44 (7)	39–49 (5)	51 (2)
	M. neglecta	14–22 (3)	21–36 (33)	25–41 (8)	36–48 (13)	45–50 (11)	51 (2)	48 (1)
	M. wireni	22–24 (6)	24–30 (6)	24–39 (27)	30–40 (14)	31–40 (8)	35–40 (3)	37–43 (4)
	M. arctia	17–21 (6)	19–27 (5)	20–30 (9)	19–31 (11)	27–36 (6)	29–36 (8)	29–37 (12)
DHH	*M. viridis*	16–22 (12)	31–46 (24)	38–57 (19)	42–57 (18)	52–61 (6)	55–69 (5)	62 (1)
	M. neglecta	16–26 (3)	25–42 (28)	28–46 (7)	41–57 (12)	55–63 (11)	58–67 (2)	58 (1)
	M. wireni	26–29 (5)	28–39 (4)	30–52 (27)	35–53 (10)	38–52 (7)	43–51 (4)	44–57 (4)
	M. arctia	18–23 (4)	23–29 (4)	21–35 (9)	24–39 (6)	37–45 (5)	38–45 (8)	37–46 (11)
Br	*M. viridis*	3–17 (13)	30–57 (27)	45–121 (19)	50–142 (18)	53–131 (5)	108 (1)	76 (1)
	M. neglecta	1–21 (7)	16–37 (31)	24–43 (8)	43–64 (14)	53–69 (11)	60 (2)	60–63 (2)
	M. wireni	12–26 (8)	41–50 (2)	78–169 (7)	50 (1)	–	–	165 (1)
	M. arctia	9–15 (7)	15–24 (4)	13–33 (11)	17–33 (12)	24–34 (6)	26–32 (8)	27–37 (11)
NO*	*M. viridis*	e1–m2 (14)	b2–m2 (26)	m2 (19)	m2 (19)	b2–m2 (7)	m2 (5)	m2 (2)
	M. neglecta	e1–m3 (15)	e1–m3 (33)	b2–m4 (10)	e2–e4 (9)	m3–m4 (10)	e3–m4 (3)	e3–b4 (2)
	M. wireni	b2–m2 (8)	m2–m3 (3)	m2–b4 (23)	b3–m4 (12)	e2–m5 (5)	b3–m3 (2)	b3–e3 (2)
	M. arctia	m1–b2 (5)	e1–b2 (3)	m1–b2 (11)	m1–m2 (12)	e1–m2 (4)	e1–m2 (8)	e1–m2 (12)
Br–VHH	*M. viridis*	−8–−2 (12)	3–25 (25)	13–80 (19)	18–98 (18)	10–89 (2)	66 (1)	25 (1)
	M. neglecta	−6–−2 (5)	−11–4 (34)	−5–7 (7)	0–18 (15)	4–24 (11)	9 (2)	12 (1)
	M. wireni	−9–2 (6)	17–21 (2)	47–130 (7)	20 (1)	–	–	123 (1)
	M. arctia	−8–−4 (7)	−5–−1 (4)	−8–11 (9)	−7–3 (11)	−7–4 (6)	−6–2 (8)	−8–5 (11)
Br–DHH	*M. viridis*	−11–−2 (13)	−4–16 (23)	5–68 (19)	8–88 (18)	1–70 (5)	52 (1)	14 (1)
	M. neglecta	−10–−6 (4)	−16–−4 (26)	−10–−1 (7)	−8–7 (14)	−7–12 (11)	−7–2 (2)	2–6 (2)
	M. wireni	−13–−4 (5)	11–13 (2)	42–117 (7)	15 (1)	–	–	108 (1)
	M. arctia	−10–−6 (4)	−9–−3 (4)	−15–−6 (6)	−14–4 (9)	−15–−8 (5)	−15–−7 (8)	−15–−5 (11)
DHH–VHH	*M. viridis*	0–5 (12)	3–10 (24)	5–16 (19)	8–15 (18)	9–19 (6)	7–20 (5)	11 (1)
	M. neglecta	2–4 (4)	2–8 (26)	3–10 (7)	3–11 (14)	6–15 (11)	16–17 (2)	10 (1)
	M. wireni	4–6 (5)	4–10 (4)	5–13 (24)	5–13 (9)	7–14 (7)	5–12 (3)	6–15 (4)
	M. arctia	1–5 (4)	2–4 (4)	1–8 (9)	4–12 (6)	9–12 (5)	7–12 (8)	6–13 (11)

Set. – Number of setigers in the case of complete specimens; VHH – First setiger with neuropodial/ventral hooded hooks; DHH – First setiger with notopodial/dorsal hooded hooks; Br – Last setiger with branchiae; NO – Last setiger with nuchal organs; b, m, e – Beginning, middle, end of setiger, respectively; for example, m2 means that the nuchal organs reach the medial transdorsal ciliary band of setiger 2.

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non-*Marenzelleria* cf. *viridis* – Bick & Zettler 1997: 141–142, figs 3–4 (= *M. neglecta* sp. nov.).
Marenzelleria cf. *wireni* – Bick & Zettler 1997: 138–141, figs 1–2.
Marenzelleria type I – Bastrop & al. 1995, 1997, 1998; Röhner & al. 1996a, b: genetic analysis.

Material examined

Nineteen samples, ~275 specimens.

LECTOTYPE of *Sc. viridis* (here designated): USA, Massachusetts, off Martha's Vineyard, Naushon Island, 1871, coll. US Fish. Comm. (YPM 24130).

PARALECTOTYPES of *Sc. viridis*: USA, New Jersey, Cape May Co., Beesley Point, April 1871, coll. A. E. Verrill & S. I. Smith (YPM 42, 6 – not examined, could not be located). USA, New Jersey, Cape May Co., Beesley Point, April 1871, coll. A. E. Verrill & S. I. Smith (YPM 44, 18). USA, Connecticut, New Haven, 1866 [? October], coll. A. E. Verrill + class (YPM 171, 1). USA, Massachusetts, off Martha's Vineyard, Naushon Island, 1871, coll. US Fish. Comm. (YPM 796, 9).

SYNTYPES of *Sc. tenuis*: USA, New Jersey, Cape May Co., Beesley Point, April 1871, coll. A. E. Verrill & S. I. Smith (YPM 43, 4).

HOLOTYPE and PARATYPES of *M. jonesi*: Cape Henlopen, Delaware, USA, sandflats, Stn 111, coll. M. L. Jones, 8 August 1977 (USNM 80472, 1; USNM 80473, 100+).

NON-TYPE MATERIAL: Europe – Weser estuary, eulittoral, 13–16 m, 14 May 1992 (ZSRO P-36, 18); 21 May 1996 (ZSRO P-35, 8). – Scotland, Tay estuary, eulittoral, 5 October 1994 (ZSRO P-34, 35; ZMUM Pl-2237, 7); 12 December 1994 (ZSRO P-33, 27). – Ems estuary, eulittoral, fine sand, 20 June 1994 (ZMH-P 18791, 3; ZSRO P-40, 6). – Elbe estuary (ZMH-P 19071, 5). North America – Great Sippewisset Salt Marsh, Massachusetts, USA, eulittoral, June 1995 (ZSRO P-42, 11). – Cape Henlopen, Delaware, USA, eulittoral, 32‰, June 1995 (ZSRO P-43, 10). – Nova Scotia, Shelburne (ZSRO P-897, 3). – Massachusetts, Gloucester, 16 May 1959 (USNM 80483, 2). – Durham Fox Point, Massachusetts, 24 August 1962 (USNM 80485, 3).

Description

LECTOTYPE: Complete specimen. Width 1.5 mm, with 232 setigers. Prostomium bell-shaped, bilobed anteriorly. Nuchal organs reaching to anterior part of setiger 2. Branchiae gradually decreasing in length; last branchiae visible on setiger 99. Neuropodial hooded hooks from setiger 42; notopodial hooded hooks from setiger 53. Notopodial post-setal lamellae pointed on five anterior-most setigers. No anal cirri visible (probably broken).

PARALECTOTYPES: 28 incomplete specimens (no data on YPM 42). Width 1.10–2.14 mm. Prostomium rounded or bilobed anteriorly. Nuchal organs not crossing mid-segmental ciliated band on setiger 2. Disappearance of branchiae visible in three specimens only, on setigers 53, 76 and 108. Neuropodial hooks from setigers 39 to 51; notopodial hooks from setigers 50 to 69.

All material examined

Up to 95 mm long (specimen 1.1 mm wide with 221 setigers), with up to 247 setigers (specimen 1.1 mm wide and 69 mm long); maximum width 2.14 mm (incomplete specimen). Body somewhat flattened, dorsally convex, concave ventrally. Prostomium usually bell-shaped, rounded or bilobed anteriorly (Fig. 4A) in adults (bilobed in all juveniles and in most medium-sized specimens). Caruncle not pronounced, surrounded by ciliary double-looped nuchal organs, sometimes faintly demarcated and extending up to middle of setiger 2 (to the mid-segmental band of cilia connecting bases of branchiae). Usually two pairs of eyes, often deeply embedded within cuticle, in alcohol-preserved specimens sometimes invisible; commonly in a trapeziform arrangement, posterior pair closer together, sometimes with all four eyes on one line. Palps may extend to setiger 16 in fixed specimens, sometimes with brownish spots on the lateral side.

From three (specimen 2 mm long, 21 setigers) to 17 pairs of branchiae in specimens ≤0.4 mm wide and ≤45 setigers. Up to 142 pairs of branchiae in larger specimens. Branchial length decreases distinctly in posterior half of branchiate region, especially in large specimens. Branchiae become papilliform posteriorly and therefore difficult to distinguish (up to 30 pairs). Branchiae of setiger 1 sometimes shorter or equal to notopodial post-setal lamellae or may surpass notopodial post-setal lamellae by one third to one half of length. Banchiae often overlapping across dorsum in anterior half of branchiate region. Post-setal lamellae on all setigers excluding most posterior ones. Upper tip of some of most anterior notopodial post-setal lamellae sometimes not fused to branchiae, often pointed (Fig. 4C), being pointed through several segments (2–19), even after

becoming completely fused to branchiae. Notopodial post-setal lamellae becoming elongated oval to broadly rounded posteriorly (Fig. 4D–E) and acutely triangular in far posterior setigers. Neuropodial lamellae with elongated tip on first 10 setigers; rounded to quadrangular on middle setigers, often with a slightly elongated tip ventrally; acutely triangular and similar in shape to notopodial lamellae in posterior part of body.

Neuropodial hooded hooks start between setigers 16 and 51, on setigers 16–18 in juveniles after settlement ($\leq$0.4 mm wide), two to 10 per fascicle (two to three per fascicle in specimens $\leq$0.4 mm wide). Notopodial hooded hooks start between setiger 16 (juveniles) and setiger 69, two to eight per fascicle. Hooks bidentate as a rule, with only one apical tooth above main tooth (Fig. 4F); occasionally with second apical tooth; apical teeth sometimes reduced. Ventral inferior tuft of neuropodium bearing sabre setae from setiger 4, occasionally from setiger 2 or 3, two to six setae per fascicle anteriorly, decreasing in number to two to three and looking stouter from setigers 13 to 56 (setae identical on all setigers in smallest specimens). Pygidium of smallest specimens with three pairs of anal cirri, ventral pair shortest; adults with up to five or six pairs, sometimes dichotomously branched, hence may thus be odd numbered.

Gametes present from setigers 32 to 40.

Type locality

USA, Massachusetts, off Martha's Vineyard, Naushon Island.

Distribution (Fig. 3B)

Atlantic species; along the North American coast from Nova Scotia to Cape Henlopen, Scotland, North Sea. Estuaries, eulittoral.

Biology and ecology

Eulittoral; on sandy bottoms; brackish waters, salinity usually >16‰; spawning observed in the Dollard-Ems estuary, the Netherlands, from March to May (Bochert 1997).

Remarks

Marenzelleria viridis is particularly difficult to distinguish from *M. neglecta* sp. nov. Both species may occur sym- and parapatrically (for example in the Elbe estuary, North Sea; Bastrop & al. 1999). The characters most useful for identification of *M. viridis* in this case are: NO to the middle of setiger 2 (does not cross the mid-segmental ciliary band on setiger 2), Br on about one half of the total number of setigers (significantly fewer in *M. neglecta*), Br–VHH and Br–DHH (Table 1). Not all specimens under 1.0 mm wide could be reliably identified. The following characteristics can be used in the identification of small specimens: all examined smaller specimens of *M. neglecta* with nuchal organs not crossing mid-segmental transdorsal ciliary band on setiger 2 had Br–VHH $\leq$2 and Br–DHH ≤ -1 (all specimens of *M. viridis* >0.4 mm wide with Br–VHH of larger values and most of them with larger values of Br–DHH); specimens of *M. viridis* hardly ever possess more than one apical tooth on their hooks. *Marenzelleria viridis* differs from *M. arctia* in having a greater number of setigers and a longer, more slender body. It differs from *M. arctia* also by larger values of VHH, DHH, Br, Br–VHH and Br–DHH (Table 1). *Marenzelleria viridis* differs from *M. wireni* in having nuchal organs not crossing the mid-segmental ciliary band on setiger 2, Br on about one half of the total number of setigers in specimens >0.8 mm wide (instead of more than two thirds of the total number of setigers in *M. wireni*), and a greater number of setigers. Specimens <0.8 mm wide differ from *M. wireni* in having clearly bilobed prostomia.

All examined type specimens of *Sc. viridis*, *Sc. tenuis* and *M. jonesi* belong to the same species. The syntypes of *Sc. viridis* and *Sc. tenuis* were rediscovered in 1986. Thus, this is the first re-examination of the types since Verrill's (1873) original description. *Scolecolepis viridis* and *Sc. tenuis* were described in the same paper. We use the epithet "*viridis*" to name this species for two reasons: (1) Maciolek (1984) treated *Sc. tenuis* as the junior synonym of *M. viridis*; (2) syntypes of *Sc. viridis* are in much better condition than syntypes of *Sc. tenuis*. We regard it as necessary to designate a lectotype for this species to stabilize its taxonomic status.

Marenzelleria neglecta sp. nov.
Figs 2B, 3C, 5A–I, 6

Marenzelleria viridis – Maciolek 1984:51–55, fig. 2 (partim); Bick & Burckhardt 1989:239–241, fig. 1, plates VII–VIII; Sikorski & Buzhinskaya 1998:1118–1119, fig. 4.
Marenzelleria cf. *viridis* – Bick & Zettler 1997: 141–142, figs 3–4.
Marenzelleria type II – Bastrop & al. 1995, 1997, 1998; Röhner & al. 1996a, b: genetic analysis.

Material examined

Nineteen samples, 128 specimens.

HOLOTYPE: Europe, Baltic Sea – Darss-Zingst-Boddenchain, 54°25′N 12°40′E, 0.2–0.8 m, 4–6‰, November 2000 (ZMH P-24386).

PARATYPES: Europe, Baltic Sea – Darss-Zingst-Boddenchain, 54°25′N 12°40′E, 0.2–0.8 m, 4–6‰, November 2000 (ZMH P-24387, four specimens; ZSRO P-983, two specimens; ZSRO P-984, three specimens); 54°25′N 12°40′E, 0.2–0.8 m, 4–6‰, May–September 1995 (ZSRO P-38, 14 specimens; ZSRO P-39, 22 specimens; ZMUM Pl-2235, seven specimens). – R/V *Lev Titov*, Stn 55, 59°53′N 28°16′E, 21 m, silty sand, 20 July 1996 (ZISP 1/49123, one specimen); Stn 56, 59°50′N 28°11′E, 20 m, sand and clay, 20 July 1996 (ZISP 2/49124, one specimen); Stn 25, 59°51′N 28°40′E, 21 m, silty sand, 20 July 1996 (ZISP 3/49125, 1); Stn 18H, 54°41.3′N 19°52′E, 18 m, fine sand, 7.1‰, 4 August 1990 (ZISP no no., 10 specimens; ZMUM Pl-2236, 10 specimens). Europe, North Sea – Lower Elbe River, Mühlenberger Loch, 1.8 m, fine sand, 0.7‰, 15 October 1996 (ZSRO P-37, seven specimens). USA, Atlantic coast – North Carolina, Currituck Sound, eulittoral, 4‰, June 1995 (ZSRO P-44, three specimens); Georgia, Ogeechee River, eulittoral, low tide, 1–2‰, June 1995 (ZSRO P-41, three specimens).

NON-TYPE MATERIAL: Europe, Baltic Sea – Darss-Zingst-Boddenchain, 1 m, 25 March 2000 (ZSRO P-893, eight specimens). Canada – North West Territories, Tuktoyaktuk Harbor, 69°29′N 132°53′W, August 1982 (ZSRO P-894; formerly NMC-Acc. IZ 1984-031, 16 specimens). USA, Pacific coast – California, Sacramento, San Joaquin Delta, Grizzly Bay at Dolphin (SIO A660, 13 specimens; ZSRO P-896, two specimens).

Description

HOLOTYPE: Complete specimen, 1.5 mm wide, 75 mm long, 194 setigers; no eyes visible; nuchal organs extending to border of setigers 3 and 4. Neuropodial hooded hooks appear on setiger 47, notopodial hooded hooks start from setiger 56; number of branchiate setigers 53; pygidium with five pairs of anal cirri.

All material examined

Up to 2.0 mm wide, 115 mm long, with up to 250 setigers.

Prostomium bell-shaped, broadly rounded anteriorly, often incised medially. Two pairs of eyespots (pale in fixed specimens), usually arranged in line or trapeziformly with posterior pair closer together (Fig. 5A). Palps short, never extending posteriorly beyond setiger 10 in fixed specimens. Nuchal organs may reach to mid-segmental ciliary band of setiger 4 (Fig. 2B) or, exceptionally, to posterior border of setiger 4. Number of branchiae one to 69 pairs (depending on size; see Table 1): one pair of branchiae found in juvenile with 15 setigers, all specimens $\leq$0.5 mm wide have $\leq$21 pairs of branchiae. Branchiae disappear sometimes immediately, sometimes six to 10 segments after starting to decrease in length. Branchiae of setiger 1 rarely as high as notopodial post-setal lamellae, usually above lamellae by up to one third of their length. Tips of notopodial post-setal lamellae on two to nine anterior-most setigers not fused to branchiae. In most of these cases, upper tip of anterior notopodial lamellae pointed (Fig. 5C), but sometimes rounded; in latter case anterior notopodial post-setal lamellae completely fused to branchiae (specimens from Canadian Arctic). Notopodial post-setal lamellae decreasing in size, posteriorly becoming nearly triangular or oval (Fig. 5E). Neuropodial post-setal lamellae sometimes pointed anteriorly (Fig. 5C, D), becoming rounded and slightly asymmetrical at end of anterior third of body, rounded or nearly triangular posteriorly (Fig. 5E). Neuropodial hooded hooks from setigers 11 to 51, two to eight per fascicle in middle of posterior half of body (only two per fascicle in specimens $\leq$0.4 mm wide). Notopodial hooded hooks appear one to 17 segments after neuropodial hooks, i.e. from setigers 12–67, two to seven per fascicle in middle of posterior half of body. Hooded hooks bidentate (Fig. 5F), sometimes tridentate posteriorly (more usual in larger specimens), with two unpaired apical teeth in tandem above main fang (Fig. 5G–I). Ventral inferior tuft of neuropodium with sabre setae appearing from setigers 1 to 5, two to six per fascicle anteriorly, decreasing in number to two to three and becoming stouter from setigers 4 to 41. Pygidium of juveniles with four pairs of anal cirri; cirri of ventral pair shortest. Pygidium of adults with up to seven pairs of anal cirri.

Gametes present from setigers 39 to 43.

Specimens unpigmented, sometimes with small black dots on palps.

Type locality

Baltic Sea, Germany, Darss-Zingst-Boddenchain.

Etymology

The name "*neglecta*" means that the species has been misidentified and overlooked.

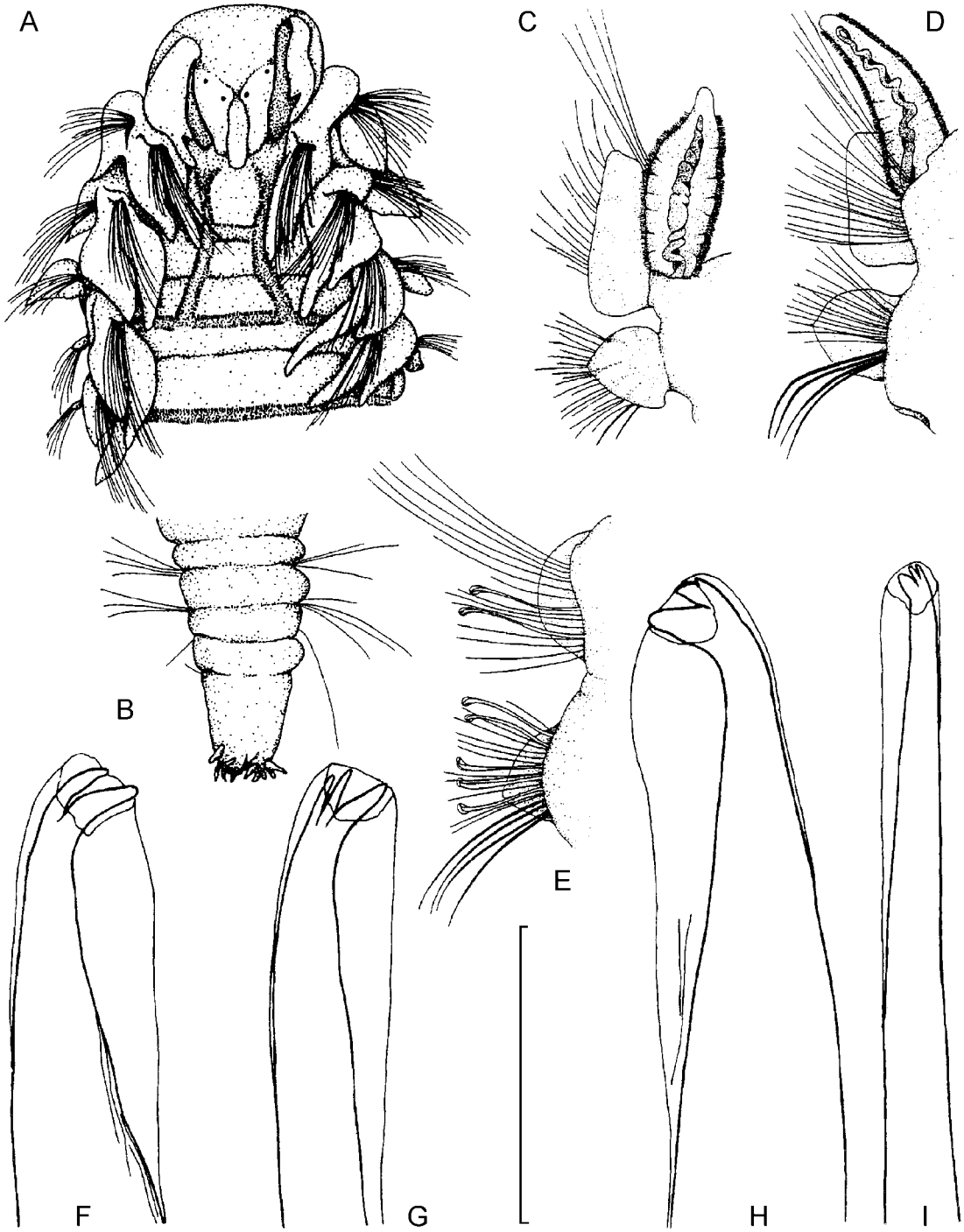

Fig. 5. *Marenzelleria neglecta* (Verrill, 1873). A. Anterior end, dorsal view. B. Pygidium, dorsal view. C. Left parapodium of setiger 3, posterior view. D. Right parapodium of setiger 45, anterior view. E. Right parapodium of setiger 70, anterior view. F. Neuropodial hook, setiger 86. G. Neuropodial hook, setiger 181. H. Neuropodial hook, setiger 147. I. Neuropodial hook, setiger 48. Material: A–E, G – Darss-Zingst-Boddenchain ZSRO P-38; F, H – Darss-Zingst-Boddenchain ZSRO P-893; I – Tuktoyaktuk Harbor ZSRO P-894. Scale (mm): A, B = 1.0; C–E = 0.8; F–I = 0.025.

Distribution (Fig. 3C)

From Durham, Fox Point (North Carolina) to Ogeechee River (Georgia) along the Atlantic coast of North America; Baltic Sea and North Sea (Elbe estuary); San Joaquin Delta, Grizzly Bay at Dolphin, California in the Pacific; Tuktoyaktuk Harbor in the Canadian Arctic.

Biology and ecology

On sandy and muddy bottoms, salinity usually 0.5–10‰ [see also Zettler (1997) for more details]; highly adapted to eutrophic conditions prevailing in brackish waters [see also Schiedek (1997) for more details]. Larvae were most abundant in plankton in the coastal waters of the Baltic Sea in September and October but occurred up to March [see also Bochert (1997) for more details]; larvae feed on phytoplankton <20 µm [see also Burckhardt & al. (1997) for more details].

Remarks

Marenzelleria neglecta can be identified by the combination of the following characters: the length of the nuchal organs (up to setiger 4) and the number of branchiate setigers in relation to the total number of setigers (about one quarter to one third). See "Remarks" for *M. viridis* and *M. arctia* and also Table 1 for more details.

All valid names listed in "Historical review" do not concern this taxon, as it is absent in the type materials. Therefore, a new name, "*neglecta*", is designated for the taxon.

Marenzelleria neglecta sp. nov. was found in coastal waters of lower salinity on both sides of the Atlantic Ocean, with one exception: Bastrop & al. (1998) found *Marenzelleria* type II (= *M. neglecta*) at Tuktoyaktuk Harbor (Canadian Arctic). All 16 examined specimens from this station were <0.9 mm wide and incomplete, which means that important diagnostic characters to

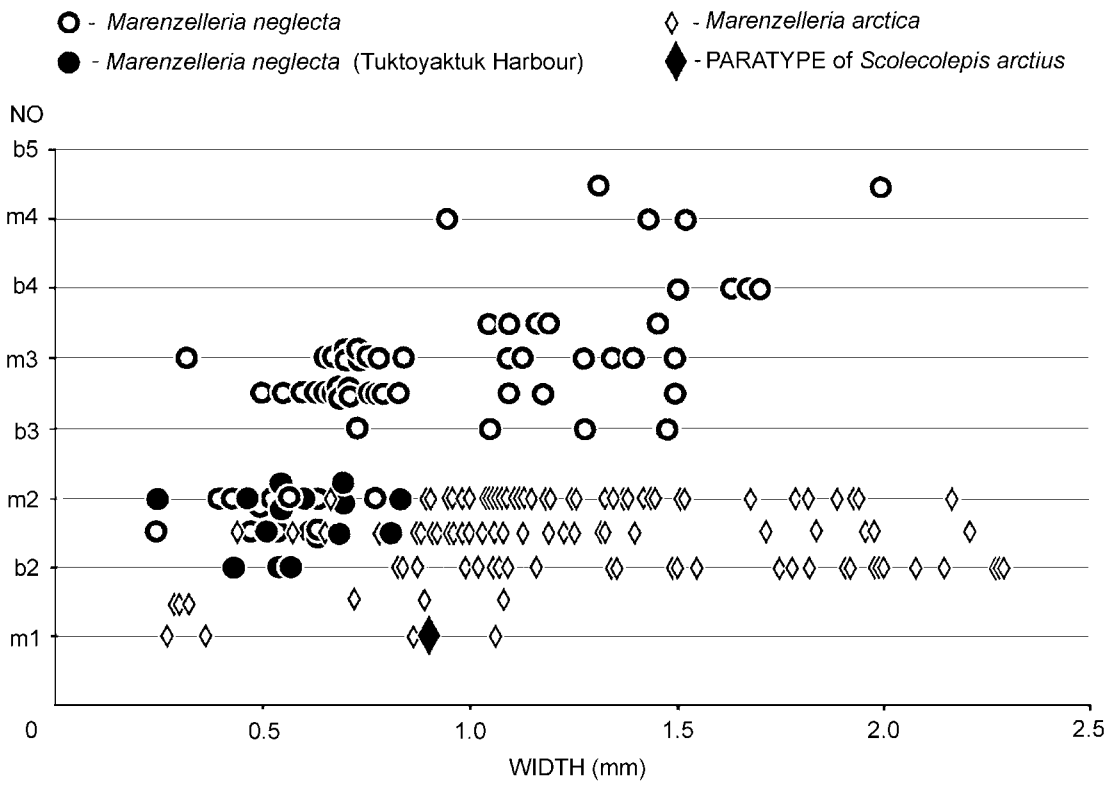

Fig. 6. Relationship between size of worm (width, mm) and length of nuchal organs (NO) in *Marenzelleria neglecta* and *M. arctia*, with special signatures for paratype of *Scolecolepides arctius* and for specimens of *M. neglecta* from Tuktoyaktuk Harbor, Canadian Arctic (m1: middle of setiger 1; b2: beginning of setiger 2; m2: middle of setiger 2, etc.).

differentiate these specimens from *M. arctia* could not be determined. However, the nuchal organs were longer than in *M. arctia* in case of comparable size (Fig. 6). We could not obtain further arctic material for genetic analysis.

Material from California was in agreement with the diagnosis of *M. neglecta*, but all specimens investigated were small; therefore some doubts about their identity remain.

Marenzelleria arctia (Chamberlin, 1920)
Figs 2D, F, 3D, 6, 7A–I

Scolecolepides arctius Chamberlin, 1920:17–18: plates III (5–7), IV (1).
Laonice annenkovae Zachs, 1925:3.
Nerine vulgaris – Wirén 1883:408 (partim).
Microspio wireni – Söderström 1920:249–250 (partim).
Laonice annenkovae – Uschakov 1939:82; 1950:200; 1955:265.
Marenzelleria wireni – Annenkova 1932:176; Vinogradov 1947:131–132; Maciolek 1984:49–51, fig. 1A–G (?partim); Sikorski & al. 1988 (partim):835–837, fig. 4a–k; ?Holmquist 1967:298–313.
Marenzelleria arctia – Stoljarov 1994:67; Burkovsky & al. 1995:69; Burkovsky & Stoljarov 1995:36; Sikorski & Buzhinskaya 1998 (partim):1115–1118.

HOLOTYPE of *Sc. arctius* Chamberlin, 1920 (not examined, unavailable for study due to postal restrictions): NMCIC (National Museum of Canada, Invertebrate Collection) 1900-8368 (two slides containing a series of parapodia). Label: Canadian Arctic Expedition station 27o, lagoon at Collinson Point, Alaska, USA. Pelagic under 5 inches (13 cm) of ice over 1 foot (0.3 m) of water.

Material examined

One hundred and one samples, about 2300 specimens from MCZ, ZISP, ZMUM and ZSRO. Two PARATYPES of *Sc. arctius*: Beaufort Sea, "Alaska: Collinson Point, Stn 27: under 5 inches of ice over 4 feet of water, coll. F. Johansen, 18 September 1913, Canadian Arctic Expedition" (MCZ no. 2194 and 2195).

LECTOTYPE and PARALECTOTYPES of *L. annenkovae*, designated by Sikorski & Buzhinskaya (1998): Barents Sea – "Murman, Kola Bay, mouth of Tuloma River, 2 June 1923" (ZISP 1/2210, 1; ZISP 2/2211, 13). "Teriberka River, 13 May 1925" (ZISP 3/13765, 10).

NON-TYPE MATERIAL: Barents Sea – Kola Bay, Mouth of Tuloma River, low-tide mark, silty sand, 17 July 1999 (ZSRO P-892, 170). White Sea – Kandalaksha Bay, estuary of Chornaya River, summer 1991 (ZMUM Pl-838, 3); summer 1997 (ZMUM Pl-2240, 7); summer 1998 (ZSRO P-895, 31). Kara Sea – Dikson Bay, "*Vega*" Expedition, Stn 19, 73°09.9′N 80°20′E, fine, very soft light brown clay, 4–5 fm, 9 August 1878 (SMNH 2041, 4) = SYNTYPES of *M. wireni*. – Mouth of Yenisey, eastern coast, 72°43′N, 300 m off shore, 31 August 1927 (ZISP 1/25658, 1). – 73°09.9′N 80°20′E, Sever Bay, Stn 7, 10 m, 1 October 1930 (ZISP 8/25665, 1). – R/V *Sibiryakov*, Stn 5, 72°24.5′N 80°51.5′E, brown ooze, pieces of algae, 7 August 1933 (ZISP 16/8664, 1). – R/V *Dm. Mendeleev*, Stn 4416, Mouth of Ob, 71°45′N 73°03.5′E, clayey silt, 18 m, 26 September 1993 (ZMUM Pl-289, 154). – R/V *Polarstern*, Stn 13, 73°35′N 80°06′E, 20 m, clay, 31.59‰, –0.49°C, August 1993 (ZISP 9/49456 and 10/49457, 2; ZMUM Pl-2238 and Pl-2239, ∼80; ZSRO P-327, 20). – Mouth of Yenisey, August 1993, coll. Komendantov (ZISP 11/49458-20/49467, 576). East Siberian Sea – Chaun Bay, Mouth of Chaun River, 2–3 km off shore, silt, 4.1 m, 14 August 1967 (ZISP 4/16576, 26); Mouth of Palyavoom River, sand, 0.67 m, 21 August 1967 (ZISP 5/16577, 8). – Russian Polar Expedition, Stn 77, south of Kotelniy Island, silty sand, gravel, 3–4.5 m, 17 September 1903 (ZISP 5/25662, 1). Bering Sea – Mouth of Anadyr River, silt, 3.7–4.47 m, 11.6°C, 1 August 1970 (ZISP 6/39681, 11); Stn 103, silt, 4.47 m, 11.6°C, 1 September 1970 (ZISP 7/40436, 15). – Avachinskaya Inlet, estuaries of Avacha and Paratunka Rivers, Stn 552, 554, sandy silt, detritus, 0.5–1 m, 1932–1935 (ZISP 10/25667, 9). – Mouth of Kamchatka River, Nerpichye Lake, 5–20‰, 1961 (ZISP 20/11664, ∼70). – Avachinskaya Inlet, 1988 (ZMUM 65 samples without no., ∼1000).

Description

PARATYPES: MCZ no. 2194 contains one anterior fragment (Fig. 7A, E), 0.9 mm wide, neuropodial hooded hooks from setiger 20, three per neuropodium; notopodial hooded hooks from setiger 25, two per notopodium; 22 pairs of branchiae; nuchal organs reaching middle of setiger 1, ventral inferior tuft of neuropodium bearing sabre setae from setiger 5; MCZ no. 2195 contains middle fragment only.

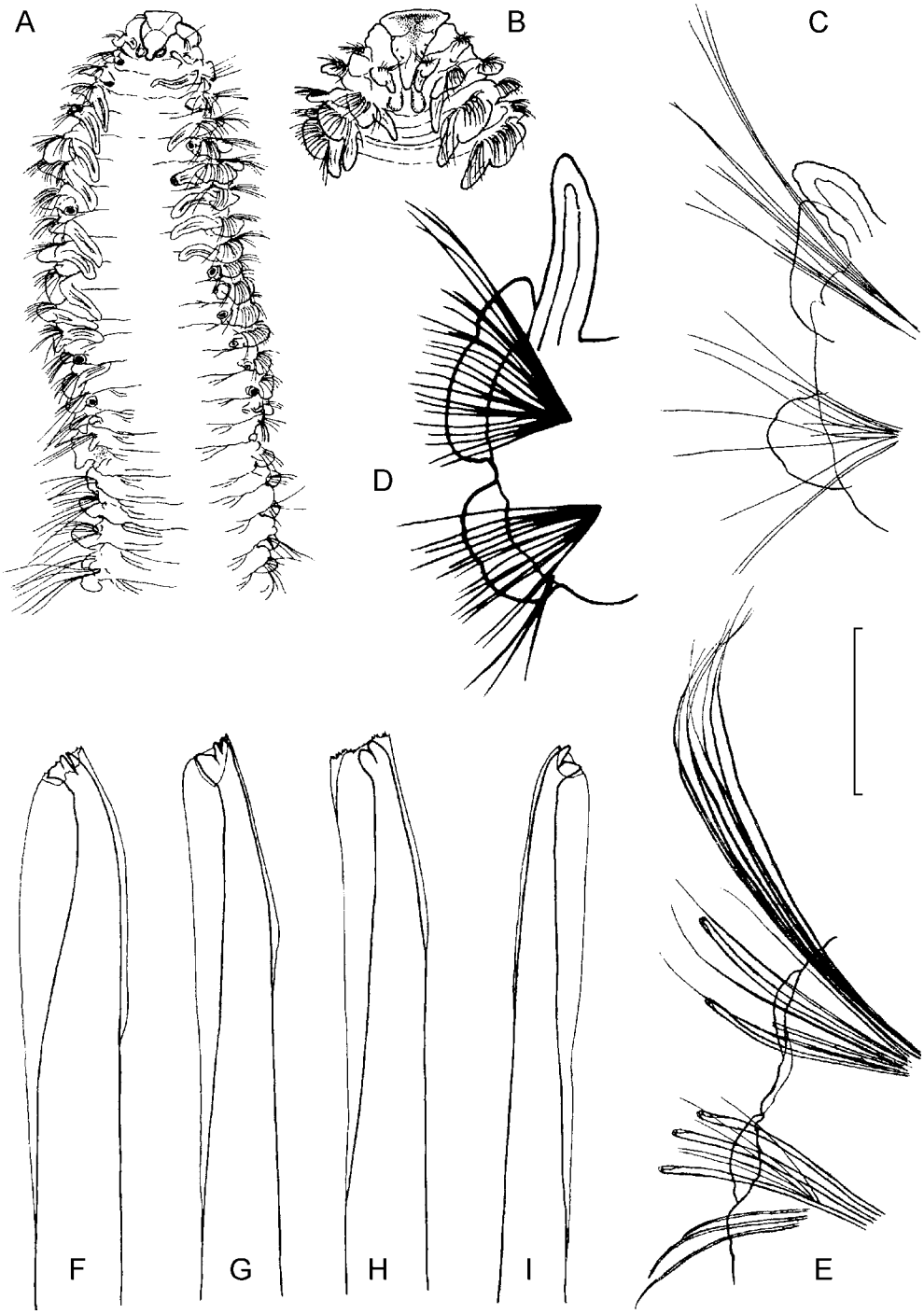

Fig. 7. *Marenzelleria arctia* (Chamberlin, 1920). A. Anterior end, dorsal view. B. Anterior end, dorsal view, pigmentation of prostomium shown. C. Right parapodium of setiger 1, anterior view. D. Right parapodium of setiger 13, anterior view. E. Right parapodium of setiger 33, anterior view. F–H. Hooks from the same neuropodium, setiger 69. I. Notopodial hook, setiger 51. Material: A, E – Paratype MCZ 2194; B – ZISP 2/2211; C – ZISP 14/8662; D – ZISP 1/2210, lectotype of *Laonice annenkovae*; F–I – ZSRO P-892. Scale (mm): A = 1; B = 1.4; C, E = 0.3; D = 0.5; F–I = 0.015.

All material examined

Up to 2.3 mm wide (ZISP 10/25667). The width of 2.6 mm mentioned by Sikorski & Buzhinskaya (1998) for a specimen from the East Siberian Sea (ZISP 5/25662) was erroneous. Up to 56 mm long and with up to 121 setigers.

Prostomium triangular- to bell-shaped, sometimes slightly incised anteriorly. Two pairs of eyespots usually trapeziformly arranged, posterior pair closer together (Fig. 7A, B). Eyespots bright in young specimens, in large specimens often invisible or obscured deeply embedded within cuticle. Posterior part of prostomium often distinctly raised, forming short caruncle that may extend to setiger 1. Nuchal organs short (Fig. 2D), resemble pair of epaulettes, may reach to mid-segmental ciliary band connecting bases of branchiae of setiger 2. Occasionally it appeared to reach end of setiger 2, but after careful examination it turned out that it never crosses mid-segmental ciliary band. Raised strip (not always obvious) between "epaulettes" of nuchal organs look in some specimens like extension of caruncle (Fig. 2D).

Last branchiae on setigers 9–49 (Table 1). Up to five of the posterior-most pairs of branchiae sometimes lower or equal to notopodial post-setal lamellae. Branchiae of setiger 1 surpass notopodial post-setal lamellae by one third to two thirds of their length (Fig. 7C). Branchiae longest on 20 anterior-most setigers in large specimens (Fig. 7D). Distal tip of several of anterior-most notopodial post-setal lamellae sometimes not fused to branchiae; often more or less pointed for several segments (up to setiger 30) even after becoming completely fused to branchiae. Upper margins of anterior notopodial lamellae sometimes rounded, often completely fused to branchiae (most frequently observed in material from Far East and Eastern Siberian Sea). Notopodial post-setal lamellae becoming round (Fig. 7E) or sometimes nearly triangular posteriorly. Neuropodial post-setal lamellae round anteriorly, sometimes slightly pointed on two to three of anterior-most setigers, becoming slightly asymmetrical with upper part wider than lower part at end of anterior third of body, more rounded (Fig. 7E) or nearly triangular at end of body, similar to notopodial lamellae.

Neuropodial hooded hooks start at setigers 17 to 42, two to seven per fascicle (only two per fascicle in specimens $\leq$0.4 mm wide). Notopodial hooded hooks start at setigers 17–51, two to seven per fascicle. Hooded hooks bi- or tridentate (usually tridentate on posterior segments) sometimes unidentate on posterior-most setigers (Fig. 2F); tridentate hooks may appear quite strange and rather variable (Fig. 7F–I). Ventral inferior tufts of neuropodium bearing sabre setae appear from setigers 1 to 6, two to five setae per fascicle anteriorly, decreasing in number to two and becoming stouter from setigers 7 to 33 (before setiger 11 only in specimens $\leq$0.6 mm wide).

Pygidium of smallest specimens with three pairs of anal cirri, ventral cirri shortest; adults with up to five pairs of anal cirri, individual cirri sometimes bifurcated, resulting in an odd number.

Specimens often with a characteristic pattern of pigmentation: dark stripe along prostomium, usually broadening anteriorly (Fig. 7B), may be pale in fixed specimens. Nothing is known about variation in this character.

Gametes present from setigers 25 to 31.

Type locality

Alaska, Collinson Point.

Distribution (Fig. 3D)

Arctic and Kamchatka estuaries. Recorded from the mouth of the Amur (Uschakov 1948, 1955), but the material no longer exists. Incorrectly reported from Franz Josef Land (Sikorski & Buzhinskaya 1998), re-identified as *M. wireni*.

Biology and ecology

Found on depths up to 20 m on silty, sandy or mixed bottoms in a wide range of temperatures and salinities. The highest density (1260 individuals m^{-2} for up to 8 g m^{-2}) was found in the Yenisey estuary in silty sediments subject to extremely changeable salinity and temperature (0–31.5‰; 0–12 °C) over short periods (Sikorski & Buzhinskaya 1998). The highest biomass, 16.6 g m^{-2}, was recorded from the Tuloma river estuary, where salinity and temperature fluctuated (tidally and seasonally) from 0.06 to 22.12‰ and from –1.25 to 19 °C. A preference for silty substrate and euryhalinity was suggested by Burkovsky & al. (1995); Stolyarov (1994) and Burkovsky & Stolyarov (1995) suggested that salinities of 3–16‰ were the most favourable.

Juveniles were found on 30 April 1935 in Avachinskaya Inlet, Kamchatka (Vinogradov 1947), at the beginning of July 1999 in the estuary of Tuloma River, on 14 August 1967 and 12 August 1986 in the estuary of the Chaun River, Eastern Siberian Sea and on 31 August 1927 in the mouth of the Yenisey.

Remarks

Marenzelleria arctia differs from the other arctic species, *M. wireni*, in having shorter NO (never crossing the mid-segmental transdorsal ciliary band of setiger 2), a lower number of branchiae, and smaller arithmetical differences in Br–VHH and Br–DHH (see Table 1). *Marenzelleria arctia* strongly resembles *M. neglecta*, especially in the case of juveniles. Only specimens >1 mm wide (adults) can be distinguished reliably. It is possible to separate them by short NO (Fig. 6), small Br and also by the combination of a smaller number of setigers with a larger width than in other species (Table 1). The characteristic pattern of dark pigmentation on the prostomium (Fig. 7B) in the specimens from the Tuloma River has never been found in any other species of the genus. However, the geographical variation of this character is unknown.

To avoid probable misidentification of the pair *M. arctia–M. neglecta* in Arctic and Far East material, the differentiation of these species in samples containing only small (<1.0 mm wide) unpigmented specimens with the NO not crossing the mid-segmental ciliary band connecting the bases of the branchiae of setiger 2 (m2 in Table 1) is not recommended (see "Remarks" for *M. neglecta*).

Some doubt might be cast about the name *Sc. arctius* as the species was described from Collinson Point, which is quite close to Tuktoyaktuk Harbor, the area where *M. neglecta* has been recorded. However, the numerical characters – VHH, DHH, Br, NO – of the *Sc. arctius* paratype examined are clearly different from those of *M. neglecta* (see Fig. 6 for NO and Table 1 for the others).

We confirm the opinion of Sikorski & Buzhinskaya (1998) synonymizing *L. annenkovae* with *M. arctia*. It should be noted that *L. annenkovae* was also mentioned from the mouth of Amur River by I. Zachs (in Uschakov 1939, 1950, 1955), but the material no longer exists. In our opinion, there is a high probability that material described from Kotsebu Bay, Alaska as *M. wireni* (Holmquist 1967) belongs to *M. arctia*.

A thorough investigation is essential to describe the morphological and genetic complexity of *Marenzelleria* populations along the coasts of Canada, Alaska and the Far East.

Marenzelleria sp. A
Figs 3D, 8A–F

Marenzelleria sp. A – Bick & Zettler 1997:143.

Marenzelleria type III – Bastrop & al. 1995, 1997, 1998; Röhner & al. 1996a, b: genetic analysis.

Material examined

North Carolina, Currituck Sound (Fig. 3D), eulittoral, 4‰, coll. R. Bastrop (ZSRO P-45, one anterior fragment).

Description

Anterior fragment consisting of 127 setigers (about 45 mm long), 1.1 mm wide. Prostomium bell-shaped, dorsally incurved, making anterior margin look more or less bilobed depending on angle of view. Caruncle noticeably elevated. One pair of eyes on lateral sides of anterior caruncle. Nuchal organs extending to anterior part of setiger 3. Branchiae 90 pairs. First branchiae slightly higher than notopodial post-setal lamellae (Fig. 8A). Branchiae shorter than notopodial post-setal lamellae only on setiger 90 (Fig. 8E). On anterior 40 setigers branchiae may surpass notopodial post-setal lamellae by three quarters of their length (Fig. 8B). Six anterior-most notopodial post-setal lamellae with pointed upper tips; following lamellae have rounded margins, oval or trapeziform (Fig. 8B–E). Four anterior-most neuropodial post-setal lamellae laterally pointed (Fig. 8A), following lamellae rounded (Fig. 8B–E). Neuropodial hooks start on setiger 47, up to six per fascicle; notopodial hooks start on setiger 73, up to three per fascicle. Hooks bi- or tridentate (Fig. 8F). Ventral inferior tuft of neuropodium with sabre setae appearing from setiger 2.

Remarks

This is the only species of *Marenzelleria* with DHH >70 and with so great a distance between the start of ventral and dorsal hooks: DHH–VHH = 25. This specimen resembles *M. viridis* in Br and Br–VHH, but *M. viridis* has nuchal organs that do not cross the mid-segmental transdorsal ciliary band on setiger 2. It differs from *M. wireni* also in both VHH and DHH. Our morphological conclusions are supported by genetic analysis of the same sample (Bastrop & al. 1997, 1998). We tried several times to get new material from Currituck Sound (*Marenzelleria* sp. A is abundant together with *M. neglecta* without hybridization at this location) but were unsuccessful. Until such time as more complete specimens are available, the relationships of this specimen within the *Marenzellaria* group as a whole remain enigmatic.

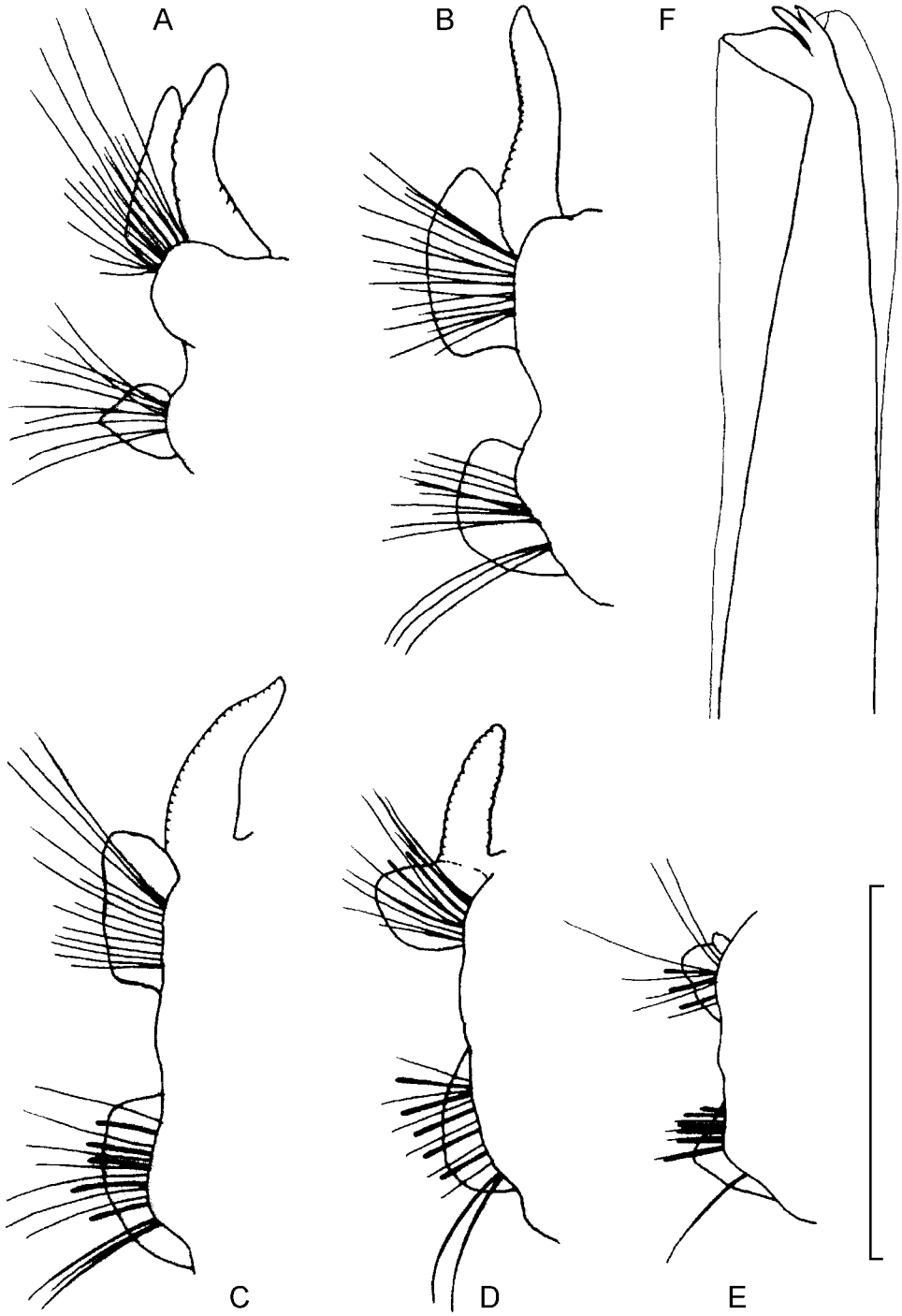

Fig. 8. *Marenzelleria* sp. A. A. Right parapodium of setiger 1, anterior view. B. Right parapodium of setiger 30, anterior view. C. Right parapodium of setiger 66, anterior view. D. Right parapodium of setiger 76, anterior view. E. Right parapodium of setiger 90, anterior view. F. Neuropodial hook, setiger 127. Material: ZSRO P-45. Scale (mm): A–E = 1.0; F = 0.03.

CONCLUSIONS

1) Five species belonging to the genus were found: *M. wireni* Augener, 1913; *M. viridis* (Verrill, 1873); *M. arctia* (Chamberlin, 1920); *M. neglecta* Sikorski & Bick sp. nov.; *Marenzelleria* sp. A. *Laonice annenkovae* Zachs, 1925 is treated as a junior synonym of *M. arctia*. *Marenzelleria jonesi* Maciolek, 1984 and *Sc. tenuis* Verrill, 1873 are synonymized with *M. viridis*, and *Spio gorbunovi* Averintsev, 1990 with *M. wireni*. A lectotype for *M. viridis* is designated. We used the name *Marenzelleria* sp. A as we had only one incomplete specimen of this taxon.

2) Two species, *M. viridis* and *M. neglecta*, were found in the European Atlantic (they immigrated there from North America): both of them inhabit the North Sea, only *M. neglecta* – the Baltic Sea; three species are known from the Atlantic North American coast: *M. viridis*, *M. neglecta* and *Marenzelleria* sp. A; one is known from the Pacific North American coast: *M. neglecta*; and three in the Arctic: *M. wireni*, *M. arctia* and *M. neglecta*. The distribution of the latter species needs more careful investigation and its co-existence with *M. arctia* needs to be confirmed.

In the Far East, *M. arctia* and possibly *M. neglecta* occur.

There is a possibility that an undescribed species, having short nuchal organs and branchiae only in the anterior part of the body, is present in the Far East and possibly in the Arctic.

3) Four species are brackish water inhabitants. *Marenzelleria wireni* occurs in normal marine salinity, but may inhabit slightly brackish conditions. *Marenzelleria arctia* sometimes inhabits areas with extremely changeable salinity, from 0 to 30‰, but prefers to breed at 5–7‰. *Marenzelleria viridis* and *M. neglecta* often share habitats in the Atlantic but diverge in their salinity preferences: *M. viridis* does not occur in salinity lower then 16‰, but *M. neglecta* prefers 0.5–10‰.

4) No single morphological character allowed us to distinguish one species distinctly from another, as all characters overlap. A combination of characters must be used to diagnose any given species. Only large worms can be reliably identified. We cannot at this time recommend any method to identify small specimens (under 0.8–1.0 mm wide) – only genetic analysis and autecological investigations may provide solutions to this problem. Some problems with *M. arctia* and *M. neglecta* in the Arctic and Far East could not be solved using traditional morphological methods. Genetic methods may be quite helpful in this situation as an additional character to separate the species reliably. However, this would force us to modify the collecting process: before fixation the material would have to be divided to fix one part with formaldehyde for morphology and the other part with ethanol for genetic analysis.

We could not identify a single non-numerical morphological character capable of distinguishing species in the genus. The length of the first branchiae, the shape of post-setal lobes, the shape of the hooks, the shape of the pygidium are variable and may be useful only in certain cases. The shape of the hooks, usually so helpful in Spionidae, is nearly useless in *Marenzelleria* because of the wide variation of this character (Figs 1E–F, 2E–F, 5F–I, 7F–H) even in the same specimen and on the same parapodium. All numerical characters used are size dependent (Table 1, Fig. 6). The intervals of variation of all these characters overlap in all species (Table 1), mainly in small specimens. All the characters have low taxonomic value separately. The length of nuchal organs is a useful character in the genus. The nuchal organs do not cross the mid-dorsal ciliary band on setiger 2, which is a specific character that separates *M. viridis* and *M. arctia* from other members of the genus.

Size-dependent characters depend on width, length and number of setigers, but species that have their own pattern of growth and proportions may, with age, increase their width or length (number of setigers is also characteristic of length as usual). This may even happen with specimens of the same species living under different conditions. For example, it is quite noticeable in the case of *M. wireni* (see Remarks on *M. wireni*). Another example is the wide variation in Br in *M. viridis*.

5) We suggest the following species key for specimens >1.0 mm wide.

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1 DHH–VHH > 20 . . . . . ***Marenzelleria* sp. A**
– DHH–VHH ≤ 20 . . . . . **2**
2 Nuchal organs crossing the mid-segmental ciliary band on setiger 2 . . . . . **3**
– Nuchal organs not crossing the mid-segmental ciliary band on setiger 2 . . . . . **4**
3 Br–DHH ≥ 14 . . . . . ***Marenzelleria wireni***
– Br–DHH < 14 . . . . . ***Marenzelleria neglecta***
4 Br > 40 . . . . . ***Marenzelleria viridis***
– Br < 40 . . . . . ***Marenzelleria arctia***

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