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ORIGINAL PAPER

A contribution to the taxonomy of *Spio* (Spionidae, Polychaeta, Annelida) occurring in the North and Baltic Seas, with a key to species recorded in this area

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Abstract In order to resolve taxonomic problems known from literature and diagnostic practices, *Spio* species currently recognised in the North Sea and the Baltic Sea have been re-examined. *Spio* species recorded in the area of interest are *S. decoratus*, *Spio* cf. *filicornis, S. goniocephala, S. martinensis*, and *S. armata*. *Spio decoratus* is restricted to the North Sea, whereas *S. armata* occurs only in the Baltic Sea. Revised descriptions with illustrations and notes on the distributions, as well as remarks on size-dependent differences of characters, are presented for all species. Specimens of *Spio* from the North and Baltic Seas, which are assigned to *S. filicornis* based on current taxonomic literature, exhibit significant morphological differences, and are here regarded as two different species. A definite assignment of specimens from the two morphological distinct groups to one of the known *Spio* species was impossible based on the material available. The significance of diagnostic characters used for the identification of *Spio* spp. is discussed. An identification key to *Spio* species found in the investigation area is provided.

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Introduction

Within the Spionidae, about 28 species of the genus *Spio* Fabricius, 1785 are currently considered valid (Maciolek 1990; Blake 1996; Sikorski 2001). However, *Spio* species show great morphological similarity, and usually only a few characters have been used to separate them (Maciolek 1990). Such characters include the shape of the anterior margin of the prostomium, the length of the branchiae on the first chaetiger, the first appearance as well as the number of neuropodial hooded hooks, and the number of apical teeth on these hooks. Because many taxonomic character states are shared by different species, unambiguous identification of *Spio* species is often very difficult and several authors have indicated the need for a generic revision (Holmquist 1967; Foster 1971; Blake and Kudenov 1978; Maciolek 1990; Worsaae 1999).

The present paper deals with *Spio* species from the North and Baltic Seas. According to Bergfeld and Kröncke (2003) six species occur in this region: *Spio filicornis* (Müller, 1776), *S. goniocephala* Thulin, 1957, *S. armata* (Thulin, 1957), *S. decoratus* Bobretzky, 1870, *S. martinensis* Mesnil, 1896, and *S. multioculata* Rioja, 1918. Several taxonomic problems have been discussed in relation to these species. For example, both *S. martinensis* and *S. goniocephala* have been considered junior synonyms of *S. filicornis* [Söderström 1920 and Hartmann-Schröder (cited in: Bick and Gosselck 1985)]. *Spio armata* was considered as *incertae sedis* by Maciolek (1990) and later synonymised with *S. goniocephala* by Hartmann-Schröder (1996).

Böggemann (1997) doubted records of *S. decoratus* from northern waters. *Spio multioculata* has been recorded only once in the investigation area (as larvae from the Gullmar Fjord, Kattegat, Sweden) by Hannerz (1956), but he himself had doubts about his findings.

The study presents revised species descriptions of *Spio* found in the North and Baltic Seas including new illustrations and notes on their distribution. Moreover, we document that certain morphological characters are size-dependent, and their usefulness in diagnoses is discussed. An identification key to all *Spio* known from the investigation area is provided, and a major step towards a revision of the genus is taken.

Material and methods

The material examined in this study comes predominately from several regions in the North Sea and in the Baltic Sea. Also, *Spio* specimens from West Greenland were examined. In addition, the types of *S. armata* and *S. goniocephala* were studied.

Polychaetes were investigated using light and scanning electron microscopy (SEM). Shirlastain A was applied to improve the visualisation of some characters, e.g. tiny or papillate branchiae on chaetiger 1, and the length and shape of nuchal and metameric dorsal ciliated organs. Measurements of width refer to the distance between the distal-most structures on the widest chaetiger seen in dorsal view (without parapodia and chaetae). Drawings were made using a camera lucida attached to a light microscope; the anterior ends were drawn without camera lucida. Since the capillaries of the species under consideration are similar, capillaries were illustrated only for *S. goniocephala*.

Because of taxonomic problems mentioned in the introduction, information on distribution given in this paper is only based on material investigated here. For the same reason, it was abstained from the presentation of synonymy lists for the two species listed as *Spio* cf. *filicornis* (either from the North Sea or from the Baltic Sea) in this paper. Additional information included in the diagnoses from the literature is indicated as such.

For SEM studies specimens were dehydrated in a graded ethanol series, critical-point dried, attached to aluminium stubs, sputter coated with gold palladium and examined with a Zeiss DSM 960 A scanning electron microscope.

The material examined was borrowed from the following museums and institutions: Landesamt für Natur und Umwelt des Landes Schleswig-Holstein, Flintbek, Germany (LANU); MariLim, Kiel, Germany (ML); Institut für Angewandte Ökologie, Broderstorf, Germany (SBRO); Senckenberg Museum Frankfurt, Germany (SMF); Zoologisk Museum, Københavns Universitet, Denmark (ZMUC); Zoologische Sammlung der Universität Rostock, Germany (ZSRO). Type material was borrowed from Zoologiska Museet, Lunds Universitet, Sweden (L).

Results

Spionidae, Grube, 1850
Genus *Spio* Fabricius, 1785
Type species: *Nereis filicornis* Müller, 1776
Type locality: Iluilârssuk, near Frederikshaab (Paamiut), Westgreenland
Synonym: *Paraspio* Czerniavsky, 1881; type species: *Spio decoratus* Bobretzky, 1870, by monotypy. *Euspio* McIntosh, 1915; type species: *Euspio mesnili* McIntosh, 1915.

Description Prostomium anteriorly rounded or slightly incised, lacking frontal or lateral horns; eyes present or absent; digitiform occipital tentacle absent, but posterior portion of prostomium may be raised or inflated. Paired recurved nuchal organs extending onto chaetiger 2 or 3. Metameric dorsal ciliated organs present. Branchiae present from chaetiger 1, continuing throughout body, branchiae completely separate from or basally fused with notopodial lamellae, branchiae often reduced in size on chaetiger 1. Notochaetae all capillaries; neurochaetae capillaries anteriorly, capillaries, hooded hooks and inferior sabre chaetae on middle and posterior chaetigers. Pygidium with four anal cirri.

Spio armata (Thulin, 1957)
Figures 1, 9f, 11, 12
Microspio armata Thulin, 1971: 57–61, Fig. 4.
Spio armata—Hartmann-Schröder 1971: 302–304, Fig. 102.—Sikorski 2001: 319–321, Figs. 1–11.
Type material. Holotype: Øresund, between Landskrona and Ven, Sweden, several middle fragments (L 916/3745).

Non-type material Baltic Sea: 54°21.99′N, 11°15.63′E, 26 May 1997, sand, 17 m, two specimens (ZSRO-P 390); 54° 34.32′N, 11°20.14′E, 25 June 1997, sand/mud, 27 m, two specimens (ZSRO-P 483); 54°35.191′N, 10°57.231′E, 20 August 2004, coarse sand, 17 m, one specimen (ZSRO-P 1667); 54°36.860′N, 11°00.753′E, 21 August 2004, one specimen.

Description Only fragments available; maximum number of chaetigers 59 (width 0.53 mm), maximum width 0.63 mm (anterior fragment with 42 chaetigers).

Prostomium anteriorly bluntly rounded or slightly convex, anterior part distinctly extended; posterior end short, extending to chaetiger 1, tapered (Fig. 1a); two pairs of black eyes, arranged trapezoidally, anterior pair crescent-

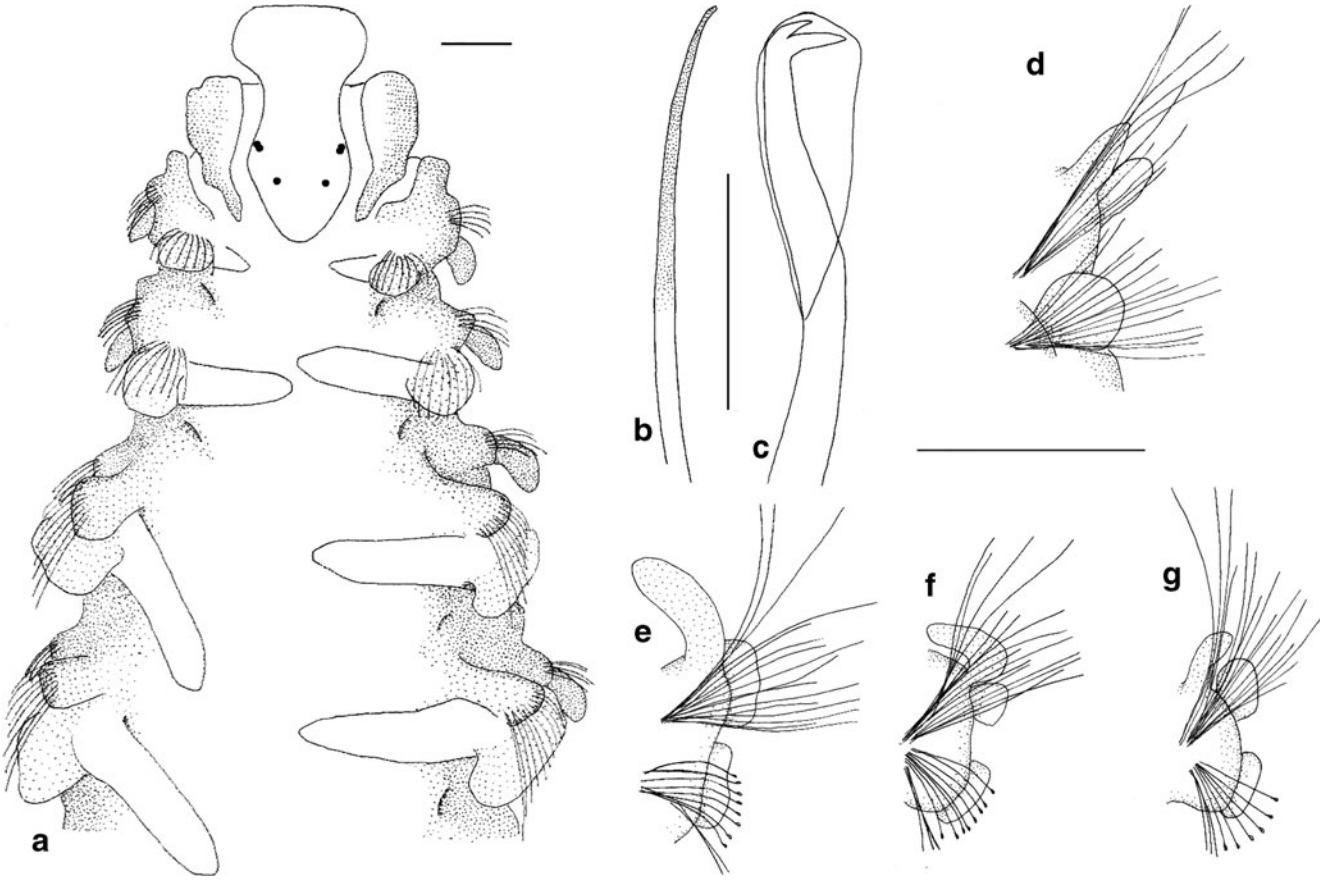

Fig. 1 *Spio armata* (Thulin, 1957). **a** Anterior end, dorsal view (pigment typical for the species (see diagnosis) partially lacking in illustrated specimen); **b** ventral sabre chaeta from chaetiger 34; **c** neuropodial hooded hook from chaetiger 34; **d** chaetiger 1 anterior view; **e** chaetiger 24, anterior view; **f** chaetiger 34, anterior view; **g** chaetiger 48, anterior view. (*Scale bar*: **a** 125 μm; **b, c** 64 μm; **d** 320 μm; **e–g** 640 μm)

shaped or rounded, posterior pair oval; prostomium distinctly separated from peristomium by a furrow (Fig. 1a).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Fig. 9f). Metameric dorsal ciliated organs double-paired, present from between branchiae 3 and 4, posterior extension not known (Fig. 9f).

Branchiae present from chaetiger 1 until almost to the end of the body, only the last eight to ten chaetigers without branchiae; branchiae on chaetiger 1 small, slightly longer or as long as notopodial postchaetal lamellae; branchiae with narrow base, tapered distally (Fig. 1a), becoming thinner and shorter in posterior chaetigers; on anterior chaetigers, branchiae fused basally with notopodial postchaetal lamellae, increasingly separated from lamellae in subsequent chaetigers (Fig. 1d–g); branchiae not touching mid-dorsally on anterior chaetigers; length of branchiae decreasing posteriorly.

First notopodium shifted dorsally. Notopodial postchaetal lamellae in anterior chaetigers oval, becoming shorter and rounded in subsequent chaetigers, on posterior chaetigers lamellae large, rounded (Fig. 1d–g). Neuropodial postchaetal lamellae rounded in chaetiger 1 (Fig. 1d), oval in other anterior chaetigers, becoming smaller and shorter in posterior chaetigers (Fig. 1e–g).

Alcohol-preserved specimens with dark brown pigment on anterior part of body: pigmented patches between peristomium and first chaetiger; scattered pigment dorsolaterally before and/or behind transverse ciliary bands and around metameric dorsal ciliated organs; longitudinal pigmented stripes on peristomium indistinct; median pigmented patch laterally between parapodia and on edges of notopodial postchaetal lamellae, close to branchiae.

Notopodial chaetae all limbate capillaries; capillaries of anterior chaetigers arranged in two rows: capillaries of anterior row short, broad, uniformly granulated (as in *S. goniocephala*, Fig. 5f), capillaries of posterior row longer, thinner, lacking granulations (as in *S. goniocephala*, Fig. 5g); additional superior fascicle of very long and thin capillaries without granulations; capillaries of posterior chaetigers arranged in irregular rows, in last three to five posterior-most chaetigers row not clearly discernable. Neuro-

podia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; capillaries of anterior neuropodia arranged in two rows similar to notopodial chaetae; from chaetiger 17 posterior row replaced by single row of six to eight hooded hooks, accompanied by alternating short, thin, alimbate non-granulated capillaries (as in *S. goniocephala*, Fig. 5e); hooks bidentate, strongly curved, slightly narrowed subdistally, with long hood and conspicuous large main fang at nearly right angle to shaft (Fig. 1c); inferior fascicles with long, thin, limbate capillaries, without granulations, replaced from about chaetiger 16/17 by two to four sabre chaetae, each uniformly granulated (Fig. 1b).

Pygidium unknown.

Distribution and ecology Western Baltic Sea, Øresund (from literature: North Sea, Norwegian Sea, Arctic Ocean); sublittoral; clay, sand.

Remarks Spio armata is readily identified by the following combination of characters: short branchiae on chaetiger 1, strongly curved hooded hooks with a conspicuous large main fang present in neuropodia from chaetiger 17, co-appearance of ventral sabre chaetae and hooded hooks from chaetiger 17, and rounded notopodial postchaetal lamellae in posterior chaetigers, rather than elongate lamellae as found in other species in the North and Baltic Seas.

In *S. armata*, the first appearance of hooded hooks might vary with the size of the specimen. In Arctic specimens, hooded hooks are reported to be present from chaetiger 8 to 20, i.e., from chaetiger 8 to 11 in small specimens and from chaetiger 18 to 20 in large specimens (Sikorski 2001). Thulin (1957) observed hooded hooks to start on chaetiger 14 and 16. For this study only six anterior fragments of comparable length were available for investigation. Therefore it was not possible to demonstrate a correlation between size and the start of hooded hooks for the Baltic Sea specimens (Fig. 11), although it might exist.

The type material of *S. armata* consists of some middle fragments only, all without prostomium and pygidium. These fragments were selected among *S. filicornis* specimens and assigned to *S. armata* by Anders Eliason after the death of Thulin. The shape of the hooded hooks differs considerably between these two species. Now these fragments are actually labelled as holotype of *S. armata* and are kept in the Museum of Zoology in Lund, Sweden. Because *S. armata* was originally described from the Baltic Sea and no other species in North and Baltic Seas exhibits these hooks with long hood and conspicuous large main fang, the type material and original description are considered adequate to recognize the species. However, Maciolek (1990) considered this species to be *incertae sedis*. For this reason, additional specimens from the type-locality (Øresund) could be necessary to allow a doubtless determination of this species in the future.

Spio decoratus Bobretzky, 1870
Figures 2, 9b, 11, 12
Spio decoratus Bobretzky, 1870: 256–257, Fig. 74–77.—Giordanella 1969: 347, Fig. 1.—Guerin 1972: 330–337, Figs. 1, 2 and 3.—Dauvin 1989: 169–170, Fig. 1.—Giangrande 1992: 87–89, Figs. 2, 3 and 4.—Böggemann 1997: 120, Fig. 94.
Spio filicornis—Fauvel 1927: 43–44, Fig. 15A–G (partim).

Non-type material North Sea: 54°43.38′N, 8°03.50′E, 12 August 1997, sand, 13 m, ten specimens (ZSRO-P 442); 54°25.86′N, 8°10.13′E, 11 August 1997, sand, 18 m, six specimens (ZSRO-P 484); 60°36.99′N, 2°46.07′E, 6 May 1998, mud, 110 m, one specimen (ZSRO-P 720); 54°43.93′N, 8°03.48′E, 18 August 1998, sand, 13 m, three specimens (ZSRO-P 905); 55°17.665′N, 6°47.913′E, 13/16 May 2000, sand, 30 m, one specimen (ZSRO-P 1555); 55°08.403′N, 6°40.302′E, May 2002, muddy sand, 39 m, four specimens (SBRO-P 67); 54°02.207′N, 6°55.016′E, March 2002, fine sand, 32 m, two specimens (SBRO-P 225); 54°01.709′N, 6°50.454′E, May 2003, muddy sand, 30.5 m, four specimens (SBRO-P 1292).

Description Specimens with up to 50 chaetigers (width 0.5 mm), maximum width 0.63 mm (anterior fragment with 30 chaetigers).

Prostomium anteriorly bluntly rounded, anterior part slightly to distinctly extended; posteriorly extending to chaetiger 1, tapered (Fig. 2a); two pairs of black eyes, arranged in trapezoid or rectangle, anterior pair crescent-shaped or rounded, posterior pair oval; prostomium distinctly separated from peristomium by a furrow (Fig. 2a).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands posteriorly curved and go only partly back to the transverse ciliary band of chaetiger 2 (Fig. 9b). Metameric dorsal ciliated organs double-paired, present from between branchiae 5 and 6 (Fig. 9b); middle chaetigers with additional short transverse ciliary band between the long transverse ciliary bands connecting the branchiae (Fig. 9b).

Branchiae from chaetiger 1, continuing to near end of body; branchiae on chaetiger 1 long, almost as long as those on following chaetigers; branchiae with broad base, tapered distally (Fig. 2a), becoming thinner and shorter with narrow base in posterior chaetigers; branchiae on anterior chaetigers fused basally with notopodial postchaetal lamellae, separated from lamellae in posterior chaetigers (Fig. 2d–g); branchiae not reaching dorsal midline on anterior chaetigers, length of branchiae decreasing in subsequent chaetigers.

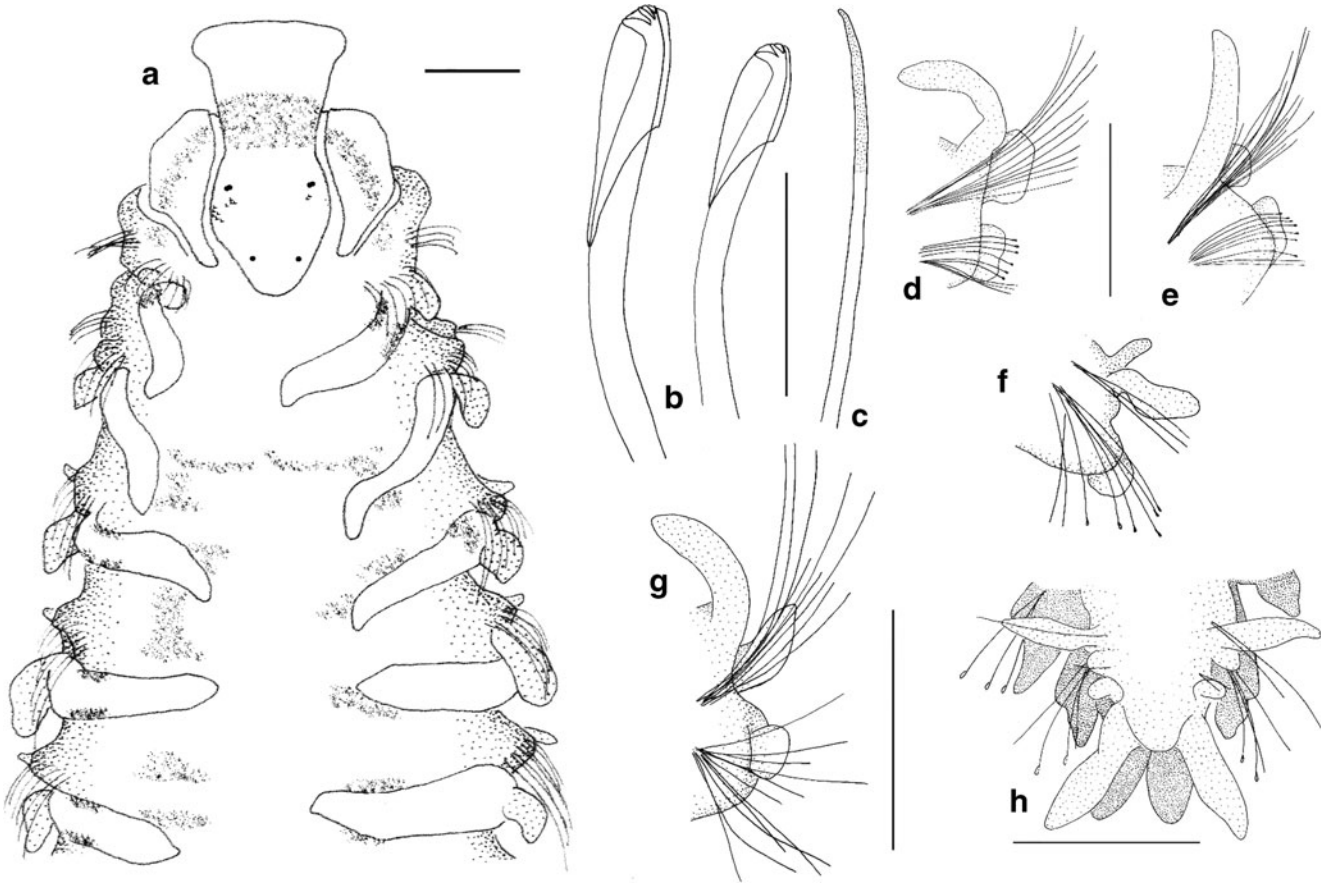

Fig. 2 *Spio decoratus* Bobretzky, 1870. **a** Anterior end, dorsal view; **b** neuropodial hooded hooks from chaetiger 34; **c** ventral sabre chaeta from chaetiger 34; **d** chaetiger 11, anterior view; **e** chaetiger 24, anterior view; **f** chaetiger 40, anterior view; **g** chaetiger 1, anterior view; **h** pygidium, dorsal view. (*Scale bar*: **a** 0.125 mm; **b, c** 64 μm; **d-f** 640 μm; **g** 320 μm; **h** 160 μm)

First notopodium shifted dorsally. Notopodial postchaetal lamella slightly pointed on chaetiger 1, oval in other anterior chaetigers, becoming shorter and rounded in subsequent chaetigers, elongated in posterior chaetigers (Fig. 2d–g). Neuropodial postchaetal lamellae rounded in chaetigers 1 and 2, oval in other anterior chaetigers, becoming smaller and shorter in middle chaetigers, rounded in posterior chaetigers (Fig. 2d–g).

Alcohol-preserved specimens with dark-brown pigment on anterior part of body: prostomium and peristomium of juveniles completely pigmented, adults dorsally with broad transverse pigmented stripe on prostomium and peristomium, longitudinal pigmented stripes between prostomium and peristomium stable in alcohol and formalin-preserved specimens; scattered pigment dorso-laterally on anterior chaetigers before and/or behind transverse ciliary bands and at the end of nuchal organs (Fig. 2a); scattered pigment ventrally on peristomium; short median pigmented stripe ventrally between anterior chaetigers; pigmented patches ventro-laterally on base of neuropodia; a median pigmented patch between parapodia of subsequent chaetigers; isolated pigmented stripes laterally before and/or behind noto- and neuropodia; one to two pigmented patches on branchiae near base.

Notopodial chaetae limbate capillaries with those of anterior chaetigers arranged in two rows: capillaries of anterior row short, broad, uniformly granulated (as in *S. goniocephala*, Fig. 5f); chaetae of posterior row longer, thinner, lacking granulations (as in *S. goniocephala*, Fig. 5g); additional superior fascicle of long, thin capillaries without granulations; capillaries of posterior notopodia arranged in irregular rows, thin, non-granulated, of different lengths. Neuropodia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; capillaries of anterior chaetigers arranged in two rows, similar to notopodial chaetae; posterior row replaced by a single row of nine to 11 hooded hooks from chaetiger 11 (Fig. 11), accompanied by alternating short, thin, alimbate, non-granulated capillaries (as in *S. goniocephala*, Fig. 5e); hooks tridentate, with long hood, slightly narrowed subdistally; third tooth distinct, rarely surmounted by fourth apical tooth (Fig. 2b); inferior fascicle with one to three long, thin, limbate capillaries, without granulations, replaced from about chaetiger 20 by two to three sabre chaetae, each uniformly granulated (Fig. 2c).

Pygidium with four anal cirri; dorsal pair longer than ventral pair or of same length; dorsal pair slender, cirriform, widely spaced; ventral pair broad and oval, closely spaced, touching each other at base (Fig. 2h).

Distribution and ecology North Sea, [from literature: Black Sea, Mediterranean Sea, Northeast Atlantic, Arctic Ocean (?)]; sublittoral; coarse and fine sand.

Remarks Spio decoratus differs from other *Spio* species in the North and Baltic Seas by its comparatively small size. Furthermore, it possesses a characteristic broad transverse pigmented band on the prostomium and peristomium and tridentate hooded hooks with a clearly discernible third tooth.

Juvenile specimens of *Spio* cf. *filicornis* (North Sea), in particular, are morphologically very similar to *S. decoratus*. Both species are conspicuously pigmented and possess tridentate hooded hooks from chaetiger 11 (Fig. 11). A character that can be used to separate these species is the furrow between the prostomium and peristomium which is present in *S. decoratus* and absent in *Spio* cf. *filicornis* (North Sea). *Spio decoratus* also differs from *Spio* cf. *filicornis* (North Sea) in having a broad transverse pigmented band on prostomium and peristomium rather than randomly distributed pigmented patches, metameric dorsal ciliated organs beginning between branchiae 5 and 6 rather than branchiae 4 and 5, and the lateral ciliary bands of the nuchal organs go only partly back to the transverse ciliary band of chaetiger 2 and not completely as in *S.* cf. *filicornis* (North Sea). In *S. decoratus* the third apical tooth of the hooded hooks is clearly visible, but is hardly discernable in *Spio* cf. *filicornis* (North Sea).

There is still uncertainty whether the specimens from the North Sea actually are *S. decoratus sensu* Bobretzky 1870 since neither type material nor material from the type locality (Black Sea) was available. The morphological characteristics of the specimens from the North Sea are in good agreement with the descriptions of *S. decoratus* from the English Channel (Dauvin 1989). However, *S. decoratus* from the Black Sea possesses bidentate hooded hooks, and the transverse pigmented band on the peristomium and peristomium is absent (Bobretzky 1870). Later Giordanella (1969) examined some material from the Black Sea and described the hooks as tridentate, modifying Bobretzky's description in this aspect.

Spio cf. *filicornis* (North Sea)

Figures 3, 9d, 10a–d, 11, 12

Non-type material North Sea: 55°17.665′N, 6°47.913′E, 15 October 2003, sand, 28 m, 14 specimens (ZSRO-P 1554); 54°59.70′N, 7°06.40′E, 15 October 2003, sand, three specimens (ZSRO-P 1861); 55°08.403′N, 6°40.302′E, May 2002, fine sand, 30 m, four specimens (SBRO-P 63); 55°08.403′N, 6°40.302′E, September 2002, sand, 37 m, four specimens (SBRO-P 64); 55°13.060′N, 6°51.297′E, September 2002, sand, 29 m, four specimens (SBRO-P 65); 54°35.571′N, 6°21.456′E, Autumn 2002, muddy sand, 40 m, two specimens (SBRO-P 445); 54°03.686′N, 7°15.390′E, August 2003, muddy sand, 25.5 m, three specimens (SBRO-P 845); 54°02.207′N, 6°55.016′E, September 2003, muddy sand, 33 m, three specimens (SBRO-P 1313).

Description Only fragments available, maximum number of chaetigers 58 (width 0.75 mm), maximum width 1.4 mm (anterior fragment with 45 chaetigers).

Prostomium anteriorly rounded, antero-lateral part slightly expanded; posterior part of prostomium pointed, extending posteriorly to chaetiger 1 (Fig. 3a); two pairs of black eyes present, with anterior pair crescent-shaped and widely spaced, posterior pair oval, closely spaced; prostomium and peristomium not distinctly separated by a furrow (Fig. 3a).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands outward curved in the range of the first transverse ciliary band, posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Figs. 9d, 10a). Metameric dorsal ciliated organs double-paired, present from between branchiae 4 and 5 continuing to branchiae 32 and 33 (Figs. 9d, 10c–d); middle chaetigers with short transverse ciliary band between metameric dorsal ciliated organs and long transverse ciliary bands connecting branchiae (Figs. 9b, 10b).

Branchiae present from chaetiger 1, continuing nearly to end of body; branchiae on chaetiger 1 long, nearly as long as those on following chaetigers; branchiae with narrow base, tapered distally (Fig. 3a), becoming thinner and shorter in posterior chaetigers; branchiae on anterior chaetigers fused basally with notopodial postchaetal lamellae; branchiae separated from lamellae in posterior chaetigers (Fig. 3b–e); branchiae not reaching dorsal midline, length of branchiae decreasing posteriorly.

First notopodium shifted dorsally. Notopodial postchaetal lamella on chaetiger 1 elongate, narrow and slightly pointed apically (Fig. 3b), in other anterior chaetigers short and wide (Fig. 3c), becoming smaller and rounded in middle (Fig. 3d) and again long and narrow in posterior chaetigers (Fig. 3e). Neuropodial postchaetal lamellae elongate and rounded on chaetigers 1 and 2 (Fig. 3b), short and wide in other anterior and middle chaetigers (Fig. 3c, d) and rounded in posterior chaetigers (Fig. 3e).

Alcohol-preserved specimens with dark-brown pigment on anterior part of body: pigmented stripes and patches on dorsal part of prostomium and peristomium; anterior chaetigers completely pigmented dorsally, pigment absent

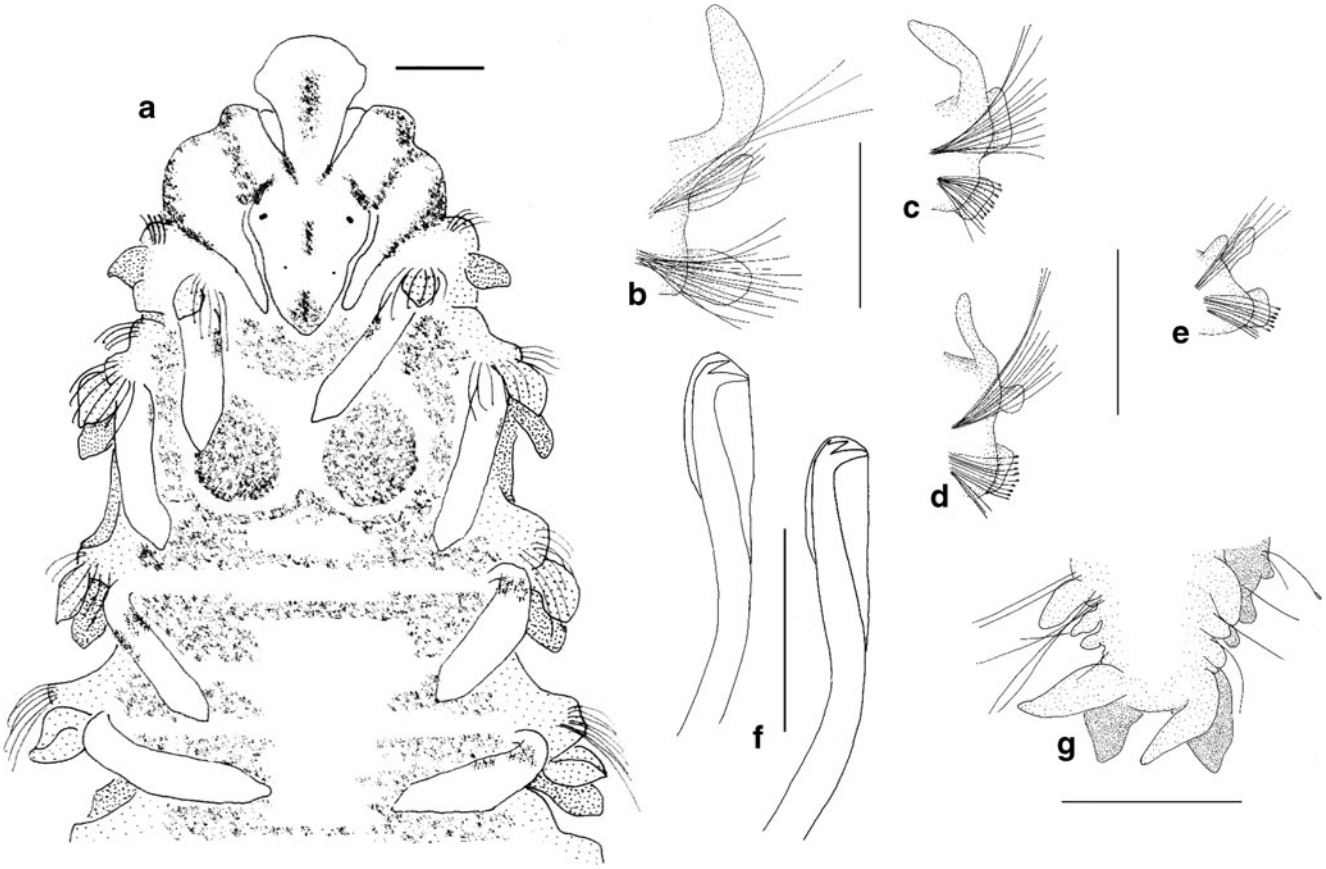

Fig. 3 *Spio* cf. *filicornis* (Müller, 1776) from the North Sea. **a** Anterior end, dorsal view; **b** chaetiger 1, anterior view; **c** chaetiger 11, anterior view; **d** chaetiger 34, anterior view; **e** chaetiger 56, anterior view; **f** neuropodial hooded hooks from chaetiger 34; **g** pygidium, dorsal view. (*Scale bar*: **a** 125 μm; **b** 320 μm; **c–e** 640 μm; **f** 64 μm; **g** 320 μm)

only where nuchal organs, metameric dorsal ciliated organs and transverse ciliary bands occur; pigmented patches present dorso-laterally anterior to and/or posterior to transverse ciliary bands and at end of nuchal organs (Fig. 3a); indistinct longitudinal pigmented stripes present on ventral side of peristomium; pigment bordering anterior chaetigers ventrally, with short median disrupted pigmented stripe, not fading in alcohol; median pigmented patch between neuro- and notopodia present; pigmented stripes present laterally before and/or behind notopodia; base of branchiae with one to two short longitudinal pigmented stripes, also visible in alcohol preserved specimens (Fig. 3a); pigmented patches on palps and large pigmented patch on base.

Notopodial chaetae all limbate capillaries; notochaetae of anterior chaetigers arranged in two rows: chaetae of anterior row short, broad, uniformly granulated (as in *S. goniocephala*, Fig. 5f); chaetae of posterior row longer, thinner, lacking granulations (as in *S. goniocephala*, Fig. 5g); additional superior fascicle of long, thin capillaries without granulations present; chaetae of posterior chaetigers arranged in irregular rows, with capillaries thin, non-granulated, with variable length. Neuropodia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; capillaries of anterior neuropodia arranged in two rows, similar to notochaetae; posterior row replaced by single row of 10–12 hooded hooks from chaetiger 11 (rarely from chaetiger 10, Fig. 11), accompanied by alternating short, thin, alimbate, non-granulated capillaries (as in *S. goniocephala*, Fig. 5e); hooks with long hood, slightly narrowed subdistally, usually bidentate, rarely (and only in juveniles) tridentate, third tooth barely visible (Fig. 3f); inferior fascicle with two to four long, thin, limbate capillaries without granulations, replaced by two to three sabre chaetae from about chaetiger 20–24, each uniformly granulated (Fig. 5d).

Pygidium with four anal cirri of similar length; dorsal pair slender, cirriform, widely spaced; ventral pair broad, and cone-shaped, closely spaced (Fig. 3g).

Distribution and ecology North Sea; sublitoral; fine sand, coarse sand, gravel.

Remarks We have abstained from naming the species, as definite assignment was impossible on the basis of the

available material. Based on previously used diagnostic characters, the species could have been identified as *Spio filicornis* (Müller, 1776). But the same applies to specimens from the Baltic Sea in this paper referred to as *Spio* cf. *filicornis* (Baltic Sea). However, specimens of *Spio* cf. *filicornis* from the North and Baltic Seas exhibit significant morphological differences and we regard them as two different species. Hence, it has to be decided whether one of the two species indeed represents *Spio filicornis*. The type material of *S. filicornis* no longer exists [see also Remarks on *Spio* cf. *filicornis* (Baltic Sea)]. An assignment of *Spio* cf. *filicornis* (North Sea) to a valid species or a description of a new species will not be possible until specimens from the *locus typicus* of *S. filicornis* near Paamiut, Greenland (see Worsaae 1999) are obtained and a neotype is designated. At this point, it should be mentioned that there is a mix-up in regard to the type-locality of *S. filicornis* in the literature. The type locality of *S. filicornis* was stated to be Denmark instead of West Greenland by Hartman (1959) and Maciolek (1990). Though Greenland in former times was part of Denmark and even today still is an autonomous country within the Kingdom of Denmark the type locality should certainly rather be stated to be Greenland. *Spio filicornis* was described by Otto Friderich Müller (1776) in his *Zoologiae Danicae Prodomus*. After a very short description, Müller (1776) noted that he had received the specimens from Greenland by Otto Fabricius. Fabricius was a missionary in the Frederikshaab colony in Greenland from 1768 to 1773, where he collected various animals. These animals have been described in more detail in his comprehensive work *Fauna Groenlandica* (1780). First illustrations of this species, and some remarks about the habitat in Greenland and the biology were given also by Fabricius (1785).

Spio cf. *filicornis* (North Sea) differs from other *Spio* species in the North and Baltic Seas by the characteristic fusion of prostomium and peristomium. Whereas in juveniles three conspicuous teeth on hooded hooks are present, the third tooth is minute or completely absent in adults. Branchiae on chaetiger 1 are nearly as large as those on subsequent chaetigers in adults, but they are small and barely as large as the notopodial postchaetal lamella in juveniles. A comparable delayed development of the first branchiae was described for *Spio setosa* Verrill, 1873: newly settled juveniles (<30 chaetigers) of this species lack branchiae on chaetigers 1 and 2 (Simon 1967, 1968). Juveniles of *Spio* cf. *filicornis* (North Sea) are very similar to *S. decoratus* (for differentiation see Remarks under *S. decoratus*).

Morphological differences between specimens of *Spio* cf. *filicornis* from the North and Baltic Seas are significant. The prostomium and peristomium are fused and pigmented patches on the peristomium are randomly distributed in North Sea specimens, whereas in specimens from the Baltic Sea the prostomium and peristomium are distinctly separated and the peristomium is dark-brown pigmented. Although specimens from the North and Baltic Seas have large branchiae on chaetiger 1 and hooded hooks first appear on chaetiger 11, there are differences in the shape of the branchiae on the anterior chaetigers and hooded hooks. In North Sea specimens, the branchiae of anterior chaetigers are large but do not touch dorsally whereas in Baltic Sea specimens they touch each other. Furthermore, the hooded hooks of North Sea specimens are bi- (adults) or tridentate (juveniles), slightly narrowed subdistally and exhibit a long hood (Fig. 3f), whereas the hooks of Baltic Sea specimens are always bidentate, not narrowed subdistally and possess a short hood (Fig. 4d). Hence, *Spio* cf. *filicornis* (North Sea) and *Spio* cf. *filicornis* (Baltic Sea) are here considered to be two different species.

Spio cf. *filicornis* (Baltic Sea)

Figures 4, 9e, 11, 12

Non-type material Baltic Sea: 54°18.405′N, 11°12.030′E, 15 October 1997, sand, 16 m, four specimens (ZSRO-P 409); 54°20.10′N, 12°04.58′E, 28 August 1997, mud, 19 m, four specimens (ZSRO-P 410); 54°10′N, 11°10′E, 29 July 1980, 22 m, three specimens (ZSRO-P 1363); 54°23.18′N, 11°57.48′E, 27 October 1995, 17 m, one specimen (ZSRO-P 1748); 54°04.490′N, 11°24.350′E, September 2003, mud, 16 m, one specimen (SBRO-P 2557); 54°10.550′N, 11°45.000′E, August 2002, mud, 17 m, two specimens (SBRO-P 2568); 54°10.100′N, 11°45.000′E, September 2004, coarse sand, 5 m, one specimen (SBRO-P 3493); 54°28.800′N, 12°15.800′E, September 2004, sand, 24 m, two specimens (SBRO-P 3523); 54°10.550′N, 11°45.000′E, February 2004, sand mud, 19.5 m, one specimen (SBRO-P 3541); 54°31.012′N, 12°18.584′E, March 2004, sand, 22 m, one specimen (SBRO-P 3542); 54°27.93′N, 12°17.750′E, February 2004, fine sand, 18 m, one specimen (SBRO-P 3543).

Additional material Greenland (Nipisat, Disko Island): 69°26.23′N, 54°13.70′W, sandy mud, 1.5 m, 13 specimens (ZMUC-POL 1769–1777).

Description Specimens with up to 38 chaetigers (width 0.65 mm), maximum width 1.1 mm (anterior fragment with 22 chaetigers).

Prostomium elongated, bluntly rounded, anterior part slightly expanded, often weakly incised; posterior part of prostomium with high, narrow, keel-shaped elevation, beginning at the level of the eyes and terminating on chaetiger 1 (not shown in Fig. 4a); three pairs of black eyes arranged trapeziformly, anterior pair crescent-shaped or oval, widely spaced, middle pair oval or irregularly shaped,

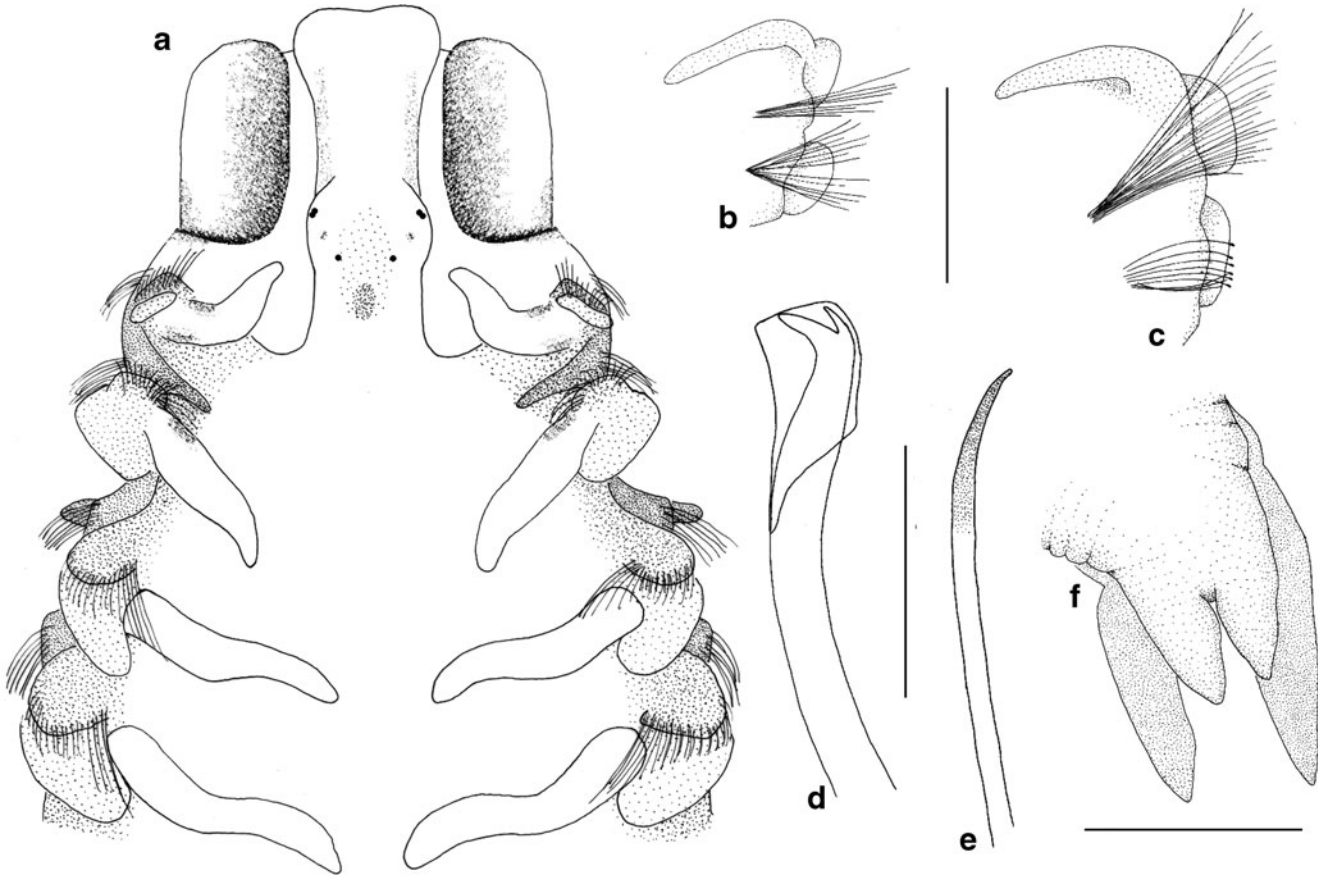

Fig. 4 *Spio* cf. *filicornis* (Müller, 1776) from the Baltic Sea. **a** Anterior end, dorsal view; **b** chaetiger 1, anterior view; **c** chaetiger 12, anterior view; **d** neuropodial hooded hook from chaetiger 24; **e** ventral sabre chaeta from chaetiger 24; **f** pygidium, ventral view. (*Scale bar*: **a** 125 μm; **b, c** 640 μm; **d, e** 64 μm; **f** 160 μm)

posterior pair oval or round, closely spaced; prostomium distinctly separated from peristomium by furrow (Fig. 4a).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands outward curved in the range of the first transverse ciliary band, posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Fig. 9e). Metameric dorsal ciliated organs double-paired extending, anterior to posterior, from between branchiae 3 and 4, and continuing on subsequent segments; posterior extent not defined (Fig. 9e).

Branchiae from chaetiger 1, continuing to near to last chaetiger; branchiae on first chaetiger nearly as long as those on the following chaetigers; branchiae with narrow base, tapering distally (Fig. 4a), becoming thinner and shorter posteriorly; branchiae on anterior chaetigers basally fused with notopodial postchaetal lamellae, separated from lamellae in posterior chaetigers; branchiae reaching midline dorsally and touching on anterior chaetigers.

First notopodium shifted dorsally. Notopodial postchaetal lamellae on anterior chaetigers oval, becoming smaller and rounded on subsequent chaetigers and appearing elongated in posterior chaetigers. Neuropodial postchaetal lamellae in anterior chaetigers oval, becoming smaller and shorter on subsequent chaetigers, rounded in posterior chaetigers.

Alcohol-preserved specimens with dark-brown pigment on anterior part of the body distributed as follows: peristomium heavily pigmented (Fig. 4a); pigmented patches dorsolaterally on anterior chaetigers before and/or behind transverse ciliary bands, around nuchal organs and metameric dorsal ciliated organs; indistinct longitudinal pigmented stripes ventrally on peristomium; pigmented border on anterior chaetigers ventrally; short median disrupted pigmented stripe and one to two pigmented patches ventro-laterally at base of neuropodia; median pigmented patch and several pigmented stripes between neuro- and notopodia; particularly conspicuous on the first two chaetigers; base of branchiae with one to two short longitudinal pigmented stripes (pattern of pigmentation not depicted in Fig. 4a); two weak longitudinal pigmented stripes on palps and a large pigmented patch on the base of palps.

Notopodial chaetae all limbate capillaries; capillaries of anterior chaetigers arranged in two rows: chaetae of anterior row short, broad, uniformly granulated (as in *S. gonioce-*

phala, Fig. 5f); chaetae of posterior row longer, thinner, lacking granulations (as in *S. goniocephala*, Fig. 5g); additionally, superior fascicle of very long, thin capillaries without granulations; capillaries of posterior chaetigers arranged in irregular rows, thin, non-granulated, of different length. Neuropodia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; capillaries of anterior neuropodia arranged in two rows, similar to notochaetae; posterior row replaced by a single row of six to eight hooded hooks from chaetiger 11 (exceptionally from chaetiger 10, Fig. 11), accompanied by alternating short, thin, alimbate, non-granulated capillaries (as in *S. goniocephala*, Fig. 5e); hooks not narrowed subdistally, with a short hood, bidentate, main fang and apical tooth well developed (Fig. 4d); inferior fascicle with two to three long, thin, limbate capillaries without granulations, replaced by two sabre chaetae from about chaetiger 20–24, each distally granulated (Fig. 4e).

Pygidium with four anal cirri; dorsal pair longer than ventral pair or of same size; dorsal pair more widely spaced than ventral pair (Fig. 4f).

Distribution and ecology Baltic Sea, North Atlantic: West Greenland; sublitoral; mud, fine sand, coarse sand.

Remarks Baltic Sea specimens of *Spio* cf. *filicornis* differ significantly from other *Spio* species in North Sea and Baltic Sea in having a heavily dark brown pigmented peristomium. The slight medial incision on the anterior margin of the prostomium, and the high, narrow, keel-shaped elevation on the posterior part of the prostomium are also useful diagnostic characters.

Spio cf. *filicornis* (Baltic Sea) is similar to *S. armata*. Both species occur in the Baltic Sea and the adults are large and robust (for differentiation see Remarks on *S. armata*).

Specimens of *Spio* cf. *filicornis* from the North and Baltic Seas exhibit significant differences and we here regard them to be different species [see Remarks on *Spio* cf. *filicornis* (North Sea)]. *Spio* cf. *filicornis* (Baltic Sea) is similar to *S. filicornis* from Øresund (Thulin 1957), the western North Atlantic (Maciolek 1990) and West Greenland (Worsaae 1999). Our study of additional material from Greenland (Nipisat, Disko Island) supports this conclusion. We have

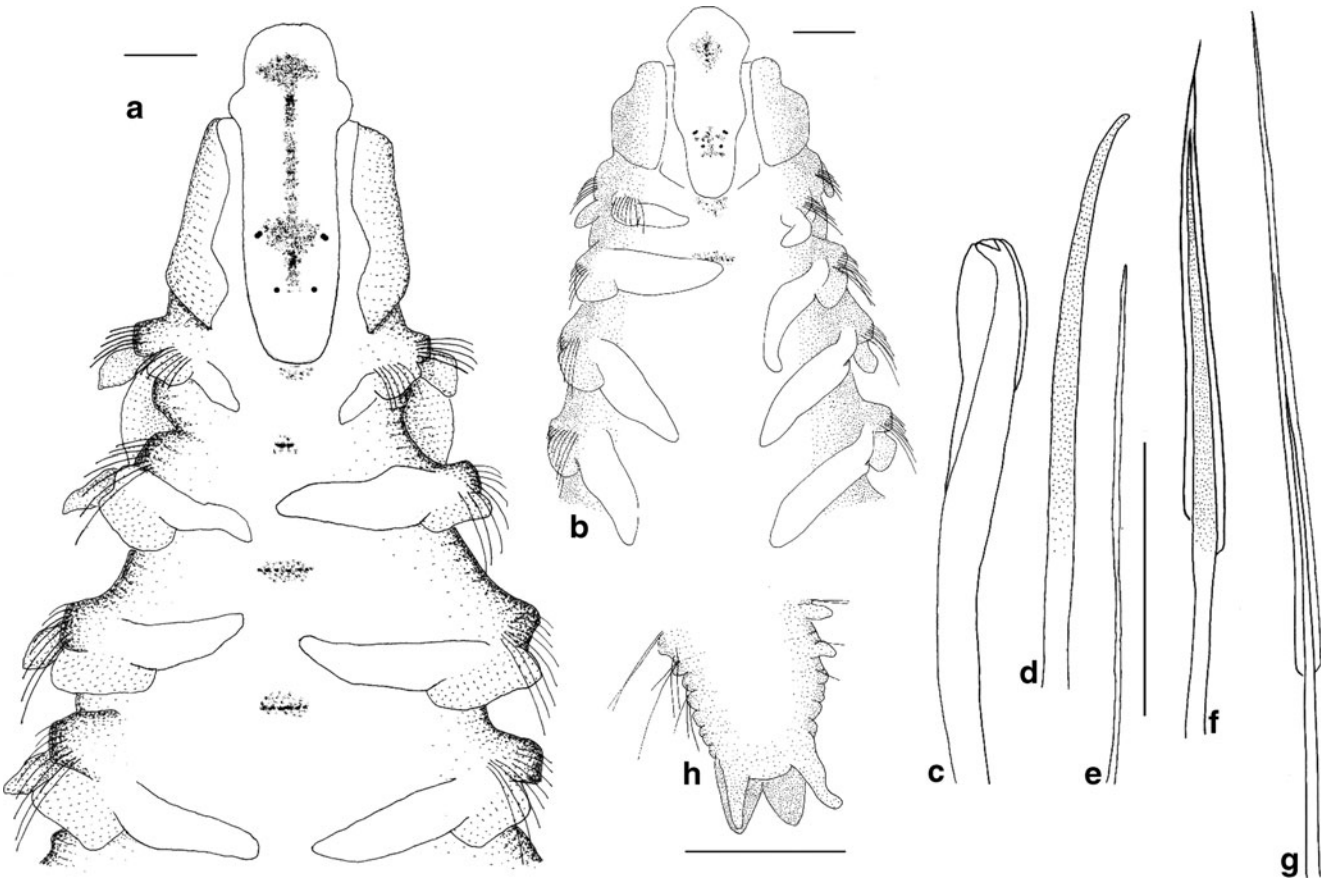

Fig. 5 *Spio goniocephala* Thulin, 1957. **a** Anterior end of a North Sea specimen, dorsal view; **b** anterior end of a Baltic Sea specimen, dorsal view; **c** neuropodial hooded hook from chaetiger 48; **d** ventral sabre chaeta from chaetiger 34; **e** short capillary from chaetiger 56; **f** capillary from anterior row of chaetae in neuropodium of chaetiger 20; **g** neuropodial capillary from posterior row of chaetae of chaetiger 20; **h** pygidium, dorsal view. (*Scale bar*: **a, b** 125 µm; **c–g** 64 µm; **h** 320 µm)

abstained from naming this species for the same reasons already mentioned for *Spio* cf. *filicornis* (North Sea) (see Remarks there).

Spio cf. *filicornis* (Baltic Sea) was usually only found in small numbers (one to three specimens per sample) when collected.

Spio goniocephala Thulin, 1957
Figures 5, 6, 8a, b, 9a, 11, 12
Spio goniocephala Thulin, 1957: 53–57, Figs. 2 and 3.—Hartmann-Schröder 1971: 301–302, Fig. 101.—Hartmann-Schröder 1996: 339, Fig. 155.—Böggemann 1997: 120, Fig. 96.—Sikorski 2001: 321, Figs. 1–5.
Spio filicornis—Eliason 1920: 40–42, Fig. 7 (partim).
Type material. Holotype: Øresund, south of Helsingør (L 916/3701); **Paratype:** Øresund, south of Helsingør, three specimens (L916/3702–3704).

Non-type material North Sea: Weser estuary May 1997, muddy sand, 19,5 m, two specimens (ZSRO-P 412); 55° 17.665′N, 6°47.913′E, 13/16 May 2002, sand, 28 m, seven specimens (ZSRO-P 1556); 53°41.513′N, 6°28.806′E, May 2003, fine sand, 20 m, one specimen (SBRO-P 501); 53°43.342′N, 6°28.683′E, May 2003, sand, 24 m, four specimens (SBRO-P 502); 53°41.513′N, 6°28.806′E, May 2003, fine sand, 20 m, ten specimens (SBRO-P 507); 53°43,.342′N, 6°28.683′E, May 2003, sand, 25 m, five specimens (SBRO-P 508); 53°43.342′N, 6°28.683′E, September 2002, sand, 22 m, 18 specimens (SBRO-P 572); 54°30.507′N, 7°51.701′E, November 2002, fine sand, 20.5 m, one specimen (SBRO-P 688). Baltic Sea: 54°10.1′N, 11°21.4′E, 25 June 1981, 23 m, one specimen (ZSRO-P 179); Mecklenburg Bight, October 1997, sand, 17 m, 29 specimens (ZSRO-P 411); 54°02.440′N, 11° 05.800′E, 20 m, ten specimens (ZSRO-P 1127).

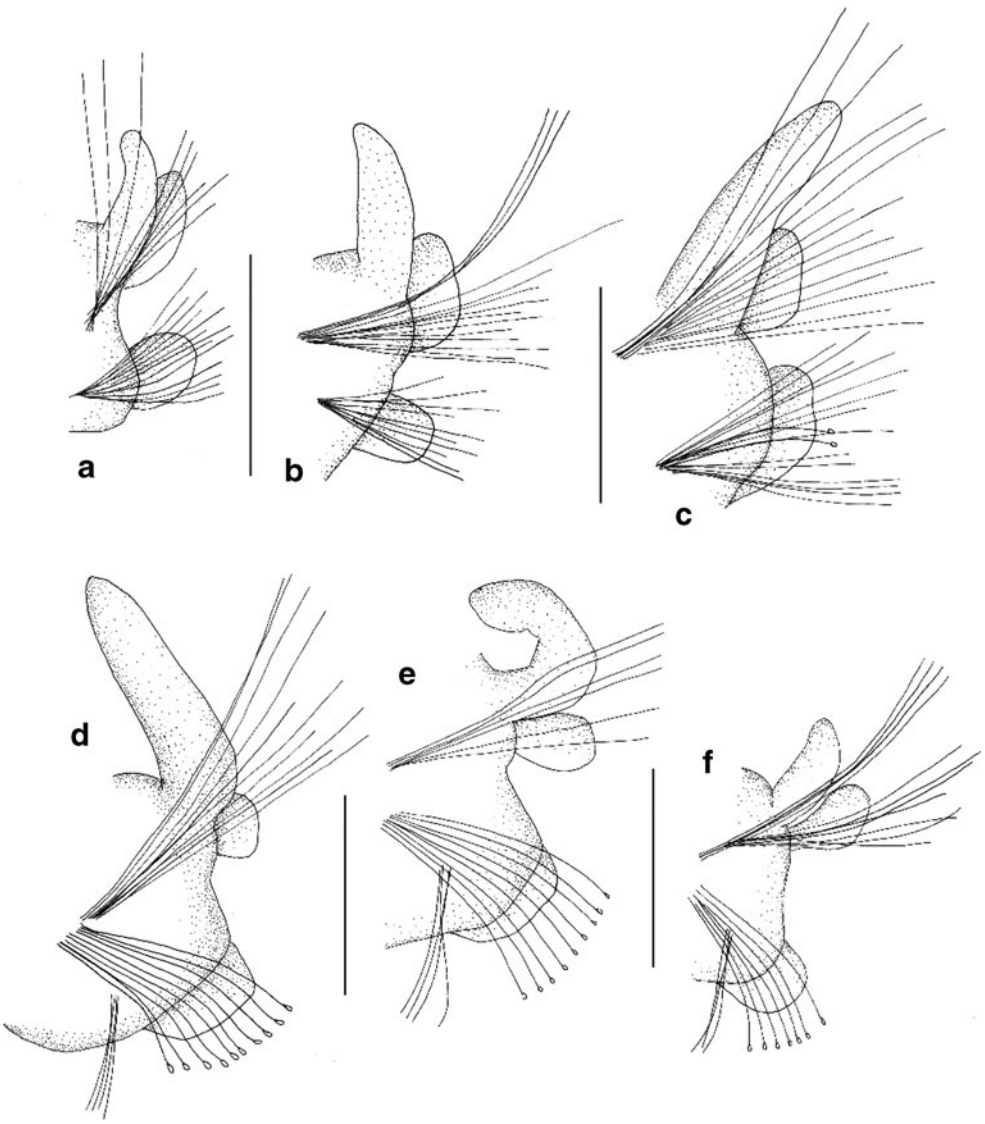

Fig. 6 *Spio goniocephala* Thulin, 1957. **a** Chaetiger 1, anterior view; **b** chaetiger 2, anterior view; **c** chaetiger 20, anterior view; **d** chaetiger 48, anterior view; **e** chaetiger 56, anterior view; **f** chaetiger 62, anterior view. (*Scale bar*: **a–f** 320 μm)

Description Specimens up to 77 (width 0.63 mm, North Sea) and up to 53 chaetigers (width 0.6 mm, Baltic Sea), maximum width 0.85 mm (North Sea, anterior fragment with 52 chaetigers) and 0.75 mm (Baltic Sea, anterior fragment with about 30 chaetigers).

Prostomium elongated, anteriorly tapered, anterior edges rounded, antero-lateral part with rounded projections (Fig. 8a); posterior part of prostomium rounded and not conspicuously elevated, extending posteriorly to chaetiger 1 (Fig. 5a, b); two pairs of black eyes, arranged trapeziformly or rectangular; anterior pair often irregularly shaped, crescent-shaped or rounded, posterior pair oval; prostomium not or little broadened in range of eyes; prostomium and peristomium distinctly separated by furrow (Fig. 5a, b).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands slightly outwardly curved in the range of the first transverse ciliary band (Figs. 8a, 9a). Paired metameric dorsal ciliated organs slightly outward curved, from between branchiae 3 and 4 (Figs. 8b and 9a).

Branchiae present from chaetiger 1, continuing nearly to last chaetiger; branchiae on chaetiger 1 small, about as half as long and wide as those on the following chaetigers; branchiae with broad base, tapered distally, becoming thinner and shorter in subsequent chaetigers, with narrow base in posterior chaetigers (Fig. 5a, b); branchiae on anterior chaetigers fused basally with notopodial postchaetal lamellae, separated from lamellae in posterior chaetigers (Fig. 6a–f); branchiae on anterior chaetigers almost reaching dorsal midline.

First notopodium shifted dorsally. Notopodial postchaetal lamellae on chaetiger 1 slightly pointed apically, oval in other anterior chaetigers, becoming shorter and rounded in middle chaetigers and then elongated in posterior chaetigers (Fig. 6a–f). Neuropodial postchaetal lamellae rounded on chaetigers 1 and 2, oval in other anterior chaetigers, becoming smaller and shorter subsequently, rounded in posterior chaetigers (Fig. 6a–f).

Alcohol-preserved specimens with dark-brown pigment on anterior part of body: prostomium of juveniles completely pigmented dorsally, adults with a dorsal median longitudinal pigmented stripe and with scattered pigment near the anterior margin, around eyes and on posterior part of prostomium (Fig. 5a, b); anterior chaetigers completely pigmented dorsally, except for nuchal organs, metameric dorsal ciliated organs and transverse ciliary bands; pigmented patches dorsally on anterior chaetigers, stable in alcohol-preserved specimens (Fig. 5a, b); two indistinct longitudinal pigmented stripes on palps; anal cirri also pigmented: ventral pair more strongly pigmented than dorsal pair; dorsal anal cirri with pigmented patch subdistally.

Notopodial chaetae all limbate capillaries; capillaries of anterior chaetigers arranged in two rows: chaetae of anterior row short, broad, uniformly granulated (Fig. 5f); chaetae of posterior row longer, thinner, lacking granulations (Fig. 5g); superior fascicle of long, thin capillaries without granulations also present; capillaries of posterior chaetigers arranged in irregular rows, thin, non-granulated, of different lengths. Neuropodia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; capillaries of anterior neuropodia arranged in two rows, similar to notochaete; from chaetiger 12 in small specimens (North Sea and Baltic Sea) and from chaetiger 23 or 20 in large specimens (North Sea or Baltic Sea) one to two hooded hooks present in posterior row, subsequently capillaries replaced by a single row of seven to ten hooks (Fig. 11), accompanied by alternating short, thin, alimbate, non-granulated capillaries (Fig. 5e); hooks bidentate, uniformly curved, slightly narrowed subdistally, with long hood, main fang and apical tooth weakly developed (Fig. 5c); inferior fascicle with three to seven (North Sea) or two to five (Baltic Sea) long, thin, limbate capillaries without granulations, replaced by three to four sabre chaetae from about chaetiger 20–22, each uniformly granulated (Fig. 5d).

Pygidium with four anal cirri of about same size; dorsal pair slender, cirriform and widely spaced; ventral pair broadened oval, touching each other at base (Fig. 5h).

Distribution and ecology Baltic Sea, North Sea, [from literature: Baffin Island (?)]; sublittoral; mud, fine sand, coarse sand.

Remarks Spio goniocephala is characterised by the tapered anterior part of its prostomium, the inconspicously elevated, posterior part of the prostomium, and the median (not dorsolateral) pigmented patches dorsally on anterior chaetigers. Branchiae on chaetiger 1 are small, about half as long and wide as those on the following chaetigers. Furthermore, neuropodial capillaries are replaced first by one to two hooded hooks and subsequently by a single row of seven to ten hooded hooks.

As in *S. armata*, the first appearance of hooded hooks is size-dependent (Fig. 11). Several authors have found neuropodial hooded hooks present from chaetiger 16–21 (Hartmann-Schröder 1996; Thulin 1957) or 16–19 (Bick and Gosselck 1985). This range has been expanded to chaetiger 12–23, and it is likely that in very small specimens hooded hooks may appear before chaetiger 12 and in larger specimens after chaetiger 23. In *S. goniocephala* the branchiae on chaetiger 1 are generally small, but in small specimens (0.25–0.38 mm width, max. 35 chaetigers) branchiae are exceptionally diminutive or papilliform and may be easily overlooked. A comparable delayed development of the first branchiae was also described for *S. setosa* Verrill, 1873 (Simon 1967, 1968), and it is also assumed to

occur in *Spio* cf. *filicornis* (North Sea) [see Remarks on *Spio* cf. *filicornis* (North Sea)].

The type material of *S. goniocephala* (Zoologiska Museet, Lund University; L916/ 3701–3704) was examined. Although the material was dried out, all diagnostic characters could still be observed and are consistent with the material from the North and Baltic Seas.

Spio martinensis Mesnil, 1896
Figures 7, 9c, 11, 12
Spio martinensis Mesnil, 1896: 122–128, VII, 1–20.—Hannerz 1956: 74–85, Figs. 24–28.—Giordanella 1969: 327, 342–343.—Fig. 6.—Rasmussen 1973: 96.—Dauvin 1989: 170–172.—Hartmann-Schröder 1996: 340.—Böggemann 1997: 121.—Bergfeld and Kröncke 2003: 27–29.—Not: Southern 1914: 95–96.
Spio filicornis—Fauvel 1927: 43–44, Fig. 15A–G (partim).

Non-type material North Sea: 54°18.00′N, 8°17.97′E, 15 December 1987, sand, 14 m, one specimen (ZSRO-P 391); 54°28.36′N, 8°48.00′E, 26 August 1997, sand, eulittoral, one specimen (ZSRO-P 485); 54°43.93′N, 8°03.48′E, 18 August 1998, 13 m, six specimens (ZSRO-P 906); 54°18.00′N, 8°18.00′E, 15 August 2005, sand, 15 m, four specimens (ZSRO-P 1853); 54°43.50′N, 8°03.05′E, 17 August 2005, sand, 14 m, eight specimens (ZSRO-P 1855); 54°35.00′N, 8°08.00′E, 16 August 2005, sand 14 m, four specimens (ZSRO-P 1856); 54°26.00′N, 8°10.00′E, 16 August 2005, sand, 19 m, four specimens (ZSRO-P 1857); 54°43.38′N, 8°41.82′E, 6 September 2005, sand eulitoral, two specimens (ZSRO-P 1858). Baltic Sea: 54°36,404′N, 12°39,448′E, March 2002, four specimens (SBRO-P 793); Wismarbucht, Februar 2003, fine to medium sand, 10 m, nine specimens (SBRO-P 809); Graal-Müritz (to the east of Rostock), Autumn 2004, fine sand, 10 m, two specimens (SBRO-P 3283); Graal-Müritz (to the east of Rostock), Autumn 2004, sand, 11 m, five specimens (SBRO-P 3295).

Description Maximum number of chaetigers 50 (width 0.5 mm), maximum width 0.63 mm (anterior fragment with 42 chaetigers).

Prostomium narrow, anteriorly rounded, anterior part sometimes slightly expanded; posterior part of prostomium

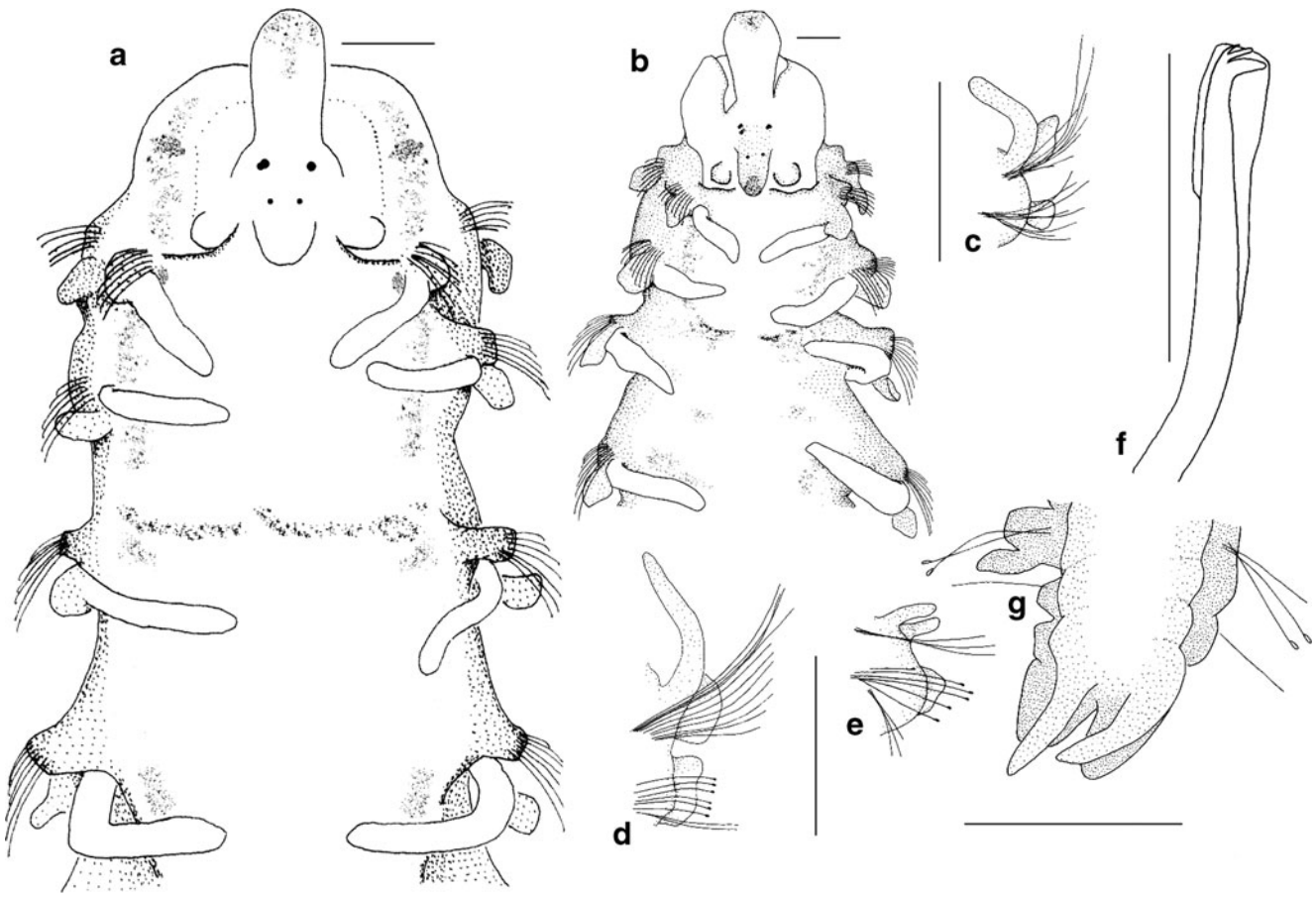

Fig. 7 *Spio martinensis* Mesnil, 1896. **a** Anterior end of a North Sea specimen, dorsal view; **b** anterior end of a Baltic Sea specimen, dorsal view; **c** chaetiger 1, anterior view; **d** chaetiger 14, anterior view; **e** chaetiger 34, anterior view; **f** neuropodial hooded hook from chaetiger 34; **g** pygidium, dorsal view. (*Scale bar*: **a, b** 125 μm; **c–e** 320 μm; **f** 64 μm; **g** 160 μm)

rounded or tapered, posteriorly extending to chaetiger 1 (Fig. 7a, b); two pairs of black eyes arranged trapezoidally, anterior pair crescent-shaped, rarely rounded, posterior pair oval; prostomium and peristomium of North Sea specimens completely separated by a depression, on Baltic Sea specimens a deep groove between prostomium and peristomium only exists anteriorly (Fig. 7a, b).

Nuchal organs with short median and long lateral ciliary bands, lateral ciliary bands posteriorly curved and go only partly back to the transverse ciliary band of chaetiger 2 (Fig. 9c); Metameric dorsal ciliated organs double-paired, indistinct from between branchiae 4 and 5 to between branchiae 5 and 6 but distinct from between branchiae 6 and 7 or 7 and 8 (Fig. 9c); its posterior extension has not been defined.

Branchiae from chaetiger 1, continuing to near end of body; branchiae on chaetiger 1 almost as long as those on following chaetigers (Fig. 7a, b); branchiae on anterior chaetigers basally fused with notopodial postchaetal lamellae, becoming separated posteriorly; minor differences in length and shape of branchiae of North Sea and Baltic Sea with North Sea specimens branchiae slender, cirriform, without wide base, slightly tapered distally, becoming thinner and shorter in posterior chaetigers (Fig. 7a); branchiae on anterior chaetigers reach the midline dorsally, touch each other; branchiae of Baltic Sea specimens with broad base anteriorly, slightly tapered distally, becoming thinner and shorter posteriorly, without broad base in posterior chaetigers (Fig. 7b); branchiae on anterior chaetigers almost reaching dorsal midline, not touching each other.

First notopodium shifted dorsally. Notopodial postchaetal lamellae on chaetiger 1 slightly pointed, in other anterior chaetigers oval, becoming shorter and rounded thereafter, notopodial lamellae elongated in posterior chaetigers (Fig. 7c–e). Neuropodial postchaetal lamellae rounded on chaetigers 1 and 2, in other anterior chaetigers oval, becoming smaller and shorter thereafter, rounded in posterior chaetigers (Fig. 7c–e).

Alcohol preserved specimens with dark brown pigment on anterior part of body: pigmented patch dorsally on anterior margin of prostomium; pigmented patches dorsolaterally on anterior chaetigers before and/or behind transverse ciliary bands; pigment indicates end of nuchal organs (Fig. 7a, b); median pigmented patch between neuro- and notopodia; row of pigmented patches on palps; anal cirri also pigmented, ventral pair more intensive than dorsal pair; on specimens from North Sea additional pigment: a median longitudinal pigmented stripe dorsally on prostomium; indistinct pigment scattered dorsally on peristomium and distinct pigmented patch at about level of eyes (Fig. 7a); pigment between peristomium and first chaetiger; a short median pigmented stripe ventrally between anterior chaetigers; pigmented stripes or patches ventro-laterally on base of neuropodia; median transverse pigmented stripe ventrally; several pigmented stripes between noto- and neuropodia; small pigmented patch at the base of palps; pigment at margin of notopodial lamellae, close to branchiae.

Notopodial chaetae all limbate capillaries; chaetae of anterior chaetigers arranged in two rows: capillaries of anterior row short, broad, uniformly granulated (Fig. 5f); chaetae of posterior row longer, thinner, lacking granulations (Fig. 5g); additional superior fascicle of very long, thin capillaries without granulations; capillaries of posterior chaetigers arranged in irregular rows, thin, non-granulated, varying length of capillaries. Neuropodia with rows of capillaries and hooded hooks as well as an inferior fascicle of capillaries; chaetae of anterior neuropodia arranged in two rows, similar to notopodial chaetae; posterior row replaced by a single row of five to eight hooded hooks from chaetiger 14 (exceptionally from chaetiger 13), accompanied by alternating short, thin, alimbate, non-granulated capillaries (Fig. 5e); hooks with long hood, slightly narrowed subdistally, tridentate, third tooth hardly visible (Fig. 7f); inferior fascicle with two to three long, thin, limbate capillaries without granulations, replaced by two to three sabre chaetae from about chaetiger 20–24, each uniformly granulated (Fig. 5d).

Pygidium with four anal cirri; dorsal pair slender, cirriform and widely spaced; ventral pair broad, oval or slightly cone-shaped, closely spaced and touching each other at the base (Fig. 7g); dorsal pair of North Sea specimens slightly longer than ventral pair and dorsal pair of Baltic Sea specimens shorter than ventral pair or of the same size.

Distribution and ecology Baltic Sea, North Sea, [from literature: northeast Atlantic, Arctic Ocean (?), northeast Pacific (?)]; sublitoral; mud, fine sand, coarse sand.

Remarks Spio martinensis is characterised by its hooded hooks present from chaetiger 14 (rarely from chaetiger 13). There are differences between the North Sea and Baltic Sea specimens in the length and shape of branchiae. Whereas the North Sea specimens possess long and slender branchiae without a wide base, specimens from the Baltic Sea have shorter, wide-based branchiae. Furthermore, only Baltic Sea specimens have the lateral margin of the prostomium slightly expanded. North Sea specimens possess a flat depression between prostomium and peristomium, whereas it is deep and limited to the anterior part in Baltic Sea specimens. The anal cirri are also slightly different.

Since type material or material from the type locality could not be tracked by the authors and is supposedly lost,

it was not possible to decide whether the specimens found in the North Sea and Baltic Sea belong to the same species or whether the assignment to *S. martinensis* is reliable. The characters found in specimens from both the North and Baltic Seas are generally similar to the original description of *S. martinensis* from the English Channel (Mesnil 1896).

Key to species of *Spio* from the North and Baltic Seas

1 Branchiae on chaetiger 1 distinctly shorter than branchiae on chaetiger 2; bidentate neuropodial hooded hooks first appear on chaetigers 16–23 (12–15 in juveniles, width <0.4 mm)..... **2**
- Branchiae on chaetiger 1 as long as those on chaetiger 2, or only slightly shorter; bi- or tridentate neuropodial hooded hooks first appear on chaetigers 11–14 in juveniles and adults..... **3**

2 Branchiae on chaetiger 1 very short, only slightly longer or as long as notopodial postchaetal lamellae; anterior part of prostomium broadly rounded, posterior part tapered; lateral ciliary bands posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Fig. 9f); metameric dorsal ciliated organs double-paired; neuropodial hooded hooks from chaetigers 17 (14–16, Thulin 1957; 8–20, Sikorski 2001), strongly curved, main fang large, of nearly right angle to shaft (Fig. 1c); inferior sabre chaetae and neuropodial hooks conjointly appear ..... ***S. armata***
- Branchiae on chaetiger 1 short, but distinctly longer than notopodial postchaetal lamellae; anterior part of prostomium tapered, posterior part broadly rounded; lateral ciliary bands slightly outward curved in the range of the first transverse ciliary band (Figs. 8a and 9a); single-paired metameric dorsal ciliated organs; neuropodial hooded hooks from chaetigers 16–23 (12–15 in juveniles, width <0.5 mm), uniformly curved, weakly developed main fang (Fig. 5c); inferior sabre chaetae first present after first appearance of neuropodial hooded hooks ..... ***S. goniocephala***

3 Neuropodial hooded hooks bi- or tridentate from chaetiger 11 (rarely 10) **4**
- Neuropodial hooded hooks tridentate, from chaetiger 14 (rarely 13); posterior part of prostomium tapered; lateral ciliary bands posteriorly curved and go only partly back to the transverse ciliary band of chaetiger 2 (Fig. 9c); metameric dorsal ciliated organs double-paired ..... ***S. martinensis***

4 Neuropodial hooded hooks bidentate; metameric dorsal ciliated organs present from between branchial pairs 3 and 4; posterior part of prostomium with distinct long, keel-shaped elevation (visible in lateral view); lateral ciliary bands outward curved in the range of the first transverse ciliary band, posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Fig. 9e); conspicuous dark-brown pigment on peristomium and no or very faint pigment on prostomium (Fig. 4a) ..... ***Spio* cf. *filicornis* (Baltic Sea)**
- Neuropodial hooded hooks usually tridentate; metameric dorsal ciliated organs present from between branchial pairs 4 and 5 or 5 and 6; posterior part of prostomium pointed or tapered; distinct brown pigment on peristomium and prostomium (Figs. 2a and 3a) **5**

5 Prostomium not distinctly separated from peristomium by a furrow (Fig. 3a); brown pigment on prostomium and peristomium in irregular patches; lateral ciliary bands outward curved in the range of the first transverse ciliary band, posteriorly curved and go nearly completely back to the transverse ciliary band of chaetiger 2 (Figs. 9d, 10a); metameric dorsal ciliated organs from between branchial pairs 4 and 5; the third tooth on the hooded hooks hardly visible (Fig. 3f, often worn down?) ..... ***Spio* cf. *filicornis* (North Sea)**
- Prostomium distinctly separated from peristomium by a furrow (Fig. 2a); broad transverse pigmented band on prostomium and peristomium (Fig. 2a); lateral ciliary bands posteriorly curved and go only partly back to the transverse ciliary band of chaetiger 2 (Fig. 9b); metameric dorsal ciliated organs present from between branchial pairs 5 and 6; distinct third tooth on the hooded hooks (Fig. 2b) ***S. decoratus***

Discussion

At least six *Spio* species occur in our study area: *S. decoratus*, *Spio* cf. *filicornis* (North Sea), *S. goniocephala* and *S. martinensis* in the North Sea, and *S. armata*, *Spio* cf. *filicornis* (Baltic Sea), *S. goniocephala* and *S. martinensis* in the Baltic Sea. Based on detailed morphological studies it was possible to find diagnostic characters for all investigated species and to provide a key for identification. Of particular importance is the discovery that specimens of the supposedly widespread *S. filicornis* belong to two different species, of which one occurs in the Baltic Sea and the other one in the North Sea. However, not all taxonomic problems have been resolved. For example, specimens of *S. martinensis* from the North and Baltic Seas differ in some respects, but are here regarded as con-specific. Taxonomic problems within *Spio* can be attributed, on one hand, to the loss or poor condition of type material, as is the case with *S. filicornis*, *S. armata* and *S. goniocephala*. On the other

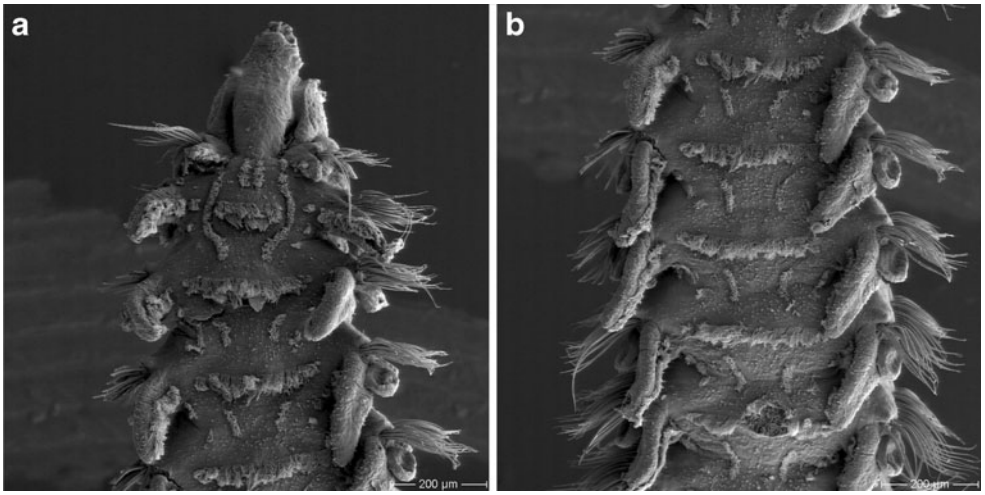

Fig. 8 *Spio goniocephala* Thulin, 1957, North Sea. **a** Anterior end, with nuchal organs and single-paired metameric dorsal ciliated organs, slightly outward curved, present from between branchial pairs 3 and 4; **b** chaetigers 3–8 with single-paired, slightly outward curved metameric dorsal ciliated organs

hand, diagnostic characters that have been previously used to differentiate *Spio* species are not sufficiently discrimantory. For example, *S. filicornis* has been characterised by a rounded, sometimes slightly incised anterior margin of the prostomium, long branchiae on first chaetigers that are of the same length as those on the second chaetiger, and bidentate hooded hooks first appearing from chaetiger 11 (e.g. Maciolek 1990). The inadequacy of this set of characters as diagnostic is revealed by the following data: out of 28 *Spio* species, 16 species possess a rounded anterior margin of the prostomium, 15 species have long branchiae on chaetiger 1, and bidentate hooded hooks from chaetiger 11 are reported for nine species (based on species descriptions in Maciolek 1990; Blake 1996, and Sikorski 2001). The distribution range of the species includes a great variety of geographically diverse regions: *S. filicornis* has been recorded in western Greenland, southern and northern Europe, including the North Sea, Baltic Sea, Black Sea and White Sea, Arctic Sea, Bering Sea, North Pacific, Red Sea, South Africa, and Ross Sea. It seems likely that the cosmopolitan species *S. filicornis* actually represents a species complex.

The fact that certain morphological characters do not serve well as diagnostic characters may also be explained by their size-dependency, or in other words, their change in the course of development. The recognition of size-dependency of character states is important and has to be considered in the species diagnosis. Within *Spio,* that concerns the shape of the caruncle, the beginning of branchiae and their length, particularly on the first chaetiger, the start and the number of hooded hooks, the number of apical teeth on these hooks, the pigmentation and the length and shape of the anal cirri (Augener 1914; Blake 1996; Day 1973; Guerin 1972; Hannerz 1956; Hartmann-Schröder 1996; Mesnil 1896; Sikorski 2001; Simon 1967, 1968; Thulin 1957). One of the most important diagnostic characters is the first appearance of neuropodial hooded hooks. Three different patterns concerning that character were found among the investigated species (Fig. 11): (1) no size-dependency of the character—hooded hooks always start at the same chaetiger; (2) a minor shift occurs and the first appearance of hooded hooks is moved posteriorly; (3) the first appearance of hooks differs considerably between juveniles (from chaetiger 11) and adults (from chaetiger 20–23). Pattern 1 was observed for *Spio* cf. *filicornis* (North Sea), *Spio* cf. *filicornis* (Baltic Sea), and *S. decoratus*. Pattern 2 applies to *S. martinensis* and pattern 3 to *S. goniocephala*. For the sixth species investigated, *S. armata*, only six specimens, all of comparable length, were available. Sikorski (2001) reported that for *S. armata* from Arctic regions, hooded hooks are present from chaetigers 8–11 in small and chaetigers 18–20 in large specimens, and Thulin (1957) found hooks to start on chaetiger 14 and 16 in this species. A correlation between size and the beginning of hooded hooks in Baltic Sea specimens may also exist.

Not only the first appearance but also the number of hooks is size-dependent: the smaller the specimens, the fewer the number of neuropodial hooks (Fig. 12). This is true for all *Spio* species occurring in both the North and Baltic Seas and it can also be assumed for all other *Spio* species. In certain cases, the number of apical teeth also varies with body size. The hooded hooks of juvenile *Spio* cf. *filicornis* (North Sea) are tridentate but usually bidentate in adults. The same observation was made by Hannerz (1956) and Bergfeld and Kröncke (2003) for *S. martinensis*. However, we cannot support this observation based on our material of *S. martinensis*.

Another important character is the length of the branchiae on the first chaetiger. This length varies depending on size of the specimens in *Spio* cf. *filicornis* (North Sea) and in *S. goniocephala*. The branchiae of *S. goniocephala* are very small and papilliform in juveniles and half as long as the branchiae on the second chaetiger in

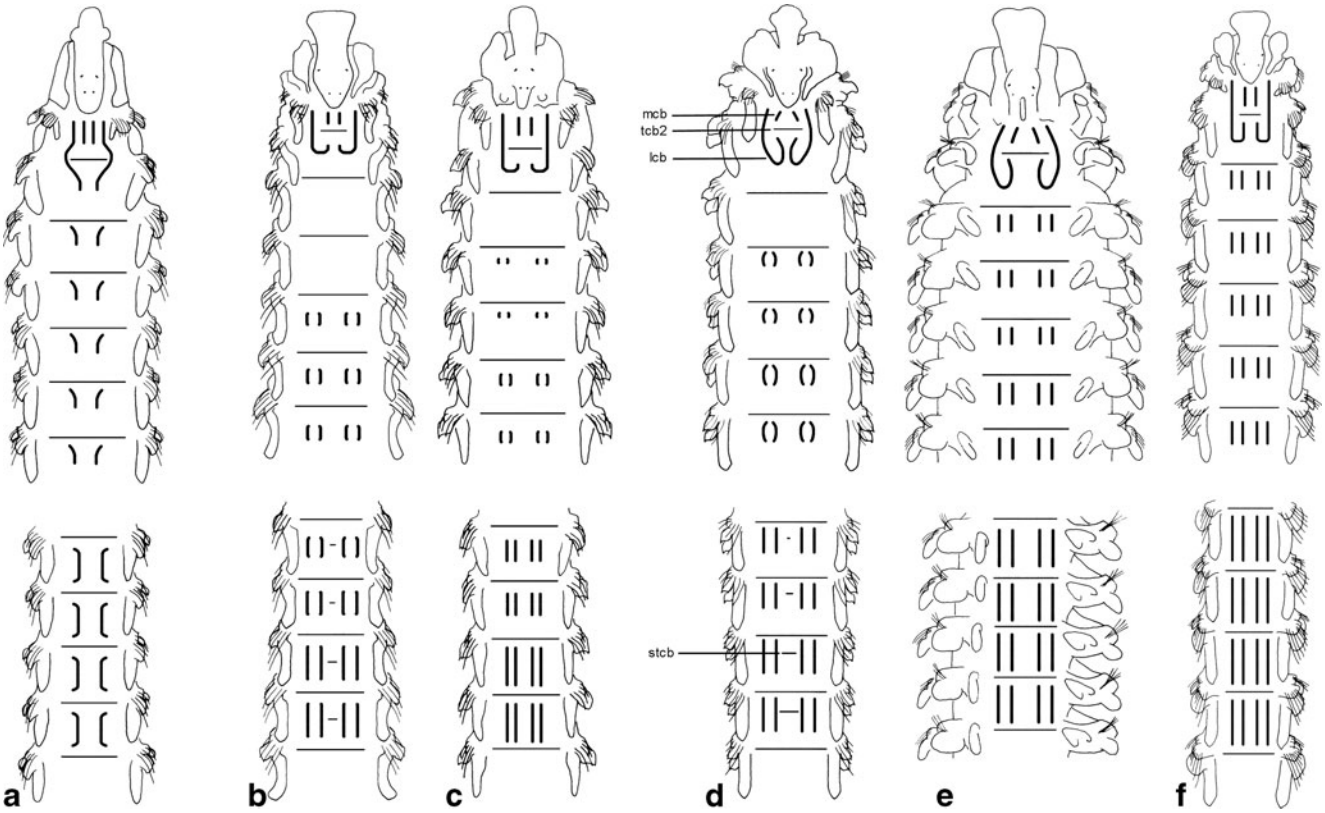

Fig. 9 Schematic representation of nuchal organs, metameric dorsal ciliated organs and transverse ciliary bands on *Spio* species from the North Sea and Baltic Sea. **a** *S. goniocephala* Thulin, 1957; **b** *S. decoratus* Bobretzky, 1870; **c** *S. martinensis* Mesnil, 1896; **d** *S.* cf. *filicornis* (Müller, 1776), North Sea; **e** *S.* cf. *filicornis* (Müller, 1776), Baltic Sea; **f** *S. armata* (Thulin, 1957) (*lcb* lateral ciliary bands of nuchal organs, *mcb* median ciliary bands of nuchal organs, *stcb* short transversal ciliary band, *tcb2* transversal ciliary band of chaetiger 2)

adults. The first branchiae on small specimens of *Spio* cf. *filicornis* (North Sea) are conspicuously shorter than those on the following chaetigers, but on adults they are usually as large as those on subsequent chaetigers. In conclusion, characters previously used as diagnostic for *Spio* species are insufficient, partly because their size-dependency has not been taken into account.

A character we found to be useful also for *Spio* are the nuchal organs, together with the metameric dorsal ciliated organs. They have already been proven extremely useful diagnostic characters in other spionid genera, e.g. in *Marenzelleria* (Bick 2005), *Spiophanes* (Meißner 2005), and *Laonice* (Sikorski 2002). The nuchal organs of *Spio* species from the North and Baltic Seas consists of two median and two lateral bands of cilia (Figs. 8a and 10a). Median ciliary bands are short, originate directly behind the prostomium and extend posteriorly to the transverse ciliary band of chaetiger 2. The lateral ciliary bands are longer, originate on the palps and extend posteriorly to the middle of chaetiger 3; they are posteriorly curved and go completely or nearly completely (e.g. *S. armata*, *S.* cf. *filicornis*; Figs. 9d–f and 10a), partly (e.g. *S. decoratus, S. martinensis*; Fig. 9b, c) or never (e.g. *S. goniocephala*; Figs. 8a and 9a) back to the transverse ciliary band of chaetiger 2. The nuchal organs and the metameric dorsal ciliated organs are readily visible well-defined structures on the epithelium in well-preserved adults. In most juveniles, they comprise lighter coloured areas on the pigmented epithelium. Shirlastain A was found particularly useful to visualise nuchal organs and metameric dorsal ciliated organs in faded or poorly preserved specimens.

Blake and Kudenov (1978) noticed that "dorsal sense organs ... are important to species concepts" and "any revision of *Spio* and *Microspio* should thus consider dorsal sense organs at the species level". This approach was used by Söderström (1920), who tried to establish the separation of the genera *Spio* and *Microspio* by means of the metameric dorsal ciliated organs, specifying the number of longitudinal ciliary bands of the metameric dorsal ciliated organs in *Microspio* as two and in *Spio* as four. The metameric dorsal ciliated organs of *Spio* spp. consists of two or four longitudinal ciliary bands arranged in a single or double row on the dorsum of the first chaetigers (Figs. 8b and 10c). According to Jelsing (2003), it belongs to the group IV (paired, metameric dorsal ciliated organs), occurring within Spionidae. Single dorsal ciliated organs

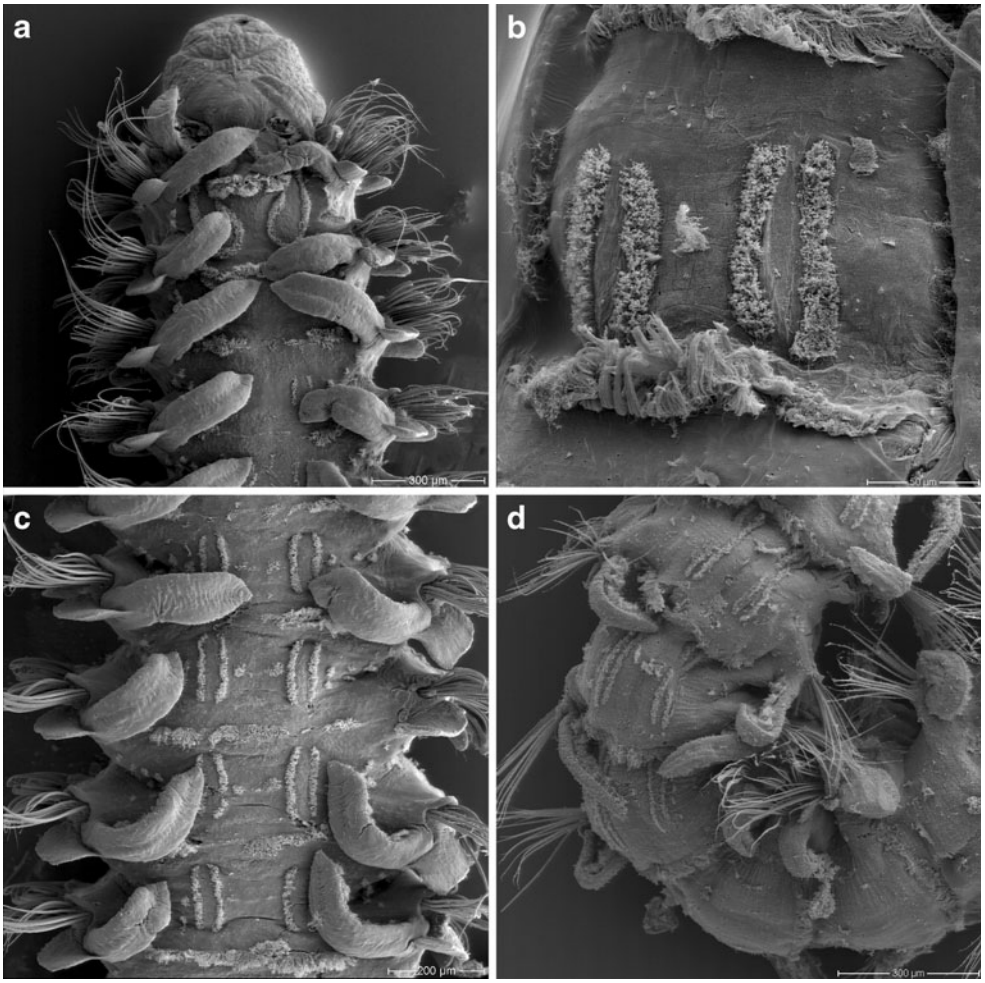

Fig. 10 *Spio* cf. *filicornis* (Müller, 1776), North Sea. **a** Anterior end with nuchal organs, and double-paired metameric dorsal ciliated organs present from between branchial pairs 4 and 5; **b** additional point-shaped transverse ciliary band on chaetiger 25; **c** chaetigers 12–15 with double-paired metameric dorsal ciliated organs, long transverse ciliary bands connecting the branchiae and additional short transverse ciliary between dorsal ciliated organs; **d** end of double-paired metameric dorsal ciliated organs on chaetiger 33

(Fig. 8b) are concave, whereas double-paired dorsal ciliated organs (Fig. 10c) consist of parallel or slightly curved ciliary bands. *Spio goniocephala* (Fig. 9a) is the only species in this region with single-paired dorsal ciliated organs; all other species have double-paired dorsal ciliated organs (Fig. 9b–f). Apart from the shape, differences also exist in the first appearance of the dorsal ciliated organs. Jelsing (2002) stated that the dorsal

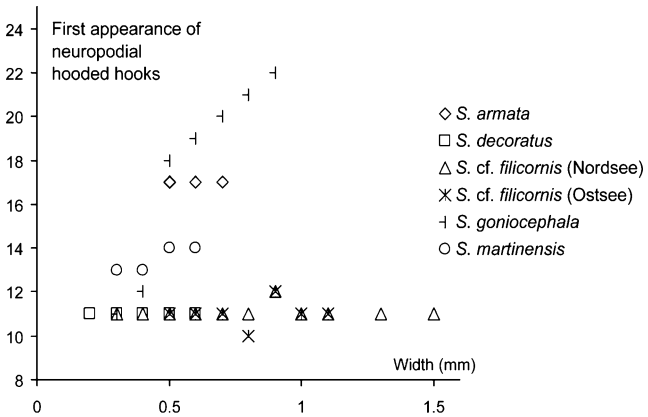

Fig. 11 Relationship between size of specimens (width in millimetres) and first appearance of neuropodial hooded hooks in *Spio* species from the North Sea and the Baltic Sea

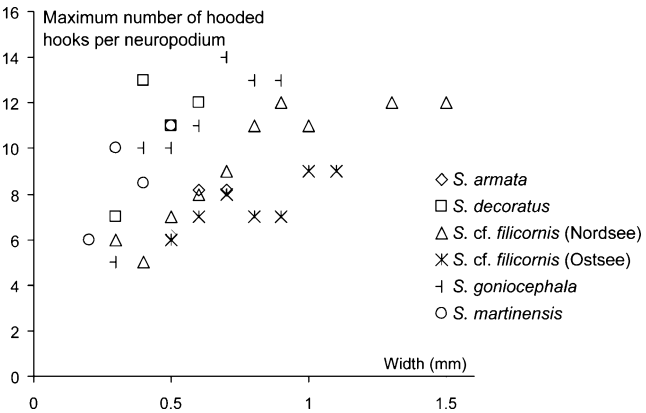

Fig. 12 Relationship between size of specimens (width in millimetres) and number of neuropodial hooded hooks in *Spio* species from the North Sea and the Baltic Sea

ciliated organs are intersegmentally located, but in fact it is difficult to define the accurate position. The branchiae have, therefore, been used as a surrogate to determine the beginning of the dorsal ciliated organs. In *Spio* species found in North Sea and Baltic Sea, they first appear from between branchial pairs 3 and 4 [*Spio armata*, *Spio* cf. *filicornis* (Baltic Sea), *S. goniocephala*] or between 4 and 5 [*Spio* cf. *filicornis* (North Sea), *S. martinensis*] or six [*S. decoratus*]. The ciliary bands of the metameric dorsal ciliated organs tend to extend in length until they are nearly as long as the corresponding chaetiger. They disappear abruptly on a middle chaetiger (Fig. 10d). It is difficult to decide whether the termination of the dorsal ciliated organs is species-specific or variable because it was not always possible to define its posterior extension.

All *Spio* species possess a transverse ciliary band connecting the opposite branchiae of the corresponding chaetiger. This ciliary band is absent on chaetiger 1, short on chaetiger 2 and fully developed from chaetiger 3 (Fig. 8a). *Spio* cf. *filicornis* (North Sea) and *S. decoratus* possess an additional shorter transverse ciliary band on middle chaetigers (Figs. 9b–d and 10b, d). First, it is a ciliated tuft situated between the longitudinal ciliary bands of the dorsal ciliated organs (Fig. 10b), then extends onto the following chaetigers to form finally the short additional transverse band (Fig. 10c, d).

Summary

The present study provides a detailed morphological study of *Spio* species found in the North and Baltic Seas. Previously used morphological characters were critically reviewed and new characters were included into the amended species diagnoses. The following characters were found to be of particular taxonomic importance: the shape of the prostomium and the type of extension of its posterior part, the presence or absence of a groove-like depression (or furrow) between the prostomium and peristomium, the shape of the nuchal organs and metameric dorsal ciliated organs (metameric longitudinal ciliary bands on the dorsum of anterior and middle chaetigers), the first appearance of sabre chaetae, and the pigment pattern on the prostomium, peristomium and anterior chaetigers. A number of taxonomic characters are size-dependent. For the species from the study region, size-dependent variation may concern the beginning and the number of neuropodial hooded hooks, the number of apical teeth on these hooks and the length of branchiae on the first chaetiger. All these characters are of taxonomic importance. As a result of the study, it was also discovered that *S. filicornis* previously reported from the North and Baltic Seas include two different species. The formal assignment of these species to either a known or a new species has to be undertaken as soon as material from the type locality of *S. filicornis* becomes available.

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