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On the identity and distribution of two species of *Marenzelleria* (Polychaeta, Spionidae) in Europe and North America

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Abstract

Discrepancies are known to exist between the reproduction biology and population genetic of various *Marenzelleria* spp. populations in North American regions and in the North Sea and Baltic Sea. Species identification is difficult, and their geographical distributions are far from clear. As the diagnostic features of the species are known to vary with growth, it was necessary to find some reference frame within which morphological differences could be understood. The total number of setigers of intact specimens and the total number of branchiate setigers of anterior fragments proved to be suitable parameters permitting morphological differentiation between previously genetically distinguished forms. The forms corresponded in several features to literature diagnoses of *M. wireni* and *M. viridis*. Additional features were found to facilitate reliable morphological differentiation between the two species. It was shown that the range of distribution of *M.* cf. *wireni* is restricted primarily to mesohaline to polyhaline regions (including the North Sea), whereas *M.* cf. *viridis* is found predominantly in oligohaline to mesohaline areas (including the Baltic Sea). This applies also to North American and, possibly, polar waters. The discovery of *M.* cf. *viridis* in an oligohaline reach of the Elbe estuary shows that the two species can exist parapatrically, at least in North Sea estuaries. Besides these two species, a third was found to occur sympatrically with *M.* cf. *viridis* in a North American estuary (Currituck Sound). No description of this species has been given as the specimen consisted only of an anterior fragment.

Introduction

In the late seventies, Elliott & Kingston (1987) discovered a spionid species in a Scottish North Sea estuary that had previously been found only in North American estuaries. Further specimens of what appeared to be the same species were found in the mid-eighties in the coastal waters of the Baltic Sea (Bick & Burckhardt, 1989). The distribution of these events in time and space led to the assumption that a North American species had immigrated to the North Sea and then extended its range of distribution to the Baltic. This assumption was hardened by the speed with which the immigrant was seen to spread within the newly colonized regions: In the Baltic virtually all suitable habitats were colonised within a few years (Gruzka, 1991; Norkko et al., 1993; Persson, 1990; Zmudzinski, unpubl. data). The immigrant was subsequently also found in other locations in the North Sea (Dekker, 1991; Gosselck et al., 1993; Kirkegaard, 1990; Leling, 1986). *Marenzelleria* soon dominated the macrofauna of the benthic communities in these areas (Essink & Kleef, 1993; Zettler, 1996).

Identification of the immigrant was beset with problems from the start. It was first identified as *M. wireni* Augener, 1913 (see Essink & Kleef, 1988; Elliott, 1983, cited in Atkins et al., 1987). However, as the range of distribution of *M. wireni* was believed to be exclusively circumpolar (Augener, 1913; Holmquist, 1973; Maciolek, 1984), this was later revoked, and the specimens found in the North Sea were identified as *M. viridis* (Verrill, 1873). This species is widespread in North American estuaries and had been transferred from *Scolecolepides* to *Marenzelleria* by Maci-

olek (1984). Atkins et al. (1987), however, noticed morphological differences between their Scottish specimens and the North American specimens described by Maciolek (1984) as *M. viridis*. As far as we know the intended morphological studies dealing with the specimens from Scottish estuaries were never published.

Besides any morphological discrepancies between European and North American specimens, life history differences were discovered between the North Sea and Baltic Sea populations; Baltic animals reproducing in autumn and North Sea animals in spring (Atkins et al., 1987; Bochert et al., 1996). This discrepancy was initially explained away more or less conclusively as the effect of abiotic factors (Bochert & Bick, 1995). However, genetic studies on several North Sea and Baltic Sea populations revealed major differences that gave reason to suspect that two different species might be involved (Bastrop et al., 1995). This suspicion was strengthened by the results of further investigations with material that included specimens from North American populations (Röhner et al., 1996b).

The above difficulties and uncertainties led to the morphological studies described here from North Sea and Baltic populations, and some specimens from North America. The work took into account the fact that a) the differences between the species of the genus *Marenzelleria* are exceedingly slight (see Maciolek, 1984) and b) important diagnostic features vary with age and size (Atkins et al., 1987; Bick, 1995). In addition, it should be noted that the type material for *M. wireni* is in relatively poor condition and that of *Scolelepis viridis* (=*Marenzelleria viridis*) no longer exists (see Maciolek, 1984: 54).

Materials and methods

The animals used for these studies were taken from various areas of the North Sea and Baltic Sea and from North American estuaries. The Baltic specimens were collected in the coastal waters of the German Baltic coast, most of them from the Darss-Zingst Bodden Chain (1992–1995). The North Sea animals came from the estuaries of the rivers Tay (October and December 1994), the Weser (May 1992 and May 1996), the Elbe (September 1994 and October 1996) and Ems (June 1994). The American specimens were collected at the following locations in North America in June 1995: Great Sippewisset Salt Marsh, Cape Henlopen, Ogeechee River and Currituck Sound. A few additional specimens were provided by museums: Zoologisches Museum Hamburg (ZMH), National Museum of Natural History (USNM), Canadian Museum of Nature (CMN). No details are available on the treatment of museum specimens apart from the fact that they were preserved in alcohol. Otherwise, all specimens collected for this study were fixed in borax-buffered formalin (4%) and preserved in alcohol.

At first, only intact animals, without any signs of regeneration, from the North Sea and Baltic Sea were examined, attention being paid primarily to the number of branchiate setigers, total number of setigers and total specimen length, as well as the setigers on which the neuropodial and notopodial hooks first appeared. Incomplete anterior fragments were also examined later on the condition that all branchiate setigers were present.

Initially the specimens from the North Sea and Baltic were designated Form I and Form II (= 'Type I' and 'Type II' in genetic study of Röhner et al., 1996b).

The specimens from North American waters were examined subsequently and compared with the specimens from the North Sea and Baltic Sea.

Results

The comparative taxonomic studies showed that the genetically differentiable Form I and Form II are also morphologically distinguishable. The specimens from North American waters can be assigned to these two forms on the basis of the same features. The features distinguishing the two forms allow conclusions to be drawn regarding the identity of previously described species. However, as some contradictions remain, the species diagnoses are corrected and augmented below.

Form I: Marenzelleria *cf.* wireni

Material examined

Europe: Franz-Joseph-Land, 3 syntypes (ZMH-PE 890), all anterior fragments; Weser estuary, 38 specimens; Tay estuary, 13 specimens; Ems estuary, 3 specimens, several fragments (ZMH-P 18791); Elbe estuary, 2 specimens, 3 anterior fragments (ZMH-P 19071); North America: Great Sippewisset Salt Marsh, 11 specimens; Cape Henlopen, 9 specimens; Durham Fox Point, 3 specimens (USNM 80485); Nova Scotia, Shelburne, 4 specimens (CMN 1973-231).

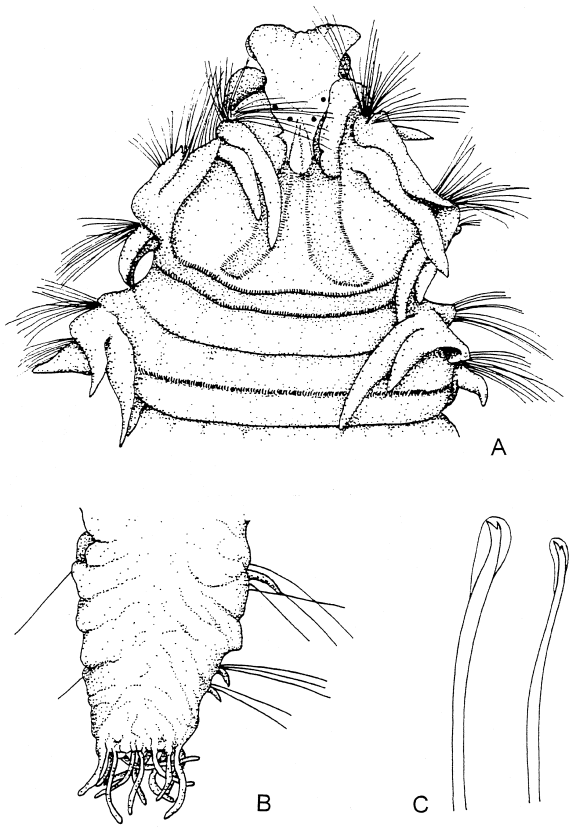

Figure 1. *M.* cf. *wireni* (210 setigers): A. anterior end, dorsal view; B. posterior end, dorsal view; C. neuropodial hooded hooks.

Description of European specimens

Specimens up to 92 mm long and 230 setigers; maximum width 3 mm. Body somewhat flattened, convex dorsally, concave ventrally. Some specimens ventrally with distinct median longitudinal groove; particulary pronounced in posterior third of body.

Anterior margin of the prostomium broadly rounded with anterior corners sometimes flared to give the prostomium a bell-shaped appearance (Figure 1A) with a slightly indented anterior margin. Prostomium terminating posteriorly in a sometimes faintly demarcated double-looped nuchal organ surrounded by cilia and extending to setiger 2. As a rule 4 (0–4) eyes, sometimes paled in alcohol-preserved specimens, usually trapeziformly arranged with posterior pair more closely spaced, but sometimes with all 4 eyes on one line. Palps relatively short, extending at most to setiger 15 in fixed specimens, sometimes with 20–30 brownish spots on the lateral side.

Branchiae present from setiger 1, number of branchiate setigers increasing with increasing animal length (Figure 5). A 2 mm specimen with 21 setigers had 3 branchiate setigers. The largest specimens had up to 91 branchiate setigers. Branchial length decreases distinctly in the posterior half of branchiate region, especially in large specimens, the branchiae finally becoming papilliform and therefore difficult to distinguish (Figure 2A–E). The branchiae touch in the dorsal median plane only on a few anterior setigers. They are basally fused with the postsetal lamella in the notopodium. Branchiae on the first setiger always longer than the notopodial postsetal lamella and sometimes about twice as long.

Postsetal lamellae on all except posteriormost setigers. In the notopodium the lamella is elongate oval with elongated tip to upper margin (Figure 2A). Posteriorly it becomes elongate oval to broadly rounded (Figure 2B–D) and then acute triangular (Figure 2E–F). Neuropodial lamella with elongated tip on the first 10 setigers. On the middle setigers it is rounded to quadratic, often with an elongated tip to its ventral part. In the posterior part of the body it is acute triangular similar to the notopodial lamella.

Capillary setae on all setigers. Dorsalmost 3–4 notosetae particularly long throughout, sometimes over twice the length of branchiae on anterior setigers. Neuropodial capillary setae about as long as those of the notopodium. Posterior to setiger 4–8 these are accompanied by distinctly longer, ventrally curved, and tapering sabre setae. Latter of granulated appearance, 2–4 per neuropodium in all but posteriormost setigers.

Hooded hooks in both neuropodia and notopodia, up to 6–8 per ramus; usually only one, rarely more (up to 4), in first hook-bearing setiger. First appearance of hooks varies with number of setigers (Figures 6 and 7). Neuropodial hooks appear from setiger 13–16 in 2–3 mm specimens with 21–28 setigers, notopodial hooks 1–2 setigers later. In specimens with more than 150 setigers, notopodial hooks usually start 10–13 setigers posterior of the neuropodial hooks. The shift in the appearance of hooks with increasing setiger number indicates that the first hooks are later shed and not replaced. In large specimens, neuropodial hooks rarely start posterior of the setiger 40 and never posterior of setiger 42. The number of hook-bearing branchiate setigers constantly increases since the development of new branchiae continues as the animals grow (Figure 8). As a rule the hooks are bidentate with a small tooth above the main tooth (Figure 1C). The small tooth is sometimes reduced. The presence of 2 small teeth is rare.

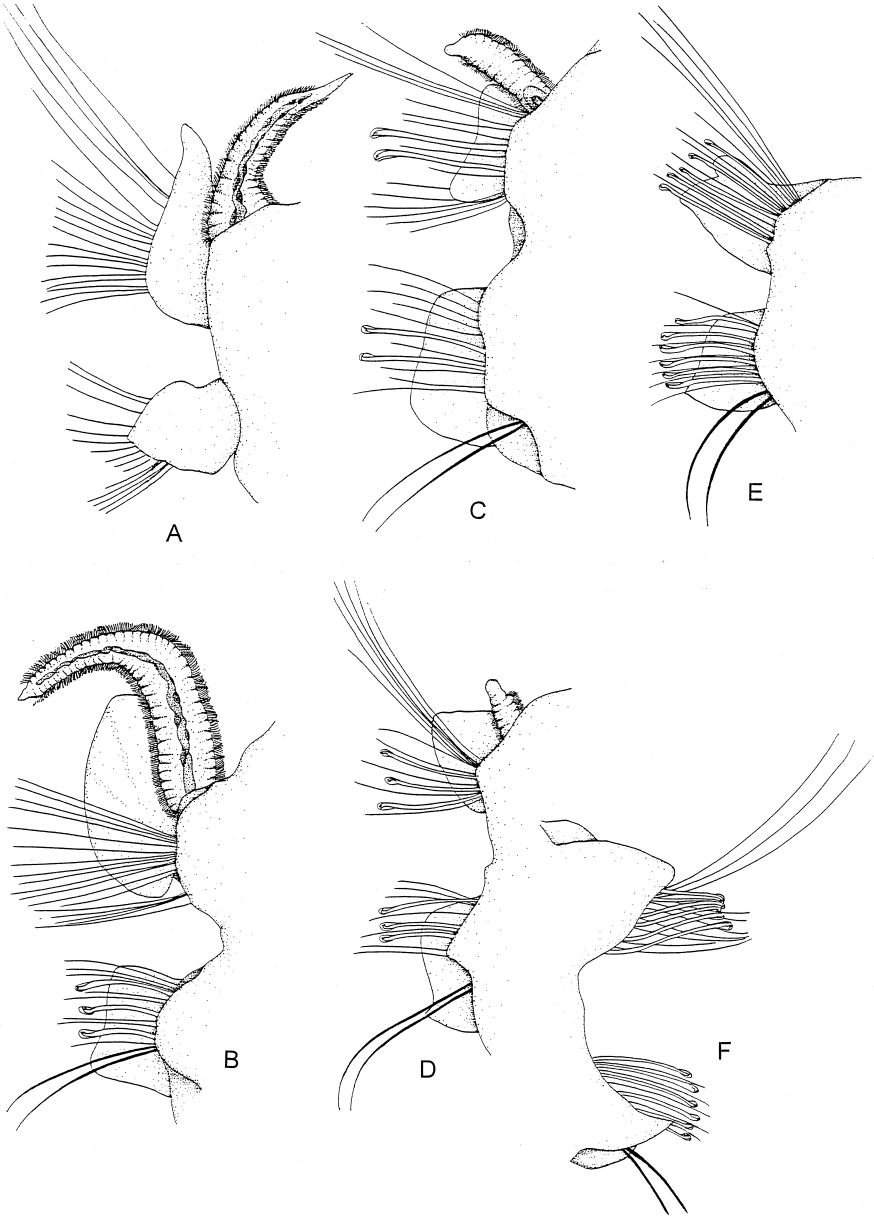

Figure 2. *M.* cf. *wireni* (210 setigers): A. setiger 3, posterior view; B. setiger 45, anterior view; C. setiger 57, anterior view; D. setiger 70, anterior view; E. setiger 82, anterior view; F. setiger 150, posterior view.

Anus terminal with anal papillae and up to 14 relatively long filamentous anal cirri (Figure 1B).

Description of North American specimens

The above description also largely applies to the North American specimens (Figure 9). Slight differences were found only in setiger number, number of branchiate setigers and the first hook-bearing setigers. A specimen with a length of 68 mm and 247 setigers had 122 branchiate setigers; the first neuropodial hook was on setiger 40 and the first notopodial hook on setiger 52. Other specimens, regrettably incomplete, had 128 and 130 branchiate setigers, i.e. about 40 more than found in European specimens. The first neuropodial (and notopodial) hooks were rarely found in later setigers than in European specimens. In one incomplete

specimen with 128 branchiate segments, the hooks began on setiger 46 (neuropodium) and 54 (notopodium). This was the latest point at which the appearance of hooks was observed in Form I specimens.

Form II: Marenzelleria *cf.* viridis

Material examined
Europe: Darss-Zingst Bodden Chain 80 specimens, Greifswalder Bodden 3 specimens, Elbe estuary 5 specimens; North America: Ogeechee River 3 specimens, Currituck Sound 4 specimens, Tuktoyaktuk Harbour (North-West Territories) 7 specimens (CMN 1984–031).

Description of European specimens
Specimens up to 115 mm long and 250 setigers; maximum width 3.2 mm. Body somewhat flattened, concave ventrally, convex dorsally, sometimes a longitudinal groove ventrally.

The anterior margin of the prostomium is broadly rounded. As a rule, the anterior corners are flared so that the prostomium is bell shaped (Figure 3A). The anterior margin is usually notched medially. SEM images show that the anterior margin of the prostomium bears 30–40 papilliform protuberances bearing cilia. The double nuchal organ extends to setiger 3 and is sometimes difficult to distinguish. The 4 (rarely less) eyes pale in fixed specimens. They are arranged in a line or at the corners of a trapezium. The palps are short and never extend posteriorly beyond setiger 10 in fixed specimens. They are unpigmented or bear up to 20 pigmented spots on the outside.

Branchiae start on the first setiger, and their number depends on the number of setigers (Figure 5). One branchia was found on a specimen with 15 setigers. Additional branchiae appear with increasing size, but even the largest specimens never had more than 65 branchiate setigers. The size of the branchiae decreases posteriorly on the last branchiate setigers and can no longer be distinguished after 5–10 further setigers (Figure 4A–C). The branchiae on the first setiger distinctly longer than the postsetal lamella of the notopodium (sometimes twice as long) and increases in size up to setiger 8–10. The branchiae touch dorsally in this area.

Postsetal lamellae on all except posteriormost setigers. The notopodial lamella is initially elongate oval with the tip pointing distinctly dorsally (Figure 4A). Posteriorly it becomes rounder, appears square and becomes triangular on the last setigers (Figure 4B–E).

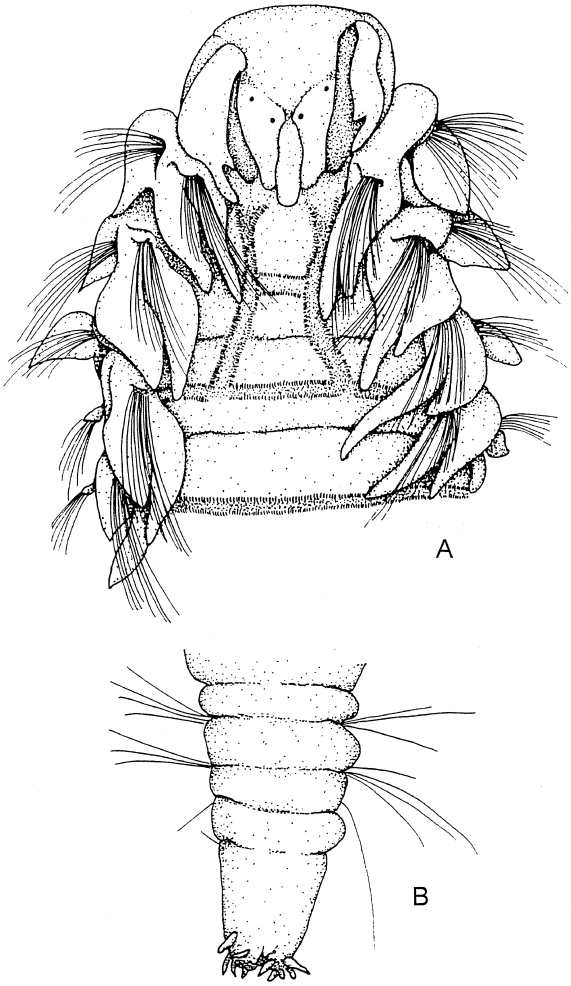

Figure 3. M. cf. *viridis* (212, 218 setigers): A. anterior end, dorsal view; B. posterior end, dorsal view.

The neuropodial lamella is oval pointed on the first 3 to 5 setigers, then becomes rounded, less frequently square and finally triangular pointed on the last setigers.

All setigers bear capillary setae. The superior dorsal setae in the notopodium are longest. These setae are particularly striking on the first setigers. Almost all setigers bear 3–6 of these long, dorsally arranged setae, which are absent only from the last setigers. Capillary setae are also found in the neuropodium. Posterior of setiger 5–10 they are accompanied by ventrally curved setae of increasing thickness. These sabre setae (usually 2–4) are present on all but the last setigers.

Hooded hooks are present in both branches of the parapodium. The first setiger on which they appear

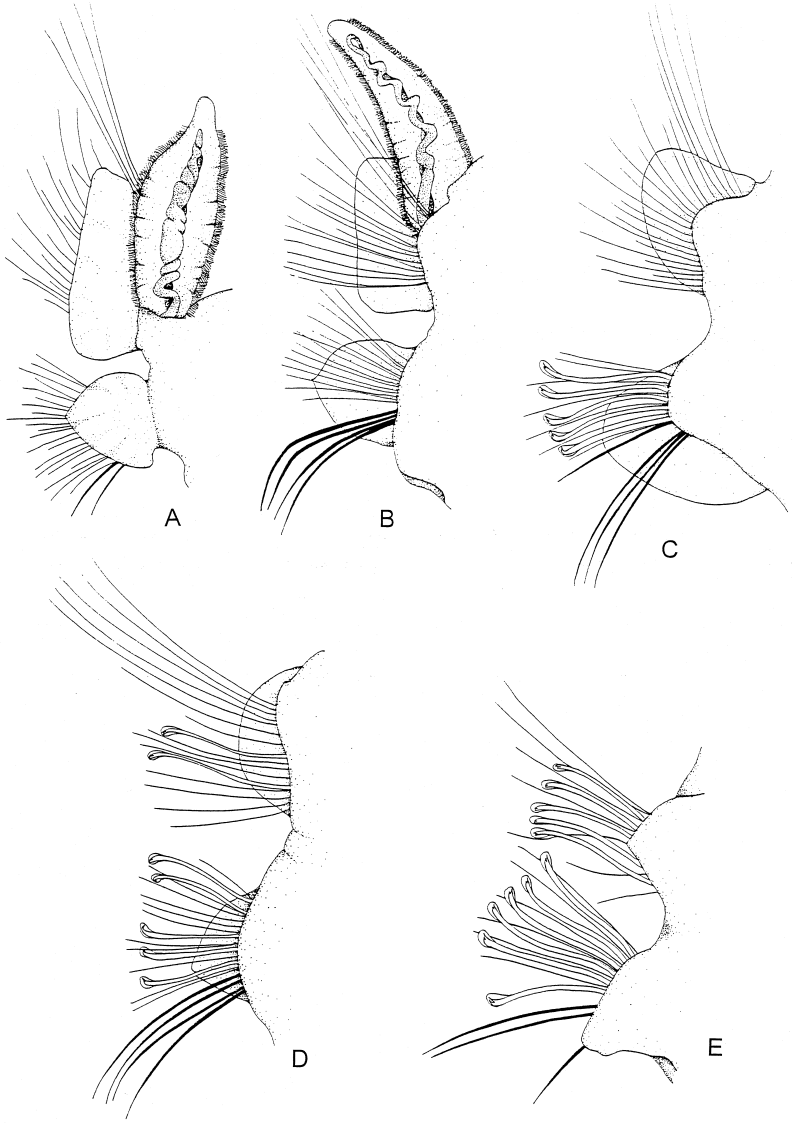

Figure 4. *M.* cf. *viridis* (210, 218 setigers): A. setiger 3, posterior view; B. setiger 45, anterior view; C. setiger 57, anterior view; D. setiger 70, anterior view; E. setiger 150, posterior view.

varies with animal size, i.e. with the total number of setigers (Figures 6 and 7). Neuropodial hooks appear from setiger 11 in 2–3 mm specimens with 20–30 setigers. On the largest specimens, the first hooks were found from setiger 48 to 52. The notopodial hooks appear 1–2 setigers posterior of the neuropodial hooks in juvenile specimens and 8–12 setigers later in adults. No specimen had more than 21 hook-bearing branchiate setigers, and most had less than 15 (Figure 8). As a rule, the hooks are bidentate, but single teeth and tridentate hooks were sometimes found.

Anus terminal and surrounded by up to 8 relatively short anal cirri besides smaller anal papilla (Figure 3B).

Description of North American specimens

With a single, distinct exception (*Marenzelleria* sp. A), the North American specimens conform to the above description of the European specimens (Figure 9).

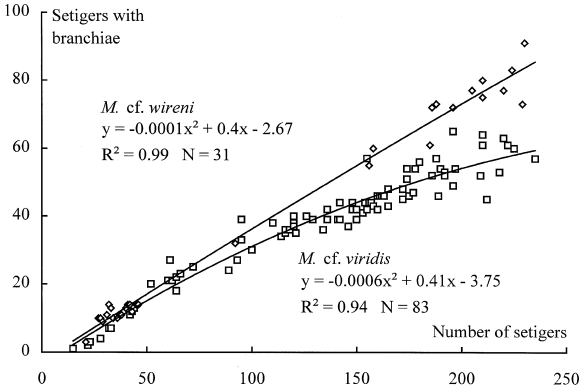

Figure 5. Relation between total number of setigers and number of branchiate setigers in *M.* cf. *wireni* and *M.* cf. *viridis.*

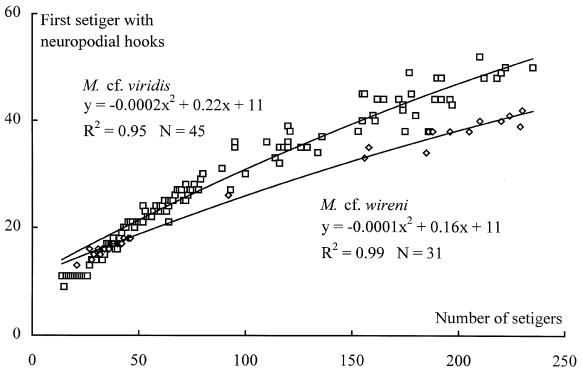

Figure 6. Relation between first neuropodial hooded hook and total number of setigers in *M.* cf. *wireni* and *M.* cf. *viridis.*

Marenzelleria *sp. A*

One fragment of a specimen (50 mm) with 167 setigers was collected in Currituck Sound alongside 3 specimens of Form II (*M.* cf. *viridis*). The fragment differed from previously described species of *Marenzelleria* in the following features: notopodial hooks begin 26 segments posterior to neuropodial hooks (setiger 47). The number of branchiate setigers (90) suggests that the fragment is of Form I (*M.* cf. *wireni*), but the presence of neuropodial hooks from setiger 47 is characteristic of Form II (*M.* cf. *viridis*). The size and shape of the nuchal organ were also as in Form II. None of the other animals we examined bore its first notopodial hook in setiger 73, as did this specimen. As the specimen exists only as a fragment, no complete description can be given.

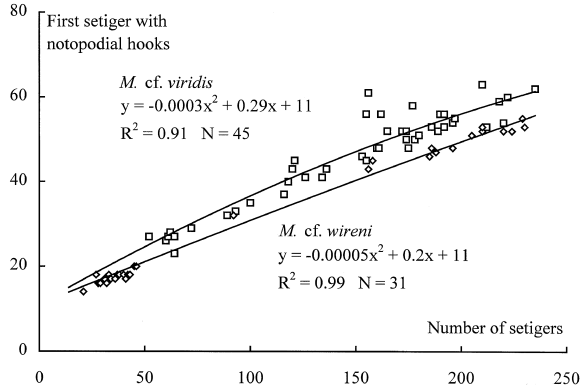

Figure 7. Relation between first notopodial hooded hook and total number of setigers in *M.* cf. *wireni* and *M.* cf. *viridis.*

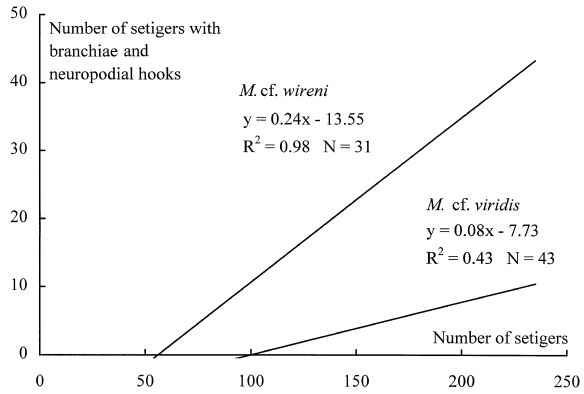

Figure 8. Relation between total number of setigers and number of hook-bearing branchiate setigers in *M.* cf. *wireni* and *M.* cf. *viridis.*

Discussion

The genus *Marenzelleria* was erected by Mesnil (1896) for spionids found by Wirén (1883) and Marenzeller (1892) in polar regions. However, no species names were given at that time. Examining further anterior fragments from Franz-Joseph Land, Augener (1913) found that they were identical in morphology and distribution to the specimens from Wirén and Marenzeller. He gave an exact description of the species, which he named *M. wireni* (type species). Augener (1913) also discussed the differences in the first setigers bearing hooded hooks to which Marenzeller (1892) had drawn attention when comparing his specimens with the animals described by Wirén. Augener suspected that in larger animals the first hooded hook appeared more anteriorly.

Later, a spionid from Collinson Point (Alaska) that closely resembled the species described by Augener

(1913) was described as *Scolecolepides arctius* (Chamberlin, 1920). However, no comparison was made with Augener's findings, so we must assume that Chamberlin was unaware of it.

Holmquist (1967) described *M. wireni* from oligohaline (0.84‰) waters in Alaska. Comparing the location of her find with the known palaearctic occurence of the species (Annenkova, 1932; Ushakov, 1955), she concluded that the spionid was a euryhaline species with a circumpolar range of distribution. Besides other spionids, she mentioned *S. arctius* Chamberlin as one of the Arctic spionids whose species status and distribution require clarification. Again, no morphological comparison with the species was undertaken.

Having examined type material of *S. arctius*, Foster (1971: 40) synonymized it with *Scolelepis viridis* [transferred to *Scolecolepides* by Hartman (1942: 13)], a species common in the eastern estuaries of North America. This action greatly expandend the distribution range of Verrill's species (Alaska, and from Newfoundland to North Carolina). According to Foster, the species should not be regarded as an Arctic, but a typical estuarine species. Unfortunately, she neither discussed similarities between *S. arctius* and *M. wireni* nor gave the locations of palaearctic finds.

Maciolek (1984) revised the two contentious genera and the species of the genus *Marenzelleria*, mentioning the presence of acicular spines in a few anterior neuropodia of *Scolecolepides* as a diagnostic feature. Lacking acicular spines, *S. viridis* was assigned to the genus *Marenzelleria* (as *M. viridis*). In contrast to Foster (1971), Maciolek abided by the assumed circumpolar distribution of *M. wireni* and a boreal distribution for *M. viridis*. She had obviously overlooked Chamberlin's (1920) work as *S. arctius* does not appear in her list of synonyms. Maciolek's diagnosis of the genus *Marenzelleria* is also inaccurate as it states that the branchiate region of all animals in this genus extends over at least half the body length. This does not apply to one of the three species dealt with in her revision: branchiae are restricted to the anterior third of the body in *M. viridis*. Moreover, this feature, like the position of the first setiger bearing hooded hooks, depends on the size of the specimens (Bick, 1995).

Marenzelleria jonesi, a new species described by Maciolek (1984), is reported to differ from the two other species primarily in the shape of the prostomium and peristomium, and in body size. In the specimens we have studied, these features vary, sometimes considerably. In our opinion, therefore, these features are diagnostically unreliable. On the other hand, the other features she names do not allow synonymity with either of the two known species. The number of branchiate segments (115) and length of the anal cirri are characteristic of *M.* cf. *wireni*, but the presence of hooded hooks from setiger 52 on seems rather to indicate *M.* cf. *viridis*. Rodi & Dauer (1996), after comparative studies, concluded that *M. jonesi* is a synonym of *M. viridis* (*sensu* Maciolek, 1984).

Lack of precise knowledge concerning the areas of distribution and the examination of fragments have given rise to considerable confusion. Holmquist (1967) pointed out that work with anterior fragments can cause false determination. They can yield no exact information about the length of the branchiate region, the presence of notopodial and neuropodial hooks and the form and number of pygidial appendages, all of which are important diagnostic features among the spionids. This alone can explain how specimens of the genus *Marenzelleria* have been assigned to *Microspio* (cf. Söderström, 1920) or *Laonice* (cf. Ferguson & Jones, 1949; Annenkova, 1932). Even exact species determination from fragments is very difficult. For this reason, little can be said concerning the assignment of finds on Sylt (North Sea) to *M. wireni* and *Microspio wireni* (=*M. wireni*) by Wohlenberg (1937) and Otte (1979) as the specimens no longer exist and no morphological description were given.

The occurrence of the immigrants in the North Sea was beset with difficulties in ascertaining the species status (cf. Introduction). It was only the population genetic studies by Bastrop et al. (1995) and Röhner et al. (1996a) that showed the presence of genetically distinct types in the North Sea and Baltic Sea. The genetic distances between them were of a magnitude otherwise found only between different species. The inclusion of North American specimens in their research programme revealed that the different genotypes found in the North Sea and Baltic Sea are also found in different regions of North America (Röhner et al. 1996b).

The morphological studies undertaken against this background and presented here allowed good discrimination between the forms found in Europe (Table 1). We now know that the species found in the oligohaline to mesohaline parts of the Baltic Sea and North Sea (Elbe estuary) fit the description of *M. viridis* (*sensu* Maciolek, 1984) quite well. It also corresponds well with Foster's (1971) description of *M. viridis* (syn. *S. viridis*), which also synonymized this species with *S. arctius*. Likewise, the species found in the mesohaline to polyhaline regions of the North Sea matches quite

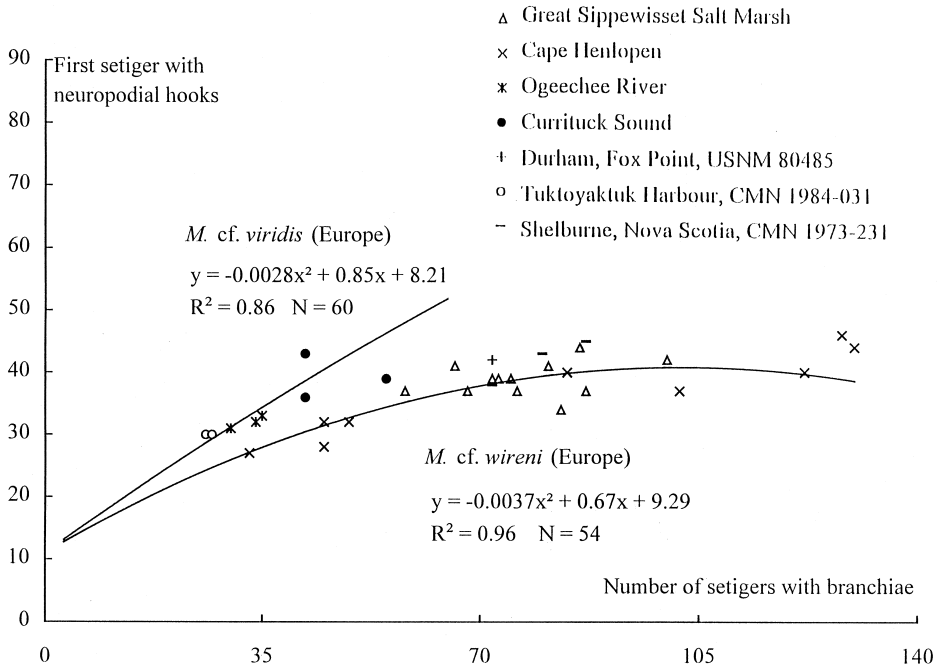

Figure 9. Relation between number of branchiate setigers and number of the setiger with the first hooded hook in the neuropodium. The regression is based on examination of specimens from various North Sea and Baltic Sea estuaries. Specimens from North America were plotted on the basis of their features.

Table 1. Diagnostic features to facilitate differentiation between adult specimens of *M.* cf. *viridis* and *M.* cf. *wireni*

Diagnostic features	*Marenzelleria* cf. *viridis*	*Marenzelleria* cf. *wireni*
Nuchal organ	up to setiger 3	up to setiger 2
Number of branchiate setigers	max. 65 setiger, i.e., less than one third of total number of setiger	max. 130 setiger, i.e., one half or more of total number of setiger
First appearance of neuropodial hooded hook	not beyond setiger 48	not beyond setiger 42 or 46
Number of hook-bearing branchiate setigers	usually less than 20 setiger	many more than 20 setiger
Anal cirri	8–10 anal cirri relatively short	12–16 anal cirri, relatively long

well with the description of *M. wireni* (*sensu* Maciolek, 1984).

None of the other currently existing descriptions based on anterior fragments or juveniles and making no reference to the size of the specimens examined can be considered reliable.

Information on the distribution of the animals might help distinguish between the species. Fritzsche (1995) has shown that the species *M.* cf. *viridis* found in the Baltic Sea (Form II) has a lower tolerance to salinity and therefore denotes it a genuine brackish water species. We have also found Form II (*M.* cf. *viridis*) in an oligohaline reach of the lower Elbe ($S = 0.5‰$). The first *M.* cf. *viridis* specimen found in a North Sea estuary, this demonstrates that the two species can at least occur parapatrically. Examination has also revealed that the specimens collected by Leling (1986) in the Elbe are definitely *M.* cf. *wireni* (ZMH-P 19071). The

specimens found in polar estuaries may thus also be of Form II (*M.* cf. *viridis*). This seems particularly likely as specimens identified as *M. arctius* (Chamberlin, 1920) in the Canadian Museum of Nature, which unfortunately consisted only of anterior fragments, agreed with this form (Figure 9). Moreover, the resemblance to the description given by Sikorsky et al. (1988) for specimens collected in Russian polar estuaries (White Sea – Kamchatka) is very strong, although the authors, in line with current views on the distribution of *Marenzelleria*, identified their material as *M. wireni*. Assignment to *M.* cf. *viridis* also seems appropriate for the specimens we studied from Ogeechee River (1–2‰) and Currituck Sound (4‰) (Figure 9). The results of our taxonomic studies are in accordance with the results of the population genetic analysis performed concurrently by Röhner et al. (1996b).

Augener's type material of *M. wireni* consists of anterior fragments only and does not allow exact determination of the branchiate region. Branchiae are present up to the last setigers of the longest fragment (78 setigers). However, it is difficult to ascertain the setiger on which hooded hooks begin as many hooks and setae are broken off. The shape and length of the nuchal organ are also difficult to determine. In view of the length of the branchiate region, at least the longest fragment appears to belong to Form I (= *M.* cf. *wireni*). The two other fragments cannot be identified unambiguously owing to the absence of important features.

Augener (1913) also falsely interpreted the previously mentioned differences in the setiger on which hooded hooks first appear. Contrary to his assumption, the first hooks appear on a later setiger in adults than in juveniles (Figures 6 and 7). This would mean that Wirén (1883), Marenzeller (1892) and Augener (1913) may have been considering different species. If this is so, both species may occur in polar regions.

The results of the morphological studies presented here and the genetic analyses of others (Röhner et al. 1996b; Bastrop et al., 1997) can account for the specimens from North America and Europe with two exceptions. First, apart from a few *M.* cf. *viridis*, the specimens collected in Currituck Sound included one genotype that corresponded to neither of the two known types and was consequently referred to a third form ('Type III' of Röhner et al., 1996b). During our studies we found one specimen (*Marenzelleria* sp. A), also from this area, with more or less clear morphological differences to the two species described here. It is impossible to say with certainty that this specimen corresponded to this third genetic form as the results of subsequent DNA analysis on part of this specimen were equivocal. Furthermore, as the specimen consisted only of a fragment, it is not possible to render a complete description and assign a name at the present.

The second exception concerns the material from New Hampshire, Durham, Fox Point (USNM 80485). Two of the three fragments in this material correspond to the Form II, *M.* cf. *viridis* (Baltic populations of Bastrop et al., 1997). DNA analysis yielded no conclusive result for the third. Morphological examination, however, revealed great similarity to Form I (*M.* cf. *wireni*) (Figure 9). Unfortunately, only one specimen could be considered reasonably identifiable including all branchiate setigers (87 setigers altogether, 72 branchiate setigers, 30 hook-bearing setigers). Another fragment (64 setigers) had 64 branchiate setigers and the hooded hooks began on setiger 41. This combination of features also seems to favour assignment to *M.* cf. *wireni* (Figure 8). So far it has been impossible to resolve this one contradiction between the genetic and morphological studies.

We have abstained from naming the two species as definite assignment was impossible on the basis of the Forms: the available type material of *M. wireni* (ZMH-PE 890) does not permit assignment, and that of *M. viridis* no longer exists. However, the two species can easily be distinguished on the basis of the diagnoses given here. Nevertheless, the description of neotypes for *M. wireni* and *M. viridis* appears necessary, and boreal and polar populations require checking with regard to their species.

This is not the first time that morphological differences have been identified after the genetic differentiation of polychaetes (e.g. Rice & Simon, 1980; Schmidt & Westheide, 1994). The example of *Marenzelleria* spp. shows once again that systematics and the distribution of species can be clarified by a combination of genetic and morphological studies. In fact, this approach seems to be very fruitful in the case of species with highly variable features and features that change in the course of development.

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