This article was downloaded by: [University of Bath] On: 13 February 2014, At: 15:31 Publisher: Taylor & Francis Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



# Journal of Natural History

Publication details, including instructions for authors and subscription information: http://www.tandfonline.com/loi/tnah20

# A new polychaete genus and species of the Kongsfjorden, Spitsbergen, Svalbard

Andreas Bick <sup>a</sup>

<sup>a</sup> FB Biowissenschaften , Allgemeine and Spezielle Zoologie , Universität Rostock , Rostock, Germany Published online: 21 Feb 2007.

To cite this article: Andreas Bick (2005) A new polychaete genus and species of the Kongsfjorden, Spitsbergen, Svalbard, Journal of Natural History, 39:32, 2987-2996, DOI: <u>10.1080/00222930500239843</u>

To link to this article: http://dx.doi.org/10.1080/00222930500239843

# PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, Ioan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <a href="http://www.tandfonline.com/page/terms-and-conditions">http://www.tandfonline.com/page/terms-and-conditions</a>

# A new polychaete genus and species of the Kongsfjorden, Spitsbergen, Svalbard

## ANDREAS BICK

FB Biowissenschaften, Allgemeine and Spezielle Zoologie, Universität Rostock, Rostock, Germany

(Accepted 27 June 2005)

#### Abstract

*Glyphochaeta laudieni*, a new genus and species of the "Spionidae", is described from the Arctic. The specimens were collected from the Kongsfjorden, Spitsbergen, Svalbard, in a marine grotto. *Glyphochaeta laudieni* was associated with colonies of unidentified Bryozoa. This new genus and species is characterized by a prostomium with frontal horns, the absence of branchiae and sabre chaetae, and the presence of grooved spines which replace hooded hooks in some chaetigers of the middle body region. These spines are associated with glandular organs situated in neuropodia. The significance of characters for determining the systematic position of *Glyphochaeta* within "Spionidae" is discussed. *Glyphochaeta laudieni* is probably related to *Pygospio elegans*.

Keywords: Arctic, glandular organ, Glyphochaeta gen. n., Glyphochaeta laudieni sp. n., grooved spine, Kongsfjorden, Polychaeta, Spionidae, Spitsbergen

#### Introduction

The "Spionidae" Grube, 1850 as currently defined comprises 38 genera and more than 450 species (Wilson 2000; Rouse and Pleijel 2001), but it is now known to represent a paraphyletic assemblage (e.g. Blake and Arnofsky 1999; Rouse and Pleijel 2001). Features that have usually been used to characterize species within this group include the shape of the prostomium, especially the anterior margin and the posterior end (caruncle); the length and shape of the nuchal organ or dorsal sense organ; the number of branchiae, their distribution and the degree of fusion of branchiae with postchaetal notopodial lamellae; the distribution and form of hooded hooks, as well as the number of anal cirri or lobes. In addition, some genera are clearly characterized by strongly modified neuro- or notochaetae anteriorly or posteriorly, e.g. species of the *Polydora* and *Atherospio (sensu* Mackie 1996) complexes, *Australospio* Blake and Kudenov, 1978, *Lindaspio* Blake and Maciolek, 1992, *Scolecolepides* Ehlers, 1907, *Spiophanes* Grube, 1860, and *Xandaros* Maciolek, 1981. In most cases the function of these modified chaetae remains to be clarified.

Published 27 September 2005.

ISSN 0022-2933 print/ISSN 1464-5262 online © 2005 Taylor & Francis DOI: 10.1080/00222930500239843

Correspondence: Andreas Bick, Universität Rostock, FB Biowissenschaften, Allgemeine and Spezielle Zoologie, Universitätsplatz 2, D-18051 Rostock, Germany. Email: andreas.bick@uni-rostock.de

Investigations of the intertidal and shallow subtidal polychaete fauna of the Kongsfjorden, Spitsbergen, yielded about 20 specimens belonging to the "Spionidae". These specimens all belong to the same species, which differs from all other spionids in having grooved chaetae in some neuropodia of the middle body region. These modified chaetae are grooved spines and are associated with glandular organs of the corresponding chaetigers. Based on this character, a new genus and species of "Spionidae" is described.

#### Material and methods

The specimens were collected in a marine grotto near Hansneset  $(78^{\circ}59.08'N, 11^{\circ}57.43'E)$ Blomstrandhalvøya, in the Kongsfjorden, Spitsbergen, between colonies of unidentified Bryozoa. The grotto is about 8 m wide and 15 m long, the opening is partially above the sea level. The water depth in the entrance of the grotto is about 6 m and in the back about 3 m. The light gradient is a major factor determining the hard bottom community here: the macroalgae Laminaria solidungula Agardh, 1868, Phycodrys rubens (Linnaeus) Batters, 1902, and Ptilota plumosa (Hudson) Agardh, 1868 dominate in the entrance of the grotto, whereas mainly sponges (Halichondria panicea (Pallas, 1766), H. genitrix (Schmidt, 1870), Haliclona viscosa (Topsent, 1888), Grantia utriculus (Schmidt, 1869), and Suberites ficus (Johnston, 1842)), but also the ascidian *Halocynthia* sp., the nephtheid soft coral Gersemia rubiformis (Ehrenberg, 1834) and Bryozoa occur in the back. The echinoderms Strongylocentrotus droebachiensis (O. F. Müller, 1776) and Henricia sanguinolenta (O. F. Müller, 1776) were also found on the wall of the grotto. The Kongsfjorden is an Arctic glacier fjord, influenced by tides (tidal range 1.5–2.0 m), bound by rocky shores, and covered by ice during the winter season. Since freshwater from glaciers and snowfields enters the shallow coastal areas at several places, brackish water overlies the marine water in summer. The salinity on the surface was between 5 and 10 psu, and between 30 and 34 psu near the bottom. More information about this fjord is given by Svendsen et al. (2002) and Hop et al. (2002). The Bryozoa colonies were scraped off from the cave wall by scuba divers at a depth between 3 and 4 m. The Bryozoa colonies and the associated fauna were preserved in a 4% formaldehyde-seawater solution. In the laboratory, samples were washed and sieved through a 0.5 mm screen. The unknown spionids and the other polychaetes were picked out under a dissecting microscope at  $10-15 \times$ magnification. Methyl green staining was employed to visualize body structures. Drawings were made using a microscope and drawing attachment. For SEM studies, specimens were dehydrated in a critical point drier, attached to a stub and sputter-coated with gold palladium. SEM observations were made with a Zeiss DSM 960 A. For histological investigations of the glandular organ, samples were infiltrated and embedded in Araldite after dehydration. Sections with a thickness of about 1 µm were cut using a Leica Reichert Ultracut S ultramicrotome and subsequently stained in a solution modified after Richardson et al. (1960). Micrographs were taken with a Zeiss-Axioplan microscope and a CCD-camera ProgRes C10 (Jenoptik). Type material has been deposited in the Zoologische Sammlung der Universität Rostock (ZSRO); catalogue numbers are given below.

#### Systematics

Family SPIONIDAE Grube, 1850 Glyphochaeta gen. nov.

Type species: *Glyphochaeta laudieni* sp. nov. Gender: Feminine.

#### Diagnosis

Body not clearly divided in different regions. Anterior margin of prostomium with frontal horns; posterior end forming a short caruncle extending to chaetiger 1; without occipital antenna; eyes present. Nuchal organ as small ciliated patch on the posterior margin of the prostomium. Peristomium well developed. Branchiae absent. Postchaetal lamellae well developed only in the anterior body region. Mid-segmental dorsal ciliated crest present. Lateral organs absent. Notopodia with capillaries. Anterior neuropodia with capillaries; neuropodia of the middle and posterior body region with hooded hooks, replaced by grooved spines in some neuropodia of the middle body region. Some chaetigers of the middle body region with glandular organs. Sabre chaetae absent. Pygidium with four anal lobes.

#### Etymology

The generic name refers to the shape of the grooved spines that replace the hooded hooks in some neuropodia of the middle body region (*glyphanos*—Greek for a carving tool or chisel; *chaite*—Greek for bristle).

## Glyphochaeta laudieni sp. nov. (Figures 1-3)

#### Type material

Holotype: Svalbard, Spitsbergen, Kongsfjorden, Blomstrandhalvøya, marine grotto near Hansneset (78°59.08'N, 11°57.43'E), grotto wall, from among Bryozoa colonies, 4 m depth, 4 September 2004 (ZSRO-P1649). Paratypes: Svalbard, Spitsbergen, Kongsfjorden, Blomstrandhalvøya, marine grotto near Hansneset (78°59.08'N, 11°57.43'E), grotto wall, from among Bryozoa colonies, 4 m depth, 4 September 2004, four specimens (ZSRO-P1650); Svalbard, Spitsbergen, Kongsfjorden, Blomstrandhalvøya, marine grotto near Hansneset (78°59.08'N, 11°57.43'E), grotto wall, from among Bryozoa colonies, 3.5 m depth, 21 June 2003, three specimens (ZSRO-P1651); Svalbard, Spitsbergen, Kongsfjorden, Blomstrandhalvøya, marine grotto near Hansneset (78°59.08'N, 11°57.43'E), grotto wall, from among Bryozoa colonies, 4 m depth, 21 June 2003, 13 specimens (ZSRO-P1652).

#### Description

Holotype complete with 35 chaetigers, total length 3.3 mm, width 0.4 mm. Paratypes between 0.8 and 4.1 mm long and 0.37 and 0.54 mm wide, with 18–35 chaetigers. Prostomium with frontal horns anteriorly, with four eyes trapeziformly arranged with posterior pair smaller and usually more closely spaced (Figures 1A, 2A); occipital antenna absent; prostomium terminating posteriorly in a small caruncle extending to the middle/ end of chaetiger 1; palps relatively short, extending at most to chaetiger 10 in preserved specimens. Very small nuchal organ as ciliated patches at the posterior margin of the prostomium (Figures 1A, 2A). Body not distinctly divided in different regions, with transversal ciliated crests dorsally and smooth surface ventrally (Figure 2B). Mid-segmental ciliated crest from chaetiger 2 to about chaetiger 10, thereafter ciliated crest at the posterior margin of chaetigers. Branchiae completely absent. Lateral organs absent. Postchaetal



Figure 1. *Glyphochaeta laudieni* gen sp. n. (A) Anterior end, dorsal view, palps broken off; (B) first chaetiger, anterior view; (C) chaetiger 10, anterior view; (D) chaetiger 12, anterior view; (E) chaetiger 15, anterior view; (F) chaetiger 16 and 17, ventral view; (G) grooved spine from chaetiger 14; (H) hooded hook from posterior chaetiger. Scale bar:  $200 \,\mu m$  (A);  $100 \,\mu m$  (B–F);  $20 \,\mu m$  (G, H).

Figure 2. *Glyphochaeta laudieni* gen sp. n., SEM micrographs. (A) Anterior end, frontal view; (B) anterior end, ventral view; (C) lateral view of chaetigers 12–15, neuropodial hooded hooks of chaetiger 12 and 13 broken off; (D) grooved spine of chaetiger 16; (E) neuropodial hooded hooks of a posterior chaetiger; (F) neuropodial hooded hooks of a posterior chaetiger; (F) neuropodial hooded hook of a posterior chaetiger, two apical teeth above the main tooth. Scale bars:  $60 \,\mu\text{m}$  (A, C);  $100 \,\mu\text{m}$  (B);  $10 \,\mu\text{m}$  (D);  $4 \,\mu\text{m}$  (E);  $3 \,\mu\text{m}$  (F).





Figure 3. *Glyphochaeta laudieni* gen sp. n., light micrographs. (A) Sagittal section through chaetiger 14 and 15 with glandular organ in chaetiger 14 and grooved spine in chaetiger 15; (B) sagittal section through chaetiger 14 with glandular organ associated with grooved spine. Scale bars:  $30 \,\mu$ m. coe, coelom; g, gut; gl, glandular organ; sp, grooved spine.

lamellae present; on chaetiger 1 tongue-like (Figure 1B); thereafter, notopodial lamella first triangular, later broadly rounded (Figure 1C-E), absent posteriorly; neuropodial lamella broadly rounded, absent when hooks appear (Figure 1C-E). Notopodia with smooth or hirsute capillaries, usually in two rows. Anterior neuropodia with smooth or hirsute capillaries, from chaetiger 8 or 9 in juveniles and from chaetiger 11 or 12 in adults additionally one or two hooded hooks (Figures 1H, 2E), usually only slightly bent, uni- or bidentate (Figure 1H); with appearance of hooks, the number of capillaries decreases considerably, one or two capillaries up to chaetiger 14 at most, in posterior chaetigers two or three neuropodial hooded hooks, uni-, bi- or sometimes tridentate (Figure 2F); spines, with longitudinal groove basally (Figures 1F, G, 2C, D) first appear on chaetiger 14 on specimens with more than 28 chaetigers in total (one specimen with 33 chaetigers without spines as an exception), only one grooved spine per neuropodium present, grooved spines replace hooded hooks from chaetiger 14 up to chaetiger 20, depending on total number of chaetigers (Table I), sometimes on posteriormost spine-bearing neuropodia one hooded hook present additionally; spines are  $10-12\,\mu\text{m}$  in diameter at the very base, posterior spines sometimes thinner; grooved spines associated with glandular organs (Figures 1F, 2C, 3B). Glandular organs about 25-35 µm in diameter (Figure 3A, B). Sabre chaetae (recurved chaetae with a broad blade in the ventralmost position of the neuropodia) absent. Pygidium with four anal lobes, maximum about 58 µm in length. No discernible methyl green or Shirlastain A® staining pattern.

#### Additional observations

The hooded hooks and spines are sometimes asymmetrically arranged. For example, hooded hooks are first present only on one side of the body, whereas the corresponding neuropodium of the other side still bears capillaries. In other cases, spines may be

		Number of chaetigers	Length (mm)	First chaetiger(s) with hooded hooks (capillaries still present)	First chaetiger with hooded hooks only	Chaetigers with grooved spines	Length of anal lobes (µm)
ZSRO-	Holotype	35	3.2	12	13	14-16	n.m.
P1649							
ZSRO-	Paratypes	18	1.1	8	10	-	32
P1650		25	1.5	10	11	-	45
		33	2.5	11-12	13	-	48
		Anterior fragment	?	9	10	14	-
ZSRO-	Paratypes	35	4.1	11-13		14-18	n.m.
P1651		Anterior fragment	?	12–13		14–20	-
		Anterior fragment	?	12–13		14–17	-
ZSRO-	Paratypes	18	0.8	11-12		-	_
P1652		22	1.0	9-11	12	-	_
		24	n.m.	11		-	_
		28	2.1	11-13		14-16	_
		32	2.2	11-13		14-17	58
		34	2.1	11–13		14-17	58

Table I. Glyphochaeta laudieni gen sp. n.: ranges of numerical characters for different specimens.

n.m., Not measured.

developed in some neuropodia, whereas hooded hooks are present on the corresponding neuropodia of the other side.

### Etymology

The species is dedicated to Dr Jürgen Laudien of the Alfred-Wegener-Institut Bremerhaven. He collected some of the specimens and he assisted us greatly during our field investigations on Spitsbergen in June 2003.

#### Geographical distribution

Species known only from the type locality.

### Discussion

*Glyphochaeta laudieni* sp. n. is unique among "Spionidae" in having grooved spines connected with glandular organs in some middle neuropodia (Figures 1F, 2C, D, 3B). The position of the species within the "Spionidae", however, is not clear. *Glyphochaeta* shares the absence of branchiae within "Spionidae"—as currently defined (excluding Apistobranchidae, Longosomatidae, Poecilochaetidae, Trochochaetidae, and Uncispionidae)—only with *Spiophanes*. Moreover, large parapodial glandular organs in the middle body region are present only in *Glyphochaeta* and *Spiophanes*. In *Spiophanes* these glandular organs are present from chaetiger 5 to about chaetiger 13–15 (Meißner and Hutchings 2003), whereas in *Glyphochaeta* they first appear from chaetiger 14. The structure of these glands is completely different as well. In *Spiophanes* the glandular organs producing "bacillary chaetae" are mainly composed of a large glandular sac and an accessory gland taking up almost the whole chaetiger (unpublished data), whereas in *Glyphochaeta* the glands are restricted to the neuropodia (Figure 3). In *Glyphochaeta* the glands probably produce a liquid secretion, and the attached grooved spines may act as a moving open drain (Figures 1F, 2C, D, 3B). A potential convergent development of glandular organs and a convergent reduction of branchiae in *Spiophanes* and *Glyphochaeta* cannot be excluded. Most characters mentioned in the diagnosis of *Spiophanes* provided by Meißner and Hutchings (2003) are absent in *Glyphochaeta*.

Comparable glandular organs have also been described in other species of spionids, for examples the "poches glanduleuses" in *Polydora* (Claparède 1870), the "podialen Drüsenorgane" in *Microspio*, *Pygospio*, and *Spio* (Söderström 1920), or the glands in the fifth chaetiger of juvenile *Polydora ciliata* (Johnston, 1838) (Hannerz 1956). These glands are usually smaller than those found in *Spiophanes* or *Glyphochaeta*, but they are also connected with neuropodial chaetae as in *Glyphochaeta* (except for *P. ciliata*). Comparative studies into homologies of the glandular structures in spionids remain to be performed.

The function of the grooved spine as a drain seems apparent, yet the function of the secretion is obscure. The specimens were found only in samples with colonies of Bryozoa. The samples from the bottom of the grotto with a high amount of detritus never contained *G. laudieni* sp. n. All specimens were found free in the samples, without any indication of a tube, so that this gland is probably not involved in formation of a tube. This assumption is reinforced by the absence of spines in juvenile specimens. Spines first appear when about 28 chaetigers have been developed (Table I). The presence of spines in adults may indicate a reproductive function. The small size of the species points to a low number of larvae and a lecithotrophic or direct development, although this hypothesis remains to be tested.

The appearance and the shape of hooded hooks have been regularly used in taxonomic descriptions. The first appearance of hooks in juveniles is most important for phylogenetic analyses. It has already been used in the cladistic analysis of Prionospio and related genera (Sigvaldadóttir 1998). The first appearance of hooks is often invariable (e.g. Polydora complex, *Pygospio*, *Streblospio*), but in other cases their presence depends to a certain extent on the total number of chaetigers (and it is only useful for identification at best, e.g. Marenzelleria, Prionospio, Spio). In G. laudieni sp. n. the hooded hooks first appear on chaetiger 8 or 9 in the smallest specimens but in chaetiger 11-12 in adults; thus, as the individuals grow, the first hooks become displaced two to four chaetigers backwards. This minor shift of hooks is probably the most common case among spionids. The first appearance of neuropodial hooded hooks at chaetiger 8 is not unusual: it has been recorded for example in certain genera of the Polydora complex and in some species of Pygospio and Streblospio. Interesting in this context is that Söderström (1920) described a transformation of bidentate hooded hooks into spoon-like hooks ("löffelförmige Borsten") in the neuropodia of chaetigers 8-11 of mature P. elegans Claparède, 1863. This transformation was also described by Berkeley and Berkeley (1954) from a single specimen from Nova Scotia and by Light (1977) from specimens from California. The California specimens exhibit spoon-like hooks in chaetiger 8 through to chaetiger 10 or 12. Hilbig (1982) provided SEM micrographs of these spoon-like hooks. The hooks possess a groove on the concave side; hoods are still present, but the hood may be opened at the concave side of the hook. Adult P. elegans from the Baltic Sea also possess these modified hooded hooks (personal observation). Some of these hooks resemble those described for *P. elegans* by Söderström (1920), whereas others resemble those found on species of the Atherospio complex (sensu Mackie 1996) (personal observation). The transformation of hooded hooks

parallels that found in *G. laudieni*, because already Söderström (1920) concluded that the development of the spoon-like hooks was a function of age and that they derived from a transformation of the bidentate hooded hooks as the specimens matured. In *Glyphochaeta*, however, the hooded hooks of chaetiger 14 and subsequent chaetigers are replaced by grooved spines without a conspicuous hood (Figure 2D), and the spines are a great deal thicker. Additional similarities with *P. elegans* are the absence of sabre chaetae, the presence of neuropodial glands, and the number and shape of anal cirri. Therefore, an assignment of *Glyphochaeta* into the third group (with *P. elegans*, the *Atherospio* complex, and *Pseudopolydora primigenia* Blake, 1983) of the strict consensus tree provided by Mackie (1996) is most likely.

#### Acknowledgements

Collecting of polychaetes in the intertidal and subtidal area of the Kongsfjorden was supported by a grant from the Deutsche Forschungsgemeinschaft (SPP 1158, Antarktisforschung mit vergleichenden Untersuchungen in arktischen Eisgebieten, BI 758/ 2-1). I would like to thank Dr Michael Assmann and Dr Jürgen Laudien, Alfred-Wegener-Institut Bremerhaven, for collecting material from the bottom and the wall of the marine grotto near Hansneset. I am thankful for the support of the Electron Microscopic Centre of the Medical Faculty of the University of Rostock. I am obliged to Dr M. Stachowitsch for scientific English copyediting.

#### References

- Berkeley E, Berkeley C. 1954. Additions to the polychaete fauna of Canada, with comments on some older records. Journal of the Fisheries Research Board of Canada 11:454–471.
- Blake JA, Arnofsky PL. 1999. Reproduction and larval development of the spioniform Polychaeta with application to systematics and phylogeny. Hydrobiologia 402:57–106.
- Blake JA, Kudenov JD. 1978. The Spionidae (Polychaeta) from the southeastern Australia and adjacent areas with a revision of the genera. Memoirs of the National Museum of Victoria 39:171–280.
- Blake JA, Maciolek NJ. 1992. Polychaeta from deep-sea hydrothermal vents in the eastern Pacific. III. A new genus and two new species of Spionidae from the Guaymas Basin and Juan de Fuca Ridge with comments on a related species from the western North Atlantic. Proceedings of the Biological Society of Washington 105:723–732.
- Claparède É. 1870. Les Annélides Chétopodes du Golfe de Naples. Supplément. Mémoires de la Société de Physique et d'Histoire Naturelle de Genève 20:365–542.
- Ehlers E. 1907. Neuseeländische Anneliden, 2. Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematisch-Physikalische Klasse, Neue Folge 5:1–31.
- Grube AE. 1860. Beschreibung neuer oder wenig bekannter Anneliden. Archiv der Naturgeschichte 26:71-118.
- Hannerz L. 1956. Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). Zoologiska Bidrag från Uppsala 31:1–204.
- Hilbig B. 1982. Beitrag zur Ultrastruktur der mit häutiger Hülle versehenen Borsten und Haken von Polychaeten und ihre Bedeutung für die Taxonomie und Systematik. Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 79:19–50.
- Hop H, Pearson T, Hegseth EN, Kovacs KM, Wiencke C, Kwasniewski S, Eiane K, Mehlum F, Gulliksen B, Wlodarska-Kowalczuk M, Lydersen C, Weslawski JM, Cochran S, Gabrielsen GW, Leakey RJG, Lønne OJ, Zajaczkowski M, Falk-Petersen S, Kendall M, Wängberg SÅ, Bischof K, Voronkov AY, Kovaltchouk NA, Wiktor J, Poltermann M, di Prisco G, Papucci C, Gerland S. 2002. The marine ecosystem of Kongsfjorden, Svalbard. Polar Research 21:167–208.
- Light WJ. 1977. Spionidae (Annelida: Polychaeta) from San Francisco Bay, California: a revised list with nomenclatural changes, new records, and comments on related species from the northeastern Pacific Ocean. Proceedings of the Biological Society of Washington 90:66–88.

- Maciolek NJ. 1981. Spionidae (Annelida: Polychaeta) from the Galápagos Rift geothermal vents. Proceedings of the Biological Society of Washington 94:826–837.
- Mackie ASY. 1996. Taxonomy and phylogeny of spioniform Polychaetes (Annelida) [PhD thesis]. Göteborg: Göteborgs Universitet. 168 p.
- Meißner K, Hutchings PA. 2003. *Spiophanes* species (Polychaeta: Spionidae) from eastern Australia—with descriptions of new species, new records and an emended generic diagnosis. Records of the Australian Museum 55:117–140.
- Richardson KC, Jarett L, Finke EH. 1960. Embedding in epoxy resins for ultrathin sectioning in electron microscopy. Stain Technology 35:313–325.
- Rouse GW, Pleijel F. 2001. Polychaetes. Oxford: Oxford University Press. 354 p.
- Sigvaldadóttir E. 1998. Cladistic analysis and classification of *Prionospio* and related genera (Polychaeta, Spionidae). Zoologica Scripta 27:175–187.
- Söderström A. 1920. Studien über die Polychaetenfamilie Spionidae [PhD thesis]. Uppsala: Uppsala Universitet. 288 p.
- Svendsen H, Beszczynska-Møller A, Hagen JO, Lefauconnier B, Tverberg V, Gerland S, Ørbæk JB, Bischof K, Papucci C, Zajaczkowski M, Azzolini R, Bruland O, Wiencke C, Winther JG, Dallmann W. 2002. The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. Polar Research 21:133–166.
- Wilson RS. 2000. Family Spionidae. In: Beesley PL, Ross GJB, Glasby CJ, editors. The southern synthesis. Fauna of Australia. Volume 4a, Polychaetes and allies. Melbourne: CSIRO Publishing. p 196–200.