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Identification keys and comments on the taxonomy of spionid polychaetes (Annelida: Spionidae) from the continental shelf of northern Europe

Vasily I. Radashevsky
A.V. Zhirmunsky Institute of Marine Biology, National Scientific Center of Marine Biology, Far Eastern Branch of the Russian Academy of Sciences, Vladivostok 690041, Russia
E-mail: radashevsky@gmail.com

Abstract Despite a long history of studies on polychaetes in shallow waters in Europe, the taxonomy of many spionids in the region remains uncertain. The present paper highlights the problems to be solved in the future and, in response to a great need for identification of European polychaetes, provides identification keys to species in 23 genera of Spionidae from the continental shelf (up to 100 m depth) of northern Europe, from Norway to Portugal.

Introduction

Despite a long and pioneering history of biological studies in European waters, the taxonomy of many polychaetous annelids in the region remains uncertain. Brief original old descriptions, absence of type material, different characters used by different authors to describe and distinguish species, ignorance of old descriptions, and misinterpretations of specific morphological and ecological characteristics have resulted in incorrect concepts of identity, taxonomy and cosmopolitan distribution of some “good old” European species of polychaetes. Re-descriptions with modern sets of taxonomic characters and keys for the identification of species are therefore needed not only to describe the biodiversity in European waters but also to monitor changes in this biodiversity due to environmental changes and introductions of non-indigenous organisms. Requests for comprehensive re-descriptions of European species comprising their morphological, ecological, reproductive and molecular characteristics also come from other regions where European species were reported to occur. Taxonomic revisions in America, Africa, Asia, Australia, etc., are not possible without complete information about old European species. New sampling techniques developed in recent decades allow better collecting, and new analytic techniques allow better examination of specimens. However, despite requests for revisions and the availability of new techniques for sampling and analysis, taxonomic studies in Europe have declined greatly in recent decades. This decline is not only because of economic problems in the region but also due to a perception that European shallow waters have been sufficiently studied. Polar, deep-water and pure molecular investigations became fashionable, while studies on the taxonomy of shallow-water organisms came to be considered outdated.

Spionids are among the most common polychaetous annelids around the world, comprising over 500 species, grouped into about 40 genera (Blake 1996a; Rouse 2001b; Radashevsky 2012). Despite their ubiquity and long history of study, the phylogenetic relationships of the Spionidae Grube, 1850 with other polychaetes and among spionid taxa remain poorly known. Previous inferences of phylogenetic hypotheses, using morphological data, have provided contradicting results (Rouse & Fauchald 1997; Sigvaldadóttir *et al.* 1997; Blake & Arnofsky 1999). Cladistic analyses of the morphological characters of the 80 polychaete families by Rouse & Fauchald (1997: fig. 73) suggested sister-group relationships between Spionidae and Trochochaetidae Pettibone, 1963, while Poecilochaetidae Hanappeared as a sister group to the Longosomatidae Hartman, 1944 and Magelonidae Cunningham & Ramage, 1888; together with Apistobranchidae Mesnil & Caullery, 1898 and Chaetopteridae Audouin & Milne Edwards, 1833, these seven taxa formed a monophyletic Spionida Dales, 1962. A cladistic analysis of the morphological characters of spiomorph polychaetes by Blake & Arnofsky (1999: figs 13C, 14) suggested close relationships between *Trochochaeta* Levinsen, 1883 and *Poecilochaetus* Claparède in Ehlers, 1875, *Heterospio* Ehlers, 1874 and *Uncispio* Green, 1982, forming a monophyletic group within the Spionidae, sister either to *Laonice* Malmgren, 1867 or *Aonidella* Maciolek in López-Jamar, 1989. The inclusion of *Poecilochaetus* and *Trochochaeta* within Spionidae was also corroborated by the presence of unpigmented ocelli of similar position and composition in the larvae of these polychaetes (Hausen 2007). Analyses using nucleotide data have been inconsistent regarding relationships among spiomorph polychaetes but all agree that Spionida is polyphyletic, as currently defined, and *Apistobranchus* Levinsen, 1883, *Chaetopterus* Cuvier, 1830, and *Magelona* F. Müller, 1858 are not closely related to Spionidae (Rousset *et al.* 2007; Struck *et al.* 2008). They confirmed the close relationships between Spionidae, *Poecilochaetus* and *Trochochaeta*, although were not able to resolve these relationships, and suggested sister-group relationships of Spionidae with Sabellariidae (Struck *et al.* 2008, 2015; Zrzavý *et al.* 2009; Capa *et al.* 2012a; Weigert *et al.* 2014; Weigert & Bleidorn 2016). A preliminary combined analysis of morphological and molecular data of spiomorph polychaetes suggests that both *Poecilochaetus* and *Trochochaeta* are nested within the Spionidae (Radashevsky unpublished). These two genera are therefore included in the present paper as members of the family Spionidae.

In the absence of a well supported hypothesis about phylogenetic relationships between spionid taxa, grouping spionid genera into higher rank taxa (subfamilies, etc.) is not currently recommended. The monophyly of the tribe Polydorini Benham, 1896 and the subfamily Spioninae Söderström, 1920 seems to be readily defined (see Blake & Arnofsky 1999; Radashevsky 2012) but requires further investigations. Remarkably, most of the genera of Spionidae have been defined not by unique morphological characters, apomorphies, but by combinations of homoplasious characteristics each shared by members of other genera.

Fauvel (1927) provided keys to 11 genera and 32 species of Spionidae from France. Nelson-Smith *et al.* (1990) provided keys to six genera and 12 species of Spionidae from the British Isles and north-western Europe, while Hartmann-Schröder (1996) provided keys to 11 genera and 43 species of Spionidae from Germany and adjacent waters, and Kirkegaard (1996) provided keys to 14 genera and 37 species of Spionidae from around Denmark. The UK Species Directory listed 60 spionid species (not all named with certainty) in 17 genera (Mackie & Erséus 1997). Of these, 12 species in 8 genera had been included in the guide by Nelson-Smith *et al.* (1990) and others in unpublished workshop keys that have formed the basis of spionid identification in British waters in recent decades. Radashevsky (2012) provided an identification key to 20 genera, listed 80 species of Spionidae reported from the British Isles, and also overviewed the morphology of adult spionids in an attempt to standardize terminology for their description. The present paper provides an updated key to 23 genera, and a series of keys to species of Spionidae recorded from the continental shelf (up to 100 m depth) of northern Europe, from Norway to Portugal.

Material and Methods

I examined most of the spionids reported in the present study in national museums in London, Edinburgh, Paris, Copenhagen, Stockholm, Reykjavik, Frankfurt-am-Mein, and in the collections of environmental consultancies: Akvaplan-NIVA (Fram Centre for Climate and the Environment, Tromsø, Norway), APEM (Letchworth, UK), Thomson Ecology (Guildford, UK) and Unicomarine (Letchworth, UK), as well as the Scottish Environment Protection Agency (SEPA) collection (Dingwall, UK). Extensive material was also collected from intertidal and shallow waters and examined alive at the Dove Marine Laboratory (Cullercoats, UK), FSC Millport Field Centre (Millport, UK), Roscoff Marine Station (Roscoff, France), BIOICE Marine Laboratory (Sandgerd'i, Iceland) and Akvaplan-NIVA. Some material was obtained from the participants of two NMBAQC Workshops on spionid taxonomy, in Cullercoats (November 2008), and Millport (October 2016). Additional material from Scotland was kindly provided by Julian Hunter, and from the North Sea, Germany, by Dagmar Lackschewitz. The characteristics of a few spionids that were not available for examination during this study were obtained from the literature.

Newly collected live worms were relaxed in isotonic magnesium chloride before examination in the laboratory. Fixed specimens were stained with solutions of methyl green and the Shirlastain A in alcohol, which contrast fine body structures and allow the study of external ciliary and internal structures including various glands. All new material has been deposited in public collections; full details will be provided in future taxonomic revisions.

Identification notes and general taxonomic remarks

The keys below refer to characters of adult, fully developed spionids as they were defined by Radashevsky (2012). Recently settled and juvenile individuals usually have not yet developed the adult features necessary for correct unambiguous identification. Such features include pigmentation, caruncle and nuchal organs, dorsal crests, arrangement and shape of chaetae and branchiae, and shape of pygidium. One of the most important taxonomic characters, branchiae, usually first appear in late larvae or early juveniles, soon after settlement and metamorphosis. In some spionids, the first pair of larval or juvenile branchiae appears on the segment in which the anteriormost branchiae will occur in the adults, while in others the two positions are different.

For example, in the larvae of many *Laonice*, *Microspio*, *Prionospio*, *Scolelepis* and *Spio*, branchiae first develop on chaetiger 3 (or even more posteriorly), and then in the juveniles branchiae develop on chaetiger 2 or on chaetigers 1 and 2, depending on the species. In larvae of *Boccardia* and *Boccardiella*, branchiae always first develop on chaetiger 7, and then in the juveniles, additional branchiae develop on chaetigers 2 or 3, and on chaetigers 4 and 6 in some species. The first branchiae in larvae and juveniles of all *Prionospio*-complex species are smooth, without appendages. Pinnules and plates develop later in ontogenesis in a specific succession in adults of certain species (*e.g.*, *Prionospio* cf. *paucipinnulata* Blake & Kudenov, 1978, see Radashevsky 2015: figs 23A & 24A-C). The shape of the pygidium changes during ontogenesis in some polydorins (e.g., *Dipolydora cardalia* (E. Berkeley, 1927), see Radashevsky 1993: fig. 11c-e), and the number of pygidial cirri usually increases with age in adults of *Laonice*, *Malacoceros*, *Marenzelleria*, *Rhynchospio*, etc. The length of the caruncle, numbers of branchiae, pygidial cirri and some other variables specified in the keys refer to the maximal values reported in the species descriptions. Small individuals have smaller values if characters are size-dependent.

One of the characteristic features of adult spionids is the arrangement of chaetae in distinct groups or rows: anterior and posterior rows, plus a dorsal superior tuft in notopodia; anterior and posterior rows plus a ventral inferior tuft in neuropodia, a so-called "three-group chaetal arrangement" (Radashevsky 2012: fig. 11). These groups are usually easily distinguished in the anterior chaetigers, where they typically comprise slender capillaries. In succeeding chaetigers, the notopodial capillaries are usually reduced in number with the groups becoming indistinct, while the neuropodial capillaries are replaced by hooks in certain patterns. Mesnil (1893: 644, 1896: 113-114, 188) was the first to recognize this characteristic feature of spionids, and Söderström (1920: fig. 164) illustrated and applied his idea in spionid descriptions. Radashevsky & Fauchald (2000: figs 1-3) described different patterns of replacement of neuropodial capillaries by hooks and for the first time distinguished an additional group of chaetae, alternating capillaries, arranged between the neuropodial hooks in many spionids. They also suggested an evolutionary transformation of segment 5 in polydorin spionids to explain the diversity of arrangement and shape of the modified chaetae and shape of the whole segment in adults. All the authors stressed the importance of application of the positional criteria to recognize homologs among the different kinds of spionid chaetae to be used for phylogenetic inferences.

The keys are at a "state-of-the-art" stage, merely a step on the way to a future taxonomic revision of the European species of Spionidae. Spionids of uncertain taxonomy are reported as sp. A, sp. B, *etc*., or using intermediate Latin abbreviations *aff.* and *cf.* to indicate that available material either shows affinity with but does not belong to the species, or its identity with the species must be confirmed in the future.

Genetic analysis, mainly nucleotide sequencing fragments of various genes, has become a powerful tool, widely used in taxonomic and phylogenetic studies at present. Sequences of gene fragments of various spionids have been steadily adding to the major genetic sequence database, GenBank (www.ncbi.nlm.nih.gov/genbank). These data should however be used with caution. Unless accompanied by morphological descriptions and reliable identification of the material, sequences may be misleading if used in a comparative analysis of newly obtained data.

Radashevsky *et al.* (2014, 2016a, b) chose to use combined sequence data from four genes to assess the taxonomic status of distant populations of various spionids and the monophyly of the genera of Spionidae. The genes comprise the mitochondrial 16S rDNA, nuclear 18S and 28S rDNA genes coding for 18S and 28S ribosomal RNA, and the protein-coding gene Histone 3 (H3). These studies is a part of a bigger ongoing project by the authors aiming to hypothesize on the phylogenetic relationships within the Spionidae based on analysis of a comprehensive set of molecular and morphological data.

Notes on the key

The genera are arranged in alphabetic order below, except for members of the tribe Polydorini Benham, 1896, which are placed at the end (this does not include *Atherospio*, which have heavy spines in the neuropodia - Polydorini have falcate spines in the notopodia). Species identification keys are followed by lists of species with references to their original description, type locality, most recent reports or re-descriptions, and general information about occurrence and habitat in northern Europe. Taxonomic problems are highlighted in *Remarks* sections preceding species identification keys. The numbers of valid species provided for each genus below are often approximate and not always the same as shown in the World Register of Marine Species (WoRMS, www.marinespecies.org). The ambiguity comes from uncertainties about the taxonomy of some populations and also from different ideas about identity and diagnoses of some species suggested by different authors. The species included are those recorded from the continental shelf (up to 100 m depth) of northern Europe, from Norway to Portugal. This has been done to give the greatest likelihood of inclusion of species present in the waters around Britain and Ireland; the keys are unlikely to be comprehensive for species from the edges of the included area.

Taxonomic account

Spionidae Grube, 1850

Key to genera of Spionidae from the continental shelf of northern Europe

1 Dorsal branchiae absent **2**

– Dorsal branchiae present **4**

2(1) Chaetae of chaetiger 1 of similar length or shorter than chaetae on the following chaetigers. Neuropodia of chaetiger 1 with one or two large crook-like spines in addition to capillaries. Neuropodia of chaetigers 2 and 3 with only capillaries .... ***Spiophanes***

– Chaetae of chaetiger 1 longer than those on the following segments and directed anteriorly, forming a structure reminiscent cephalic cage. Neuropodia of chaetiger 1 with capillaries only. Neuropodia of chaetigers 2 and 3 with heavy falcate spines **3**

3(2) Prostomium with anterioventral facial tubercle, posteriorly extended as a tri-lobed antler-like nuchal complex not attached to dorsum. Chaetiger 1 with notochaetae longer than neurochaetae. Chaetiger 4 with conical postchaetal lamellae. Postchaetal lamellae ampullaceous (flask-shaped) at least on chaetigers 7-11 .... ***Poecilochaetus***

– Prostomium anteriorly rounded, without facial tubercle, posteriorly extended as a short narrow caruncle attached to dorsum. Chaetiger 1 with neurochaetae longer than notochaetae. Chaetiger 4 with greatly expanded, serrated postchaetal lamellae. Postchaetal lamellae of anterior chaetigers flat, not ampullaceous .... ***Trochochaeta***

4(1) Chaetiger 5 with only capillaries **5**

– Chaetiger 5 with heavy spines in addition to capillaries **18**

5(4) Branchiae from chaetigers 11–14 on middle and posterior chaetigers, fused to notopodial postchaetal lamellae. One pair of dorsal appendages present on chaetiger 2 in males. Pygidium with two pairs of cirri .... ***Pygospio***

– Branchiae from chaetigers 1–3 for a variable number of chaetigers, fused to or free from notopodial postchaetal lamellae. Appendages absent on chaetiger 2 in males. Pygidium with cirri or otherwise **6**

6(5) Branchiae throughout most of body length **7**

– Branchiae limited to anterior half of body **12**

7(6) Head usually conical and distally pointed anteriorly (rounded or truncate in *S. cantabra*, *S. foliosa* and *S. tridentata*). Branchiae from chaetiger 2 (3 in small juveniles); anterior branchiae fused to notopodial postchaetal lamellae for most of their length. Pygidium fleshy, cushion-like, without cirri .... ***Scolelepis***

– Head usually rounded or truncate anteriorly (conical in *Dispio* and some *Spio*). Branchiae from chaetiger 1 or 2 (2–3 in small juveniles); anterior branchiae basally fused to notopodial lamellae or totally free from lamellae. Pygidium cirriform (small ventral pad present in addition to cirri in *Dispio*) **8**

8(7) Branchiae from chaetiger 1 (2–3 in small juveniles). Pygidium with two or more pairs of cirri **9**

– Branchiae from chaetiger 2 (3 in small juveniles). Pygidium with two pairs of cirri ... . ***Microspio***

9(8) Anterior notopodial postchaetal lamellae serrated. Lateral gills present. Posterior notopodia with capillaries only. Pygidium with small ventral pad in addition to cirri ....

Dispio

– Notopodial postchaetal lamellae entire, not serrated. Lateral gills absent. Posterior notopodia with or without hooks in addition to capillaries. Pygidium with cirri only **10**

10(9) Nuchal organs U-shaped, not metameric. Pygidium with more than two pairs of cirri. Posterior notopodia with hooks in addition to capillaries .... ***Marenzelleria***

– Nuchal organs metameric, with at least one pair of segmental metamers. Pygidium with two or more pairs of cirri. Posterior notopodia with capillaries only **11**

11(10) Prostomium with fronto-lateral horns. Pygidium with two or more pairs of cirri .... ***Malacoceros***

– Prostomium without fronto-lateral horns. Pygidium with two pairs of cirri .... ***Spio***

12(6) Single pair of branchiae on chaetiger 1. Peristomium forming distinct hood enveloping prostomium ventrally and laterally. Dorsal transverse ridge on chaetiger 2 .... ***Streblospio***

– More than one pair of branchiae on anterior chaetigers. Peristomium not forming hood around prostomium. Dorsal transverse ridge absent on chaetiger 2 .... **13**

13(12) Branchiae from chaetiger 3 (2–3 pairs) .... ***Aurospio***

– Branchiae from chaetiger 2 (more than three pairs) **14**

14(13) Prostomium conical with narrow and rounded tip anteriorly .... ***Aonides***

– Prostomium broadly rounded to truncate anteriorly **15**

15(14) Occipital antenna present on prostomium. Nuchal organs extending beyond chaetiger 3. Lateral pouches present between neuropodia of middle chaetigers .... ***Laonice***

– Occipital antenna absent on prostomium. Nuchal organs extending over 1–3 anterior chaetigers. Lateral pouches present or absent between neuropodia of middle chaetigers ... **16**

16(15) Ventral crests from chaetiger 2. Four pairs of smooth branchiae on chaetigers 2–5. Posterior notopodia with only capillaries .... ***Laubieriellus***

– Ventral crests absent. Four or more pairs of smooth or pinnate branchiae. Posterior notopodia with hooks in addition to capillaries **17**

17(16) Prostomium not flattened dorso-ventrally. Up to 12 pairs of branchiae. Pygidium with three cirri .... ***Prionospio***

– Prostomium flattened dorso-ventrally. More than 12 pairs of branchiae. Pygidium with more than three cirri .... ***Aonidella***

18(4) Chaetiger 5 with heavy falcate or aristate spines in neuropodia and only capillaries in notopodia .... ***Atherospio***

– Chaetiger 5 with heavy falcate spines in notopodia and only capillaries in neuropodia (neurochaetae sometimes absent) .... **Polydorini 19**

19(18) Chaetiger 5 only a little larger than chaetigers 4 and 6. Hooks in neuropodia from chaetiger 8; upper part of hook shaft with constriction, lower part of hook shaft bent at about right angle. Branchiae from chaetiger 7 .... ***Pseudopolydora***

– Chaetiger 5 almost twice as large as chaetigers 4 and 6. Hooks in neuropodia from chaetiger 7; upper part of hook shaft with or without constriction, lower part of hook shaft slightly curved. Branchiae from chaetigers 2–10 .... **20**

20(19) Branchiae from chaetiger 2 (from chaetiger 7 in early juveniles) **21**

– Branchiae from chaetigers 7–10 at all sizes **22**

21(20) Notopodia of chaetiger 5 with heavy falcate spines alternating with bilimbate-tipped companion chaetae. Posterior notopodia with heavy recurved spines in addition to slender capillaries .... ***Boccardiella***

– Notopodia of chaetiger 5 with heavy falcate spines and brush-topped spines. Posterior notopodia with only slender capillaries .... ***Boccardia***

22(20) Chaetiger 1 with notochaetae. Branchiae from chaetigers 7–10. Hooks accompanied by inferior capillaries at least in anterior neuropodia; upper part of hook shaft without constriction ***Dipolydora***

– Chaetiger 1 without notochaetae. Branchiae from chaetiger 7. Hooks not accompanied by inferior capillaries; upper part of hook shaft with constriction .... ***Polydora***

Aonidella Maciolek in López-Jamar, 1989

Aonidella Maciolek in López-Jamar, 1989: 107. Imajima 1992b: 57. Meißner *et al.* 2014: 208-209.

Type species. *Prionospio cirrobranchiata* Day, 1961. By Maciolek 2000: 529.

Synopsis.

Remarks. *Aonidella* Maciolek in López-Jamar, 1989 currently comprises three species. In Europe, *A. dayi* Maciolek in López-Jamar, 1989 was reported from Portugal (Gil & Sardá 1999), and *A. cirrobranchiata* (Day, 1961) was reported from Greece (Simboura & Nicolaidou 2001). Specimens from near the Isles of Scilly, UK, examined in the present study appear similar to *A. cirrobranchiata* originally described from south western Africa, but their identity requires verification.

1. *Aonidella* cf. *cirrobranchiata* (Day, 1961: 488-489, fig. 4, as *Prionospio cirrobranchiata*). Off Good Hope Cape, South Africa. Simboura & Nicolaidou 2001: 31. Rare, offshore, southwards from SW England.

Aonides Claparède, 1864

Aonides Claparède, 1864: 505. Pettibone 1963: 90. Foster 1971: 65–66. Blake & Kudenov 1978: 189. Imajima 1989: 214. Blake 1996: 100. Brito *et al.* 2006: 60.

Type species. *Aonides auricularis* Claparède, 1864 [=*Nerine oxycephala* Sars, 1862], by monotypy.

Synopsis. Adults with conical prostomium, rounded anteriorly and not extending posteriorly as a caruncle. Occipital antenna present or absent. Nuchal organs very short and indistinct. Branchiae from chaetiger 2 over anterior part of body, free from notopodial lamellae; branchial blood vessel interconnected by circular capillaries. Lateral pouches and dorsal crests absent. Posterior notopodia with hooks in addition to capillaries. Hooks bidentate to quadridentate, with only outer hood. Pygidium with two or more pairs of cirri. Digestive tract without gizzard-like structure. Main dorsal blood vessel with heart body. Excretory nephridia in anterior segments, gonoducts in fertile segments. Gonochorists, broadcast spawners. Oocytes with thick honeycombed envelope ornamented with two circles of vesicles. Spermatozoa short-headed. Larval development holopelagic, lecithotrophic.

Remarks. *Aonides* Claparède, 1864 currently comprises nine species. The oldest and the type species of the genus, *A. oxycephala* (Sars, 1862) originally described from Norway, has been reported worldwide and considered cosmopolitan. These reports, however, likely comprise a series of similar or sibling species.

Key to *Aonides* from the continental shelf of northern Europe

1 Up to 23 pairs of branchiae. Occipital antenna present. Hooks bidentate. Pygidium with up to ten cirri .... ***A. oxycephala***

– Up to 12 pairs of branchiae. Occipital antenna absent. Hooks quadridentate. Pygidium with four cirri .... ***A. paucibranchiata***

2. *Aonides oxycephala* (Sars, 1862: 64, as *Nerine oxycephala*). Norway. Sikorski 2001: 286-287, textfigs 1-9. Common, lower shore – shallow subtidal, mixed substrata; ubiquitous.
3. *Aonides paucibranchiata* Southern, 1914: 100-101, pl. 11, figs 24A-E. Clew Bay of Clare Island, Ireland. Sikorski 2001: 287-288, textfigs 1-5. Common, shallow subtidal, sand; ubiquitous.

Atherospio Mackie & Duff, 1986

Atherospio Mackie & Duff, 1986: 140. Meißner & Bick 2005: 116.

Type species. *Atherospio disticha* Mackie & Duff, 1986. By monotypy.

Synopsis.

Remarks. *Atherospio* Mackie & Duff, 1986 was established to encompass unusual spionids with aristate spines in the neuropodia of chaetigers 4 and 5, *A. disticha* from the west coast of Scotland. The worms had an anteriorly bilobed prostomium, short caruncle with an occipital antenna, a small number of branchiae beginning from chaetiger 7 and completely fused to the notopodial postchaetal lamellae, bidentate hooks with an unusually small lower tooth, and a pygidium surrounded by a ring of anal cirri. Mackie & Duff (1986) suggested that *Atherospio* was more closely related to *Pygospiopsis* Blake, 1983 than to polydorin spionids with heavy spines in the notopodia of chaetiger 5, and *Polydora guillei* Laubier & Ramos, 1974 with large acicular spines in the neuropodia of chaetiger 5. In establishing a new monotypic genus for a new species from Southern California, USA, *Pseudatherospio fauchaldi*, Lovell (1994) suggested that *Pseudatherospio*, *Atherospio* and *Pygospiopsis* are a closely related, geographically widespread complex of genera.

Polydora guillei was originally described based on two anterior fragments from Mediterranean Spain. Placing the new species within *Polydora*, Laubier & Ramos (1974) noted that it did not completely fit the diagnosis of the genus. When new material became available from the German Bight, North Sea, Germany, Meißner & Bick (2005) described additional characters for the species and referred it to *Atherospio*. They also supported Lovell's (1994) idea about close relationships between *Pseudatherospio*, *Atherospio* and *Pygospiopsis*.

Currently, *Atherospio* comprises two species, both of which occur in northern Europe. Nothing is known about the internal anatomy, gamete morphology or reproductive biology of either species. Unusually for spionids, *Atherospio* are often preserved with the proboscis everted.

Key to *Atherospio* from the continental shelf of northern Europe

1 Up to 18 aristate spines arranged in two rows in each neuropodium of chaetigers 4 and 5. Occipital antenna present. Hooks in neuropodia from chaetigers 13-15 .... ***A. disticha***

\- 1-3 large smooth acicular spines and 3-5 thinner pointed spines with short hairs or bristles on the distal end present in each neuropodium of chaetiger 5. Occipital antenna absent. Hooks in neuropodia from chaetigers 15-17 .... ***A. guillei***

4. *Atherospio disticha* Mackie & Duff, 1986: 140–144, figs 1–4. Loch Tuirnaig, west coast of Scotland. Rare, shallow subtidal, possibly more widespread.
5. *Atherospio guillei* (Laubier & Ramos, 1974: 480–484, figs 1, 2, as *Polydora guillei*). Golfo de Rosas, Mediterranean, Spain. Meißner & Bick 2005: 116–119, figs 2–5. Moderately common, shallow subtidal, sand; ubiquitous.

Aurospio Maciolek, 1981

Aurospio Maciolek, 1981a: 229-230.

Type species. *Aurospio dibranchiata* Maciolek, 1981a. By monotypy.

Synopsis.

Remarks. *Aurospio* Maciolek, 1981 currently comprises six species. A member of the *Prionospio*-complex *sensu lato*, this genus was established for the deep-water Atlantic *A. dibranchiata* Maciolek, 1981. Adults of *Aurospio* have apinnate branchiae (2 or 3 pairs) beginning from chaetiger 3, not chaetiger 2, as for most *Prionospio* adults.

Prionospio ockelmanni Pleijel, 1985, originally described from Öresund, Sweden, was considered a junior synonym of *P. banyulensis* Laubier, 1966 by Sigvaldadóttir (1992). Later, Sigvaldadóttir (1998) transferred *P. banyulensis* to *Aurospio*. Paterson *et al.* (2016) described two new deep-water *Aurospio* species, one from the deep north-eastern Atlantic and another from the Mediterranean, and discussed the status of the genus.

Key to *Aurospio* from the continental shelf of northern Europe

1 Two pairs of branchiae on chaetigers 3 and 4; branchiae on chaetiger 3 longer than those on chaetiger 4. Median eyes small, similar in size to lateral eyes. Hooks in neuropodia from chaetigers 9-11 .... ***A. dibranchiata***

– Three pairs of branchiae on chaetigers 3-5 almost equal in length. Median eyes distinctly larger than lateral eyes. Hooks in neuropodia from chaetigers 12-13 .... ***A. banyulensis***

6. *Aurospio dibranchiata* Maciolek, 1981a: 230-238, figs 1–3. Argentine Basin, deep South Atlantic. Sigvaldadóttir 2002a: 209–210. Offshore, mud.
7. *Aurospio banyulensis* (Laubier, 1966: 258; 1968: 99-105, figs 10–15, as *Prionospio banyulensis*). Cap d'Osne, Banyuls, Mediterranean, France. Sigvaldadóttir 1998: 185, 186; 2002a: 210. Moderately common, subtidal mixed substrata, mud; probably ubiquitous.

***Dispio* Hartman, 1951**

Dispio Hartman, 1951: 86. Foster 1971a: 72. Blake & Kudenov 1978: 191.

Type species. *Dispio uncinata* Hartman, 1951. By monotypy.

Synopsis.

Remarks. Adults of *Dispio* Hartman, 1951 are usually big and muscular, living in sand or muddy sand on the intertidal or in shallow water. The worms exhibit high morphological variability, both ontogenetic and individual, which has never been described in literature. Identification of the species is therefore often confusing and ambiguous. Typically for such situations, the older and the type species of the genus, *Dispio uncinata* Hartman, 1951, originally described from the Gulf of Mexico, has since been reported from several different regions and is considered widespread.

Until 2016, *Dispio* comprised nine species. In an attempt to revise the genus, Delgado-Blas & Diaz-Diaz (2016) ignored two species poorly described by Friedrich (1956) from El Salvador and Brazil, and in their place, described five new species from the same region, thus making the taxonomy of the group even more confusing.

In Europe, *D. uncinata* Hartman, 1951 was reported from Spain (Ibáñez Genis 1973) and Italy (Lardicci 1989), and *D. magna* (Day, 1955) was reported from Greece (Simboura & Nicolaidou 2001). Specimens from Newquay, south west England, examined in the present study appear similar to *D. uncinata*, but their identity requires verification.

8. *Dispio* cf. *uncinata* Hartman, 1951: 86–90, pl. 22, figs 1–5, pl. 23, figs 1–4. Gulf of Mexico, Florida, USA. Rare, intertidal, sand; southwards from SW England.

***Laonice* Malmgren, 1867**

Laonice Malmgren, 1867: 200. Söderström 1920: 220. Foster 1971a: 69. Blake & Kudenov 1978: 204. Maciolek 2000: 533-536. Sikorski 2003a: 317, 2003b: 1179-1180, 2011: 201. Radashevsky & Lana 2009: 268.

Type species. *Nerine cirrata* M. Sars, 1851. By Malmgren 1867: 200.

Synopsis. Adults with rounded prostomium, anteriorly free or fused to peristomium, posteriorly extending as a long, low caruncle. Occipital antenna usually present, rarely absent. Median eyes usually large, complex. Nuchal organs long, U-shaped. Branchiae from chaetiger 2 over most of anterior part of body, free from notopodial lamellae; branchial blood vessels interconnected by circular capillaries. Lateral interneuropodial pouches usually present. Dorsal crests present or absent on postbranchiate segments. Notopodia with only capillary chaetae (except *L. sarsi* having hooks in addition to capillaries in posterior notopodia). Hooks in neuropodia bidentate to multidentate, with only outer hood. Pygidium with more than two pairs of cirri. Digestive tract without gizzard-like structure. Main dorsal blood vessel apparently without heart body. Excretory nephridia in anterior segments, gonoducts in fertile segments. Gonochorists, broadcast spawners. Oocytes with thick honeycombed envelope ornamented with two circles of vesicles. Spermatozoa short-headed. Larval development holopelagic, planktotrophic.

Remarks. *Laonice* Malmgren, 1867 currently comprises 35 valid species. Adults move freely in sediment near the surface, have strong body musculature and easily break apart upon fixation, thus fragments are usually present in samples. The size-dependent relationships of various characters, therefore, remain uncertain for many species. Sikorski (2003a) provided an identification key to eight *Laonice* species occurring in the Arctic and North Atlantic. Radashevsky & Lana (2009) overviewed the morphological features used in the identification of *Laonice*, while Sikorski (2011) and Sikorski & Pavlova (2016) provided an overview of all *Laonice* species and highlighted taxonomic problems to be solved.

Key to *Laonice* from the continental shelf of northern Europe

1 Prostomium fused with peristomium at anterior margin. Caruncle to chaetiger 35. Branchiae to chaetiger 37. Dorsal crests present on post-branchiate chaetigers. Sabre chaetae in neuropodia from chaetigers 9-21. Hooks in neuropodia from chaetigers 14-35, absent in notopodia. Hooks quadridentate or quinquedentate, with two small upper teeth situated side by side, and one to two tiny median superior teeth above main fang. Lateral interneuropodial pouches from chaetigers 6–25 to end of body. Pygidium with up to 20 cirri ....
....
L. bahusiensis

– Prostomium free from peristomium at anterior margin. Caruncle to chaetiger 14. Branchiae to chaetiger 34. Dorsal crests absent on post-branchiate chaetigers. Sabre chaetae in neuropodia from chaetigers 10-26. Hooks in neuropodia from chaetigers 16-39, in notopodia from chaetigers 33-96. Hooks bidentate or tridentate, with two small upper teeth situated side by side above main fang. Lateral interneuropodial pouches from chaetigers 4–33 to chaetigers 15-91, absent on posterior 19-52 chaetigers. Pygidium with up to 17 cirri ....

....

L. sarsi

9. *Laonice bahusiensis* Söderström, 1920: 4-7, 81-83, 93, 98, 99, 110, 114, 128, 134, 195, 223, figs 78-82. Gullmarfjord, Bohuslän, Sweden. Sikorski 2001: 290-291, textfigs 1-9; 2002: 413-418, fig. 4; 2003a: 320-325, figs 2B, 3A-I, 4A,B, 5A,B, 6F. Common, shallow sand and mixed substrata.
10. *Laonice sarsi* Söderström, 1920: 223-225, figs 129, 130 (*Part.*). N Flatholmsrännan, Gullmaren, Sweden. Sikorski 2001: 295-297, textfigs 1-5; 2003a: 338-340, figs 2B, 6A-E, 8A-J. Common, offshore, mud.

Laubieriellus Maciolek, 1981

Laubieriellus Maciolek, 1981b: 829-831.

Type species. *Laubieriellus grasslei* Maciolek, 1981. By author's designation.

Synopsis.

Remarks. *Laubieriellus* Maciolek, 1981 currently comprises two species. One of them, *L. salzi* (Laubier, 1970), has been reported in grey literature from northern Europe, but the identity of the worms requires verification.

11. *Laubieriellus salzi* (Laubier, 1970: 183-189, figs 1-3, as *Prionospio salzi*). Ashdod, south to Tel Aviv, Mediterranean, Israel. Rare.

Malacoceros Quatrefages, 1843

Malacoceros Quatrefages, 1843: 8-10. Fauchald 1977: 24. Blake & Kudenov 1978: 195. Imajima 1991a: 5. Sikorski 1994a: 21-22. Hourdez *et al.* 2006: 594. Delgado-Blas & Díaz-Díaz 2013: 182. Meißner & Götting 2015: 382.

Type species. *Spio vulgaris* Johnston, 1827. By Pettibone 1963b: 98.

Synopsis. Adults with fronto-lateral horns on prostomium. Occipital antenna absent. Nuchal organs entire or metameric. Branchiae from chaetiger 1 through most of body, fused to notopodial lamellae at least basally; branchial blood vessels not interconnected by capillaries. Lateral pouches and dorsal crests absent. Notopodia with only capillaries. Neuropodia with capillaries, hooks and sabre chaetae. Hooks unidentate to quadridentate with only outer hood. Pygidium with anal cirri. Digestive tract without gizzard-like structure. Main dorsal blood vessel without heart body. Nephridia serving both excretory and gamete-releasing functions. Gonochorists, broadcast spawners. Oocytes with thick honeycombed envelope ornamented with one circle of vesicles. Spermatozoa short-headed. Larval development holopelagic, planktotrophic.

Remarks. *Malacoceros* Quatrefages, 1843 is a confusing genus within the Spionidae; its diagnosis has suffered from different interpretations (see reviews by de Saint-Joseph 1894: 66-67; Mesnil 1896: 144-149; Söderström 1920: 215; Pettibone 1963: 98). The genus currently comprises 17 species occurring all over the world, mainly on the intertidal and in shallow coastal waters. Two species, *M. samurai* Hourdez, Desbruyères & Laubier, 2006 and *M. jennicus* Graff, Blake & Wishner, 2008 are associated with hydrothermal vents in the southern East Pacific Rise and in the Caribbean, respectively. Preliminary molecular analysis suggested that, as currently defined, *Malacoceros* is polyphyletic (Radashevsky unpublished).

The type species of the genus, *Spio vulgaris* was originally described from Berwick-Upon-Tweed, Northumberland, England, by Johnston (1827). The original description was brief and not illustrated. First illustrations and more morphological details of the species were provided by Johnston (1838, 1865). Despite the brevity of the original description, Johnston (1827: 335) provided some particular details of the palp morphology: "Antennae two, setaceous, white, obscurely spotted, half an inch long, approximate at the base, placed on the vertex, contortile, and capable of being rolled up in a spiral form", which shows that he carefully examined these organs. Notably, Johnston (1827, 1838, 1865) did not describe a basal sheath on the palps of the worms. Johnston (1827: 336) also reported important ecological characteristics for the species: "The *Spio vulgaris* inhabits the sea shore, and the **margins of our river** (River Tweed, VIR), a little **below high-water mark**. It prefers a soil composed of **sand and mud, and in which the latter rather preponderates** (emphasis by VIR). It is found lurking under stones, or burrowing in the soil. ... The animal is used in this neighbourhood as a bait to take the fry of the Coal-fish..." Johnston (1827) reflected the common occurrence of the worms in the name of the species.

The generic breakdown of the Spionidae was not yet settled in nineteenth century, and *Spio vulgaris* was placed by different authors within *Nerine*, *Malacoceros*, *Scolecolepis* and *Scolelepis* (Johnston 1838; Quatrefages 1843, 1866c; Malmgren 1867; Mesnil 1896). Revising spionids from northern France, Mesnil (1896) was uncertain about the morphological characteristics of *Nerine vulgaris* Johnston, 1827. He referred to it as "l'espèce la plus énigmatique du genre" (Mesnil 1896: 146) but noted that it matched his emended diagnosis of *Scolelepis*. Mesnil (1896: 147) referred to *Scolelepis* three species "bien connues", *S. girardi* (Quatrefages, 1843), *S. ciliata* (Keferstein, 1862), *S. fuliginosa* (Claparède, 1868), and one species "énigmatique", *S. vulgaris* (Johnston, 1827). Mesnil (1896) referred pigmented worms from northern France to *S. fuliginosa* originally described from the Gulf of Naples by Claparède (1868, as *Spio fuliginosus*). He also proposed to refer *Spio laevicornis* described from Sebastopol Bay, Black Sea, Crimea, Russia, by Rathke (1837), and *Colobranchus tetracerus* described from Brittany by Schmarda (1861) to this genus. Moreover, Mesnil (1896: 138) distinguished two varieties within *S. fuliginosa*: *microchaeta* for worms from Naples described by Claparède (1868), and *macrochaeta* for worms from the English Channel.

McIntosh (1909, 1915a) distinguished only two species with fronto-lateral horns on the prostomium occurring in British waters: *Scolecolepis vulgaris* (Johnston, 1827) and *S.*

fuliginosus (Claparède, 1868). To the former species he referred *Malacoceros girardi* Quatrefages, 1843, *Colobranchus tetracerus* Schmarda, 1861, and *C. ciliatus* Keferstein, 1862, while to the latter species he referred *Spio laevicornis* Rathke, 1837. Remarkably, for *S. vulgaris*, McIntosh (1909, 1915a, b) described and/or illustrated palps with basal sheaths and tridentate hooks with two upper teeth arranged one above the other, while for *S. fuliginosus* he described and/or illustrated palps without basal sheath and tridentate hooks with two upper teeth arranged side by side.

Fauvel (1927) distinguished three species with fronto-lateral horns on the prostomium occurring in French waters: *Scolelepis fuliginosa* (Claparède, 1868), *S. ciliata* (Keferstein, 1862), and *S. girardi* (Quatrefages, 1843). He questionably referred *Colobranchus tetracerus* Schmarda, 1861 to *S. ciliata*, and *Spio vulgaris* Johnston, 1827 to *S. girardi*. Fauvel (1927: 28) separated the three species according to the presence of tridentae (*S. girardi*) or bidentate hooks numbering four (*S. fuliginosa*) or 7-12 (*S. ciliata*) per neuropodium. Remarkably, for *S. girardi*, Fauvel (1927: 31) noted palps "entourés à la base d'un calice du côte interne".

Guérin & Kerambrun (1984) examined adult, gamete and larval morphology, ecology, genetics and biochemical compositions of several Atlantic and Mediterranean populations of *Malacoceros fuliginosus* and suggested the existence of three forms. One was indigenous to the Atlantic, one to the Mediterranean, and one common to both locations. The authors suggested the use of the term "*Malacoceros fuliginosus* complex" to designate these relationships and emphasized the need for a complete re-examination of the genus *Malacoceros*.

Hartmann-Schröder (1996) distinguished three species with fronto-lateral horns on the prostomium occurring in German waters: *Malacoceros fuliginosus* (Claparède, 1868), *M. tetracerus* (Schmarda, 1861), and *M. vulgaris* (Johnston, 1827). She used mainly the same characters as Fauvel (1927) but referred worms with tridentate hooks to *M. vulgaris* and those with bidentate hooks to *M. fuliginosus* (4-10 hooks per neuropodium, beginning from chaetigers 30-57) and *M. tetracerus* (7-12 hooks per neuropodium, beginning from chaetigers 20-28). Hartmann-Schröder (1996) did not mention *M. girardi* Quatrefages, 1843 but referred *Scolelepis girardi* by Fauvel (1927) to synonymy of *M. vulgaris*.

Read & Bellan (2011) considered *M. vulgaris* as a synonym of *M. fuliginosus* (Claparède, 1868), but *M. girardi* Quatrefages, 1843 and *M. laevicornis* (Rathke, 1837) as valid species.

Sikorski (1992) described a new *Malacoceros* species, *M. jirkovi* from the Norwegian Sea but later placed it within *Spio* (Sikorski 2013). Meißner & Götting (2015) did not accept the new combination and re-assigned it back to *Malacoceros*. The uncertain generic assignement of this species results from the limited information available about its morphology and reproductive biology. New data about internal anatomy and gamete morphology will help to resolve the taxonomic position of *M. jirkovi*.

A revision of *Malacoceros* from northern Europe will be provided elsewhere (Radashevsky unpublished). Herein, the names are applied according to the species concepts provided in the original descriptions.

Key to *Malacoceros* from the continental shelf of northern Europe

1 Branchiae free from notopodial postchaetal lamellae, absent on posterior third of body. Pygidium with two pairs of cirri in individuals of all sizes. Sabre chaetae in neuropodia from chaetigers 5-6 .... ***M. jirkovi***

– Branchiae fused with notopodial postchaetal lamellae at least on anterior chaetigers, present along most of body. Pygidium with two pairs of cirri in small individuals (usually up to 50 chaetigers); large individuals with at least three pairs of pygidial cirri. Sabre chaetae in neuropodia after chaetiger 6 .... **2**

2(1) Bases of palps enveloped by a thin sheath. Up to 22 white chromatophores usually present on each palp in live individuals (invisible in fixed specimens). Nuchal organs comprising a pair of straight ciliary bands on sides of caruncle and a pair of entire serpentine ciliary bands on dorso-lateral sides near notopodial bases from front of chaetiger 1 almost to end of body. Hooks tridentate, with two upper teeth one above the other, accompanied by anterior-row capillaries, alternating capillaries between hooks, and inferior sabre chaetae ....

....

M. girardi

– Bases of palps free, without sheath. White spots on palps present or absent. Nuchal organs comprising a pair of U-shaped ciliary bands on sides of caruncle and short paired segmental metamers from chaetiger 2 on some anterior chaetigers. Hooks tridentate, with two upper teeth arranged side by side, accompanied only by alternating capillaries and inferior sabre chaetae **3**

3(1) Pigmentation absent on palps and body. Segmental nuchal metamers ciliated semi-ovals. Hooks up to 10 per neuropodium .... ***M. tetracerus***

– Up to 28 white chromatophores usually present on each palp, and one pair of white chromatophores present on lateral sides of peristomium below palps in live individuals (invisible in fixed specimens). Dark pigment usually present in foregut and scattered on anterior chaetigers (absent in small individuals with less than 100 chaetigers). Segmental nuchal metamers ciliated ovals. Hooks up to 7 (usually 3-5) per neuropodium .... ***M. vulgaris***

12. *Malacoceros girardi* Quatrefages, 1843: 10-13, pl. 3, figs 1-6. Îles Chaussey, Brittany, English Channel, France. Moderately common, intertidal to shallow mixed substrata; ubiquitous.
13. *Malacoceros jirkovi* Sikorski, 1992: 105-108, textfigs A-F. Norwegian Sea. Rare, subtidal; possibly northern.
14. *Malacoceros tetracerus* (Schmarda, 1861: 66-67, textfigs a-d, pl. XXVI, figs 210, 210a, as *Colobranchus tetracerus*). Brittany, northern France. Sikorski 1994a: 27-30, figs 3-4. Sikorski 2001: 300-301, textfigs 1-6. Moderately common, intertidal and shallow mixed substrata; ubiquitous.
15. *Malacoceros vulgaris* (Johnston, 1827: 335-336, as *Spio vulgaris*). Berwick-upon-Tweed, Northumberland, UK. Common, intertidal and shallow mud and mixed substrata, often in areas of organic enrichment; ubiquitous.

Marenzelleria Mesnil, 1896

Marenzelleria Mesnil, 1896: 120. Sikorski & Buzhinskaya 1998: 1111-1112. Sikorski & Bick 2004: 255. Blank & Bastrop 2009: 311-318.

Type species. *Marenzelleria wireni* Augener, 1913. By Augener 1913: 265.

Synopsis.

Remarks. *Marenzelleria* Mesnil, 1896 probably evolved in the Arctic region (Blank & Bastrop 2009) and currently comprises five species occurring in the Arctic and in boreal waters in the Atlantic and the Pacific. It was unknown in northern Europe before the 1970s, *Marenzelleria* were first recorded in the North Sea in late 1970s-early 1980s and in the Baltic Sea in 1985 (see reviews by Zettler 1997 and Blank *et al.* 2008). The first records of invasion were followed by rapid development of these non-indigenous worms in the region in the 1990s-2000s. The unexpected emergence of *Marenzelleria* stimulated numerous studies on their distribution, morphology, reproductive biology, physiology, ecology, bioturbation and genetics (e.g., *Aquatic ecology* 1997, Vol. 31, No. 2; Zettler 1996, 1997; Blank *et al.* 2004, 2005, 2006; Sikorski & Bick 2004; Bick 2005a; Orlova *et al.* 2006; Thomsen *et al.* 2008; Maximov 2010, 2011, 2015; Beukema & Dekker 2011; Karlson *et al.* 2011; Quintana *et al.* 2011; Renz & Forster 2013; Maximov *et al.* 2014; Kauppi *et al.* 2015; etc.). Some of these studies, however, were hampered by identification uncertainties (see Blank *et al.* 2008). Bastrop & Blank (2006) and Blank *et al.* (2008) suggested that molecular characters should be used for certain identification. Using PCR/RFLP analysis and PCR/sequencing (fragments of the mitochondrial *16S*, *COI* and *Cytb* genes), they distinguished three species of *Marenzelleria* occurring in the North and Baltic seas: *M. arctia*, *M. neglecta* and *M. viridis*, provided molecular key for their identification, and clarified their distribution in the region.

The identification of *Marenzelleria* specimens, using morphological characters only, is still problematic. Sikorski & Bick (2004: table 1) and Bick (2005: 271) suggested characters to identify intact mature individuals with body widths more than 1.2 mm. No characters have been suggested so far to identify smaller and incomplete specimens or larvae. The identification key to *Marenzelleria* provided by Bick (2005a) was used as a base for the key given below.

Key to *Marenzelleria* from the continental shelf of northern Europe (mature adults with body width more than 1.2 mm)

1 Branchiae throughout most of body. Nuchal organs to middle of chaetiger 4. Up to 180 chaetigers in total .... ***M. wireni***

– At least posterior one third of chaetigers abranchiate. Nuchal organs to middle of chaetiger 4 or shorter **2**

2 Nuchal organs to middle of chaetiger 4. Up to 65 branchiate chaetigers (less than one third of body). Up to 210 chaetigers in total .... ***M. neglecta***

– Nuchal organs not extending beyond chaetiger 2 .... **3**

3 30-40 branchiate chaetigers. Less than 100 chaetigers in total .... ***M. arctia***

– 60-130 branchiate chaetigers. Up to 240 chaetigers in total .... ***M. viridis***

16. *Marenzelleria arctia* (Chamberlin, 1920: 17–18, pl. III, figs 5–7, pl. IV, fig. 1, as *Scolecolepides arctius*). Lagoon at Collinson Point, Alaska, Camden Bay, Beaufort Sea, USA. Sikorski & Buzhinskaya 1998: 1115-1118, figs 2, 3. Sikorski 2001: 302-303, textfigs 1-6. Sikorski & Bick 2004: 268-271, figs 2D, F, 3D, 6, 7A-I.
17. *Marenzelleria neglecta* Sikorski & Bick, 2004: 264–268, figs 2B, 3C, 5A–I, 6. Darss–Zingst–Boddenchain, Germany, Baltic Sea. Unpublished records from Thames in shallow mixed substrata, low salinity; non-native.
18. *Marenzelleria viridis* (Verrill, 1873: 345, 600–601, as *Scolecolepis viridis*). Off Martha's Vineyard, Naushon Island, Massachusetts, USA. Maciolek 1984a: 51-55, fig. 2 (*Part.*). Sikorski & Bick 2004: 261-264, figs 2C, 3B, 4A-F. Recorded as a non-native from the Tay Estuary, Scotland.
19. *Marenzelleria wireni* Augener, 1913 (*Part.*): 264-267, figs 1, 2. West Bay off Flagstaff, Cape Flora, Franz-Joseph Land, Kara Sea. Maciolek 1984a: 49-51, fig. 1. Sikorski & Buzhinskaya 1998: 1112-1115, fig. 1. Sikorski & Bick 2004: 255-261, figs 1A-F, 2A, 3A. Bick 2005a: 269-270, fig. 3.

Microspio Mesnil, 1896

Microspio Mesnil, 1896: 119, 174. Fauvel 1927: 42. Blake & Kudenov 1978: 231. Maciolek 1990: 1128. Blake 1996a: 160.

Spio (*Microspio*): Foster 1971a: 33.

Type species. *Microspio mecznikowiana* (Claparède, 1868). By Söderström 1920: 247.

Synopsis.

Remarks. *Microspio* Mesnil, 1896 currently comprises 18 species. Adult *Microspio* appear similar to those of *Spio* but differ from them mainly in branchiae beginning from chaetiger 2 instead of chaetiger 1. Notably, in juveniles of many species of both groups, branchiae begin on chaetiger 3 and later appear on anterior chaetiger(s) (Hannerz 1956); thus, even generic identification of small worms may be confusing.

Two *Microspio* species were reported from northern Europe: *M. atlantica* and *M. mecznikowiana*. Adults of both species have tridentate hooded hooks in their neuropodia, with two upper teeth situated in a vertical row above the main fang. The superior tooth on the hooks of *M. atlantica* is tiny, closely applied to the lower tooth, and can only be observed with high magnification.

Key to *Microspio* from the continental shelf of northern Europe

1 Hooks in neuropodia from chaetiger 9. Prostomium anteriorly bilobed to slightly incised .... ***M. atlantica***

– Hooks in neuropodia from chaetiger 11. Prostomium anteriorly rounded to slightly incised **_M. mecznikowiana_**

20. *Microspio atlantica* (Langerhans, 1880: 89, as *Spio atlanticus*). Madeira, Portugal. Moderately common, shallow mixed substrata; ubiquitous.
21. *Microspio mecznikowiana* (Claparède, 1868: 324–325, pl. XXIII, fig. 2, as *Spio mecznikowianus*). Gulf of Naples, Mediterranean, Italy. Rare, offshore.

Poecilochaetus Claparède in Ehlers, 1875

Poecilochaetus Claparède in Ehlers, 1875: 9-13. Fauvel 1927: 67. Blake 1996e: 227. Rouse 2001a: 266-268.

Type species. *Poecilochaetus fulgoris* Claparède in Ehlers, 1875. By monotypy.

Synopsis.

Remarks. Claparède (in Ehlers 1875) established a new genus for a new species, *Poecilochaetus fulgoris* Claparède, 1875, but was in doubt about its relationships with other polychaetes. He noted its possible affinity with the Spionidiens (= Spionidae Grube, 1850) or Ariciens (Ariciea Audouin & Milne Edwards, 1829 = Orbiniidae Hartman, 1942) but concluded that the adults of *P. fulgoris* were so aberrant that it was impossible to place them in a family. Levinsen (1883) was the first to suggest the affinity between *Poecilochaetus* and *Disoma* Örsted, 1843 (= *Trochochaeta* Levinsen, 1883). Following this idea, Mesnil (1897) established a new family Disomidae Mesnil, 1897 to encompass the two genera, *Disoma* and *Poecilochaetus*. In a revision of the Spionidae, Söderström (1920) placed *Disoma* Örsted and *Poecilochaetus* in a new subfamily Disominae Söderström, 1920 within the family Spionidae. Based on the morphology of the larvae, Hannerz (1956) established a new family Poecilochaetidae for the only genus *Poecilochaetus*, and placed *Disoma* Örsted within the monogeneric family Disomidae. Studies on the morphology, biology and phylogenetic relationships of *Poecilochaetus* with other spionids were reviewed by Blake (1996e) and Rouse (2001a). Rouse (2001a: 268) noted that "The name Poecilochaetidae is essentially a redundant name since it only contains *Poecilochaetus*" and placed *Poecilochaetus* as an individual taxon within the Spionida Dales, 1962. Eibye-Jacobsen (2005) performed a phylogenetic analysis of morphological characters of 24 species of *Poecilochaetus* and discussed the possible evolution of some features. There is more on the taxonomy of *Poecilochaetus* in the introduction section above.

Poecilochaetus currently comprises 31 valid species. Kitamori (1965), Orensanz (1976), Pilato & Cantone (1976), and Read (1986) provided identification keys to the species described up to 1986. Santos & Mackie (2008) summarized and discussed taxonomic characters of all described *Poecilochaetus* species.

In north European waters, only *P. serpens* Allen, 1904 has been reported by various authors. Allen (1904) described details of adult morphology while Thorson (1946) and Hannerz (1956) described the gametes and pelagic larvae of *P. serpens*.

22. *Poecilochaetus serpens* Allen, 1904: 79-151, figs 1-66. Plymouth, England, UK. Common, subtidal sand; ubiquitous.

Prionospio Malmgren, 1867 *sensu lato*

Prionospio Malmgren, 1867: 201. Blake & Kudenov 1978: 211–212. Maciolek 1985: 329, 332. Wilson 1990: 245–246.

Type species. *Prionospio steenstrupi* Malmgren, 1867, by monotypy.

Synopsis.

Remarks. *Prionospio* Malmgren, 1867 and closely related spionids constitute the most diverse and complicated group within the Spionidae. The group currently comprises more than one hundred species occurring worldwide from the intertidal to the abyss. Historically treated together and referred to as a generic *Prionospio* complex, for a long time the genus was not explicitly defined and no single character or group of characters was suggested to support its monophyly. Different generic breakdowns of the complex were suggested by various authors based on different suites of external morphological characteristics of adults and ideas about their weight for taxonomy (e.g., Foster 1971; Blake & Kudenov 1978; Maciolek 1985; Wilson 1990; Blake 1996). All those groupings have been considered artificial, convenient for identification purposes rather than reflecting phylogenetic relationships.

The phylogenetic generic analysis by Sigvaldadóttir (1998) suggested monophyly of the group containing *Prionospio* Malmgren, 1867 *sensu stricto*, *Minuspio* Foster, 1971, *Aquilaspio* Foster, 1971, and *Apoprionospio* Foster, 1969. More than 80 valid species of these taxa were referred to *Prionospio* Malmgren, 1867 *sensu lato* with further generic division based on branchial form discouraged. In agreement with this conclusion and in the absence of an explanatory phylogenetic hypothesis, Wilson (1990) dispensed with subgenera, and Radashevsky (2015) suggested re-description of the *Prionospio* complex species using a diverse set of morphological characteristics to accumulate information for future phylogenetic analyses.

The morphology and taxonomy of some European *Prionospio* was described and discussed by Mackie (1984), Sigvaldadóttir (1992, 1998, 2002a), and Sigvaldadóttir and Mackie (1993). The identification keys presented below are based on their descriptions and the author's examination of new material. Further studies are required to clarify the taxonomy of some European *Prionospio*, especially those which are referred to names originally described from distant regions, e.g., *P. dubia* from South Africa, *P. ehlersi* from Morocco, and *P. multibranchiata* from British Columbia, Canada.

Prionospio cirrifera has been reported from all over the world after its original description from the Kara Sea by Wirén (1883). The taxonomy of Arctic and boreal *Prionospio* with several pairs of smooth apinnate branchiae from chaetiger 2, and sabre chaetae in neuropodia from chaetiger 10 was discussed by Mackie (1984), Maciolek (1985), and Sigvaldadóttir (2002a), but uncertainties remain. Northern European *Prionospio* with these characteristics may comprise two similar species and are, therefore, referred to as *P. cirrifera* complex.

The creation of identification keys to *Prionospio* involves a common problem of choice of major characters to distinguish the species. The shape and arrangement of branchiae were traditionally used in "academic" studies, searching for principal differences between species and reflection of phylogenetic relationships between them. In practice, however, these features are useless when branchiae are lost during sampling and following treatment of specimens. To satisfy both the "academic" and "practical" interests, two key formats are given below.

Key to *Prionospio* from the continental shelf of northern Europe (with shape and arrangement of branchiae as major diagnostic characters)

1 Branchiae all apinnate **2**

– Branchiae apinnate and pinnate **3**

2(1) Branchiae 4 to 7 pairs. Sabre chaetae in neuropodia from chaetiger 10. Hooks in neuropodia from chaetigers 10-17, in notopodia from chaetigers 18-48. Lateral interneuropodial pouches present from chaetigers 3-10 to chaetigers 9-28 or absent. Neuropodial postchaetal lamellae of chaetiger 2 ventrally pointed and elongated .... ***P. cirrifera* complex**

– Branchiae 6 to 13 pairs. Sabre chaetae in neuropodia from chaetigers 12-17. Hooks in neuropodia from chaetigers 13-21, in notopodia from chaetigers 20-52. Lateral interneuropodial pouches absent. Neuropodial postchaetal lamellae of chaetiger 2 ventrally rounded ..... ***P.* cf. *multibranchiata***

3(1) Branchiae on chaetigers 2 and 5 pinnate, on chaetigers 3 and 4 apinnate **4**

– Pinnate/apinnate branchiae in another combination **6**

4(3) Sabre chaetae in neuropodia from chaetigers 11-22. Eyes absent. Dorsal crests absent. Branchiae on chaetiger 2 two to three times length of other pairs. Neuropodial postchaetal lamellae of chaetiger 2 ventrally rounded, not elongated. Caruncle to end of chaetiger 1. Hooks in neuropodia from chaetigers 13-22, in notopodia from chaetigers 25-70 .... ***P.* cf. *dubia***

– Sabre chaetae in neuropodia from chaetiger 10. Eyes present. Dorsal crest(s) present on some postbranchiate chaetigers. Branchiae on chaetigers 2 and 5 of similar size. Neuropodial postchaetal lamellae of chaetiger 2 ventrally elongated and pointed **5**

5(4) Median eyes very large. Caruncle to end of chaetiger 1. Pinnate branchiae at least twice length of apinnate pairs. High dorsal crest present on chaetiger 7 only. "Pockets" between notopodia on anterior chaetigers absent. Hooks in neuropodia from chaetigers 10-14, in notopodia from chaetigers 18-45 .... ***P. fallax***

– Median eyes small, similar in size to lateral eyes. Caruncle to end of chaetiger 2. Pinnate branchiae 1.5-2.5 times length of apinnate pairs. Low dorsal crests from chaetiger 6 to chaetigers

16-18; crests initially conspicuous, slightly higher on chaetiger 7, gradually decreasing thereafter. Rear of each notopodium from chaetiger 4 to chaetigers 9-13 basally linked to face of following notopodial lamella by thin membranous fold, forming apparent series of small, ventrally open, "pockets". Hooks in neuropodia from chaetigers 15-17, in notopodia from chaetigers 43-58 .... ***P. steenstrupi***

6(3) Three pairs of pinnate branchiae on chaetigers 2, 3 and 5 .... ***P. plumosa***

– One pair of pinnate branchiae **7**

7(6) Branchiae with digitiform pinnules on chaetiger 2; shorter apinnate branchiae on chaetigers 3-5. Lateral interneuropodial pouches from chaetigers 2-4 to mid body. Low dorsal crests on several chaetigers from chaetiger 7. Sabre chaetae in neuropodia from chaetigers 17-19. Hooks multidentate, in neuropodia from chaetigers 18-22, in notopodia from chaetigers 37-40 .... ***P. ehlersi***

– Branchiae with plate-like pinnules on chaetiger 5; shorter apinnate branchiae on chaetigers 2-4. Lateral interneuropodial pouches absent. Prominent dorsal crest on chaetiger 7 only. Sabre chaetae in neuropodia from chaetiger 11. Hooks bidentate, in neuropodia from chaetigers 14-21, in notopodia from chaetigers 22-40 .... ***P. caspersi***

Key to *Prionospio* from the continental shelf of northern Europe (with shape and arrangement of dorsal crests and sabre chaetae as major diagnostic characters)

1 Dorsal crest present on chaetiger 7 .... **2**

– Dorsal crest absent on chaetiger 7 .... **6**

2(1) High dorsal crest present on chaetiger 7 only. Median eyes large or small. Caruncle to end of chaetiger 1 .... **3**

– Low to moderate dorsal crests present on chaetiger 7 and several successive chaetigers. Median eyes small. Caruncle to end of chaetiger 1 or chaetiger 2 .... **5**

3(2) Median eyes very large. Pinnate branchiae on chaetigers 2 and 5; apinnate branchiae on chaetigers 3 and 4 shorter, robust, flattened. Sabre chaetae in neuropodia from chaetiger 10. Hooks in neuropodia from chaetigers 10-14, in notopodia from chaetigers 18-45 ....
....
P. fallax

– Median eyes small. Pinnate and apinnate branchiae on chaetigers 2-5 otherwise **4**

4(3) Sabre chaetae in neuropodia from chaetiger 10. Branchiae with digitiform pinnules on chaetigers 2, 3 and 5; apinnate branchiae on chaetiger 4 shortest. Hooks multidentate, in neuropodia from chaetigers 10-12, in notopodia from chaetigers 30-44 .... ***P. plumosa***

– Sabre chaetae in neuropodia from chaetiger 11. Branchiae with plate-like pinnules on chaetiger 5; shorter apinnate branchiae on chaetigers 2-4. Hooks bidentate, in neuropodia from chaetigers 14-21, in notopodia from chaetigers 22-40 .... ***P. caspersi***

5(2) Sabre chaetae in neuropodia from chaetiger 10. Caruncle to end of chaetiger 2. Rear of each notopodium from chaetiger 4 to chaetigers 9-13 basally linked to face of following notopodial lamella by thin membranous fold, forming apparent series of small, ventrally open, "pockets". Lateral interneuropodial pouches absent. Pinnate branchiae on chaetigers 2 and 5; apinnate branchiae on chaetigers 3 and 4 shorter, robust, flattened. Hooks in neuropodia from chaetigers 15-17, in notopodia from chaetigers 43-58 .... ***P. steenstrupi***

– Sabre chaetae in neuropodia from chaetigers 17-20. Caruncle to end of chaetiger 1. . Notopodial pockets absent. Lateral interneuropodial pouches from chaetigers 2-4 to midbody. Pinnate branchiae on chaetiger 2; shorter apinnate branchiae on chaetigers 3-5. Hooks in neuropodia from chaetigers 18-22, in notopodia from chaetigers 37-40 .... ***P. ehlersi***

6(1) Eyes absent. Pinnate branchiae on chaetigers 2 and 5; apinnate branchiae on chaetigers 3 and 4 shorter, robust, flattened. Capillary chaetae of chaetiger 2 longer than on other anterior chaetigers. Sabre chaetae in neuropodia from chaetigers 11-22. Neuropodial postchaetal lamellae of chaetiger 2 ventrally rounded, not elongated. Caruncle to end of chaetiger 1. Hooks in neuropodia from chaetigers 13-22, in notopodia from chaetigers 25-70 .... **P. cf. *dubia***

– Two or more pairs of eyespots present; median eyes small to large (multiple eyespots). Branchiae all apinnate. Capillary chaetae of chaetiger 2 same length as on other anterior chaetigers **7**

7(6) Sabre chaetae in neuropodia from chaetiger 10. Hooks in neuropodia from chaetigers 10-17, in notopodia from chaetigers 18-48. Branchiae 4 to 7 pairs. Caruncle to end of chaetiger 2. Lateral interneuropodial pouches absent or present from chaetigers 3-10 to chaetigers 9-28. Neuropodial postchaetal lamellae of chaetiger 2 ventrally pointed and elongated ***P. cirrifera*** **complex**

– Sabre chaetae in neuropodia from chaetigers 12-17. Hooks in neuropodia from chaetigers 13-21, in notopodia from chaetigers 20-52. Branchiae 6 to 13 pairs. Caruncle to middle of chaetiger 2. Lateral interneuropodial pouches absent. Neuropodial postchaetal lamellae of chaetiger 2 ventrally rounded .... **P. cf. *multibranchiata***

23. *Prionospio caspersi* Laubier, 1962: 135-148, figs 1-3. Venice, Mediterranean, Italy. Britayev *et al.* 1991: 5-8, fig 1. Rare, offshore.
24. *Prionospio cirrifera* complex Wirén, 1883: 409-410. Kara Sea. Mackie 1984: 36-40, figs 1, 2, table 1. Sigvaldadóttir 2002a: 211-213. Common, subtidal mud; ubiquitous.
25. *Prionospio* cf. *dubia* Day, 1961: 489–490, fig. 3j–n, as *Prionospio malmgreni* var. *dubia*. Off Western Cape, South Africa. Wilson 1990: 249–250, figs 9–15. Sigvaldadóttir & Mackie 1993: 211–215, figs 6–8, tables 1 & 2. Moderately common, subtidal mud, mainly offshore.
26. *Prionospio ehlersi* Fauvel, 1928a: 10-11, fig. 1. Morocco, off Atlantic coast. Maciolek 1985: 345-347, fig. 7. Rare, offshore.
27. *Prionospio fallax* Söderström, 1920: 235–237, figs 135, 144 & 145. Islandsberg, Gullmaren, Sweden. Common, subtidal mud; ubiquitous.

28. *Prionospio* cf. *multibranchiata* E. Berkeley, 1927: 414, pl. 1, fig. 1. Station Flat, Nanaimo, Vancouver Island, British Columbia, Canada. Mackie 1984: 40-42, fig. 3. Maciolek 1985 (*Part.*): 365-367, fig. 15. Moderately common, subtidal mud; ubiquitous.
29. *Prionospio plumosa* M. Sars, 1872: 410; 1873: 63-68, pl. XVII, figs 13-29, as *Prionospio plumosus*. Christianiafjord, Norway. Rare, offshore.
30. *Prionospio steenstrupi* Malmgren, 1867: 201–202, pl. 10, fig. 55. Skagafjördur, Hofsós, Iceland. Sigvaldadóttir & Mackie 1993: 204–207, figs 1, 2, 5, tables 1, 2. Sikorski 2001: 308-309, textfigs 1-10. Sigvaldadóttir 2002a: 213-214. Rare, offshore.

Pygospio Claparède, 1863

Pygospio Claparède, 1863: 37. Fauvel 1927: 45. Uschakov 1955: 268. Foster 1971a: 28-29. Fauchald 1977b: 25. Blake 1996a: 164. Hartmann-Schröder 1996: 330.

Type species. *Pygospio elegans* Claparède, 1863. By monotypy.

Synopsis.

Remarks. *Pygospio* Claparède, 1863 currently comprises two described species and two species awaiting description and clarification (Radashevsky *et al.* 2016a). Adults have branchiae on middle chaetigers, only capillary chaetae in notopodia, bidentate hooded hooks in neuropodia, and pygidium with four conical cirri.

Pygospio elegans Claparède, 1863 is the only *Pygospio* species reported from northern Europe. Adults are unique among spionids in having spoon-like hooded hooks in anterior neuropodia.

31. *Pygospio elegans* Claparède, 1863: 37–38, pl. XIV, figs 27–31. Saint Vaast la Hougue, Normandy, northern France. Common, intertidal and shallow inshore, mud, sand and mixed substrata, particularly where reduced salinity; ubiquitous.

Scolelepis Blainville, 1828

Scolelepis Blainville, 1828: 492. Pettibone 1963: 92. Foster 1971a: 58-59. Blake & Kudenov 1978: 175. Light 1978: 98-99. Maciolek 1987: 17. Sikorski & Pavlova 2015: 10-11.

Aonis sensu Audouin & Milne Edwards, 1833. *Fide* Malmgren 1867a: 198; 1867b: 89. Not Savigny 1822.

Nerine Johnston, 1838: 68-70. Type species *Nerine coniocephala* Johnston, 1838. By Quatrefages 1843: 9. *Fide* Pettibone 1963: 91.

Pseudomalacoceros Czerniavsky, 1881: 361. Type species *Malacoceros longirostris* Quatrefages, 1843 (=*Lumbricus squamatus* Müller, 1806). By monotypy. *Fide* Pettibone 1963: 91.

Nerinides Mesnil, 1896: 119, 152. Type species *Nerine longirostris sensu* Saint-Joseph, 1894 (=*Lumbricus squamatus* Müller, 1806; not *Malacoceros longirostris* Quatrefages, 1843). By Mesnil 1896: 152.

Asetocalamyzas Tzetlin, 1985: 296. Type species *Asetocalamyzas laonicola* Tzetlin, 1985. By monotypy. *Fide* Vortsepneva *et al.* 2008: 414.

Parascolelepis Maciolek, 1987: 33. Type species *Nerinides tridentata* Southern, 1914. By Maciolek 1987: 33.

Type species. *Lumbricus squamatus* Müller, 1806. By monotypy.

Synopsis. Adults with elongated, conical, usually pointed, rarely rounded or trilobed snout. Occipital antenna present or absent. Two pairs of small red eyes usually arranged in a transverse line. Nuchal organs short, U-shaped. Palps with basal sheath which upper edge smooth or decorated with short papillae. Branchiae from chaetiger 2 through most of body, basally or entirely fused to notopodial postchaetal lamellae; branchial blood vessels not interconnected by capillaries. Lateral pouches and dorsal crests absent. Notopodia with only capillaries or with hooks in addition to capillaries; notopodial postchaetal lamellae entire throughout or bilobed in posterior segments. Neuropodia with capillaries and hooks; sabre chaetae absent; neuropodial postchaetal lamellae entire throughout or bilobed in posterior segments. Hooks unidentate to multidentate, with only outer hood; shaft slightly curved or bent in upper part. Pygidium oval disc or cushion, entire or divided in two or more lobes. Digestive tract without gizzard-like structure. Main dorsal blood vessel without heart body. Nephridia serving both excretory and gamete-releasing functions. Gonochorists, usually broadcast spawners; rarely, males forming spermatophores; rarely, sexual dimorphism (*S. vasaha* Eibye-Jacobsen & Soares, 2000) and dwarf males (*S. laonicola*). Oocytes with thick honeycombed envelope ornamented with one circle of vesicles. Spermatozoa usually short-headed, rarely with needle-like acrosome and elongated nucleus. Larval development usually holopelagic and planktotrophic, rarely mixed, partly in gelatinous cocoons and then planktotrophic. Larvae with mid-ventral pointed appendage formed by lateral peristomial lips elongated and fused anteriorly, internally supported by conspicuous fibres.

Remarks. *Scolelepis* Blainville, 1828 is one of the largest and most problematic genera within the Spionidae; its diagnosis has suffered from different interpretations (see reviews by de Saint-Joseph 1894: 66-67; Mesnil 1896: 170-171; Söderström 1920: 215; Pettibone 1963: 98; Maciolek 1987: 16). The genus currently comprises about 90 species occurring all over the world, mainly in the intertidal and in shallow coastal waters. The adults of *Scolelepis* usually have an elongated and pointed snout which has traditionally been referred to as a pointed prostomium and considered to be one of the diagnostic characters of the genus. The larvae are unique among polychaetes in having the prostomium drawn out into a conical tip, anteriorly tapered, rounded or truncate, and antero-ventrally concave; the prostomium partly encloses a longer mid-ventral pointed appendage formed by lateral peristomial lips that are elongated and fused anteriorly and internally supported by conspicuous fibres (Hannerz 1956). During settlement and metamorphosis, the larval peristomial appendage elongates anteriorly and extends far beyond the prostomium, forming the tapered adult snout. Basally, the peristomial appendage becomes greatly swollen and fused with the (also enlarged) antero-lateral parts of the prostomium. The two structures remain separate dorsally in early juveniles, but become completely fused in adults, concealing their true origin (Radashevsky unpublished). In a very few species, the larval peristomial appendages do not elongate and, together with the prostomium, form short, conical, anteriorly rounded or trilobed snouts (e.g., *S. cantabra*, *S. foliosa*).

The taxonomic history of the *Scolelepis* is confusing and begins with Savigny (1822), who established a new genus, *Aonis*, for *Nereis caeca* Fabricius, 1780, and Johnston (1838), who established a new genus *Nerine*. Blainville (1825: 451, 1828: 492) recognized *Aonis* Savigny, 1822 and also established a new genus *Scolelepis* Blainville, 1828 for an unusual *Lumbricus squamatus* Müller, 1806 (originally described without palps and with dorsal and ventral sides misinterpreted; the pointed head was noted as a characteristic feature). Audouin & Milne Edwards (1829: 17, 1833, 1834: 261-264) misinterpreted the diagnosis of *Aonis* Savigny, 1822 and emended it to fit the newly described (without palps and with pointed head as characteristic features) species *Aonis foliosa* Audouin & Milne Edwards, 1829. For a time after their description, the name *Aonis* was used *sensu* either Savigny (1822) or Audouin & Milne Edwards (1829).

Johnston (1838) established the genus *Nerine* to encompass *Spio vulgaris* Johnston, 1827 and *Nerine coniocephala* Johnston, 1838 (a replacement name for *Spio viridis* Johnston, 1828). As the diagnostic characters of the new genus, Johnston (1838: 68) noted a pair of palps, branchiae distributed throughout body, biramous parapodia and a stellate pygidium. By combining two spionids of different morphology within one genus: *Nerine vulgaris* with a horned prostomium and *Nerine coniocephala* with a conical snout, and not designating either as the type species, Johnston (1838) created confusion in the taxonomy of these spionids.

Quatrefages (1843: 9) proposed *N. coniocephala* to be the type (and only) species of *Nerine* Johnston, 1838. He also described two new annelids: *girardi*, with fronto-lateral horns on the prostomium similar to *N. vulgaris*, and *longirostris*, with an elongated, pointed snout similar to *N. coniocephala*. To encompass *Spio vulgaris* Johnston, 1827 and the two new species from Brittany, Quatrefages (1843) established a new genus, *Malacoceros* Quatrefages, 1843. Thus, Quatrefages (1843) resolved the confusion created by Johnston (1838) with his chimerical *Nerine* but created another chimera, *Malacoceros* combining spionids of different morphology: *M. vulgaris* and *M. girardi* with horned prostomia, and *Malacoceros longirostris* with a pointed snout, and not designating any of them as the type species.

Grube (1850: 301) placed *Nereis caeca* Fabricius, 1780 within the genus *Nephtys* Cuvier, 1817 (fam. Nephtyidae Grube, 1850). He did not recognize the genera *Scolelepis* Blainville, 1828 (probably because of poor original description) or *Malacoceros* Quatrefages, 1843 (probably overlooking Quatrefages' 1843 paper) but recognized the genera *Aonis* (Savigny, 1822) *sensu* Audouin & Milne Edwards, 1829 and *Nerine* Johnston, 1838. Within *Nerine*, Grube

(1850: 314) placed two species with horned prostomia: *N. vulgaris* (Johnston, 1827) and *N. laevicornis* (Rathke, 1837, as *Spio laevicornis*), and one species with a pointed snout: *N. coniocephala* Johnston, 1838. Grube (1850: 317, 1851: 69) also commented that *Aonis* appeared very similar to *Lumbricus squamatus* Müller.

Claparède (1864: 505) established the genus *Aonides* Claparède, 1864 and noticed that it was similar to *Aonis* Savigny but differed from the latter "par l'absence du tentacule céphalique impair et subulé, et par la condensation des branchies sur les segments de la partie antrieure du corps".

Johnston (1865) did not mention Quatrefages' (1843) paper and continued to treat *Nerine* as comprising two species: *N. vulgaris* and *N. coniocephala*. Johnston (1865: 201) noted that *N. coniocephala* might be identical with either *Lumbricus cirratulus* Delle Chiaje, 1822, *Nerine foliosa* Sars, 1851, or *Nereis foliata* (= *Aonie foliacée* Audouin & Milne Edwards, 1829).

Malmgren (1867a: 198; 1867b: 89) considered *Aonis sensu* Audouin & Milne Edwards, 1829 as a synonym of *Nerine* Johnston, 1828. He proposed *Nerine foliosa* Sars, 1851 to be the type species of *Nerine* Johnston, 1838 and suggested that *Aonis foliosa* Audouin & Milne Edwards, 1829 and *Nerine coniocephala* Johnston, 1838 might be synonyms of *N. foliosa* Sars, 1851. Malmgren (1867a: 199) was the first to re-establish *Scolelepis* of Blainville (1828), but misspelled it as *Scolecolepis* and used it in a different sense from Blainville (1828). Malmgren (1867a: 199) proposed *Spio vulgaris* Johnston, 1827 to be the type species of *Scolelepis* Blainville, 1828, placed *Malacoceros girardi* Quatrefages, 1843 as a synonym of *Scolelepis vulgaris* (Johnston, 1827), and suggested that *Colobranchus tetracerus* Schmarda, 1861 might also be a synonym of this species. In addition, Malmgren (1867) placed two species described by Sars (1851, 1862) within *Scolelepis*: *Nerine cirrata* M. Sars, 1851 (currently recognized as *Laonice cirrata*) and *Nerine oxycephala* Sars, 1862 (currently recognized as *Aonides oxycehala*).

De Saint-Joseph (1894: 66) considered *Aonis sensu* Audouin & Milne Edwards, 1829 and *Malacoceros* Quatrefages, 1843 as synonyms of *Nerine* Johnston, 1828 and, following Malmgren (1867a), referred *Nerine oxycephala* Sars, 1862 to *Scolelepis* Blainville, 1828. De Saint-Joseph (1894: 67) noted that "les trois genres *Spio*, *Nerine* et *Scolelepis* sont si imparfaitement délimités et définis qu'ils ne peuvent être que provisoires".

Mesnil (1896: 112-122) introduced a series of new taxonomic characters, consistently applied them for the generic breakdown of Spionidae and, for the first time, suggested relationships between spionid genera. He did not recognize *Malacoceros* Quatrefages, 1843 and divided all spionids into two groups, one without fronto-lateral horns on the prostomium, and another with horns (Mesnil 1896: 117). Within each group, Mesnil (1896: 117) distinguished subgroups according to the first chaetiger with branchiae, either chaetigers 1, 2 or after chaetiger 2, and the modification of chaetiger 5. Mesnil (1896: 119) referred *Nerine* Johnston, 1828 to the former group and defined it as having a rounded to pointed prostomium, branchiae from chaetiger 2 to the end of the body, notopodial postchaetal lamellae fused to branchiae, at least on anterior segments, neuropodial lamellae incised after chaetigers 30-40, hooded hooks in noto- and neuropodia, and a sucker-shaped "ventouse" pygidium. Mesnil (1896: 120) referred

Scolelepis Blainville, 1828 to the group with fronto-lateral horns on the prostomium and defined it as having branchiae from chaetiger 1 to almost the end of the body, hooded hooks only in the neuropodia, and the pygidium with cirri. He also established a new genus *Nerinides* Mesnil, 1896 to encompass the worms described by Saint-Joseph (1894: 74) under the name *Nerine longirostris* (Quatrefages, 1843). Mesnil (1896: 152) noted that *Nerinides* is similar to *Scolelepis* in having a "ventouse" pygidium, notopodial lamellae entirely fused to the branchiae, and an absence of branchiae on the first chaetiger, but differs in the absence of hooded hooks in the notopodia and having neuropodial postchaetal lamellae entire throughout the body instead of bilobed lamellae in posterior segments. Mesnil (1896: 152) also suggested that *Nerinides* is intermediate between *Spio* and *Nerine*.

Mesnil's (1896) generic diagnoses were followed by the majority of subsequent authors, including McIntosh (1915), Rioja (1918, 1931), Fauvel (1927), Hannerz (1956) and Hartman (1959), until Pettibone (1963) revised branchiate spionids with pointed heads and those with distinct fronto-lateral horns on the prostomia. Pettibone (1963) redefined *Scolelepis* Blainville, 1828 as having a pointed snout and branchiae arranged from chaetiger 2 to near the end of the body, with *Lumbricus squamatus* Müller, 1806 as the type species. Following Quatrefages (1843), she considered *N. coniocephala* Johnston, 1838 as the type species of *Nerine*, and placed *Nerine* Johnston, 1838 as a junior synonym of *Scolelepis* Blainville, 1828. Pettibone (1963) resurrected *Malacoceros* Quatrefages, 1843 as a valid genus, defined it as having a prostomium with distinct fronto-lateral horns, and designated *Spio vulgaris* Johnston, 1827 as its type species. Within the genus *Scolelepis*, she distinguished two subgenera: *S.* (*Scolelepis*), comprising 11 species in which adults had notched neuropodial lamellae in the middle and posterior segments, and *S.* (*Nerinides*), comprising seven species in which adults had entire neuropodial lamellae throughout body; *Nerine auriseta* Claparède, 1868 was considered indeterminable.

Day (1967: 482, 484) accepted Pettibone's (1963) definition of *Scolelepis* Blainville, 1828 as having a pointed snout but also followed Mesnil (1896) in recognizing *Nerinides* Mesnil, 1896 as a valid genus in which adults had pointed snouts, hooded hooks only in neuropodia, and neuropodial postchaetal lamellae entire throughout body. Hartmann-Schröder (1971) and Foster (1971) treated *Scolelepis* and *Nerinides* as two subgenera of *Scolelepis*, but Foster (1971: 62) noted that the presence of hooks in notopodia was an unstable character causing confusion in the taxonomy of these spionids. Light (1977, 1978: 98) noted that "the presence of a notch in the median and posterior neuropodia appears to be similarly highly variable between specimens from the same sample and on different sides of the same specimen, in some cases." He also treated *Scolelepis* and *Nerinides* as subgenera but noted that the distinction between them, as defined by Pettibone (1963), "is a doubtful one, but is retained until further studies are completed" (Light 1978: 98). Light (1978: 99), however, suggested that "the two subgenera can be readily distinguished by the configuration of the neuropodial hooded hooks: *Scolelepis* (sensu stricto) has hooks that are unidentate falcigers, or bi- or tridentate with short, conical, or blunt or flangelike apical teeth and bearing a short, stubby, conical main fang; those of the subgenus

Nerinides are multidentate, with sharp, naillike apical teeth and a very long, thin, tapering main fang".

Blake & Kudenov (1978: 176) considered "it to be increasingly difficult to maintain 2 subgeneric or generic categories based on such tenuous and variable characteristics" and considered "it to be the better course" to avoid subgeneric division "pending a re-evaluation of the taxonomic characteristics of *Scolelepis*." This approach was shared by Sikorski (1994b, 2001).

Maciolek (1987) reviewed spionids with pointed snouts and branchiae from chaetiger 2 at least partially fused to notopodial postchaetal lamellae. She agreed with Foster (1971), Light (1977, 1978) and Blake & Kudenov (1978) that considerable variation in the presence and degree of development of the neuropodial notch and in the presence of notopodial hooks within a single population of a species makes the subgeneric division of *Scolelepis* based on these characters ambiguous. Maciolek (1987: 16) noted that "Of the 47 species currently assigned to the genus, at least 16 have both notopodial hooks and a neuropodial lamellar notch, nine lack both features, and eight have one character without the companion trait. Fourteen species are incompletely known because only fragments are available." Maciolek (1987: 16), however, agreed with Light (1978) that "the hooks of *Scolelepis* do fall into two major groups, with the majority of species having the falcigers-like type." Maciolek (1987: 16) noticed that the worms described by Saint-Joseph (1894: 74) under the name *Nerine longirostris* (Quatrefages, 1843) and used by Mesnil (1896) to establish the genus *Nerinides* have falcigers-like hooks and, therefore, "the name *Nerinides* cannot be used to designate those species which have the sharp-fanged, multidentate hooks." Consequently, she proposed the name *Parascolelepis* Maciolek, 1987 for this new subgenus, and designated *Nerinides tridentata* Southern, 1914 as its type species.

The division of the *Scolelepis* into two subgenera, *S.* (*Scolelepis*) and *S.* (*Parascolelepis*) proposed by Maciolek (1987), was followed by some authors, including Hartmann-Schröder (1996), Hutchings *et al.* (1998), Delgado-Blas (2006), and Sikorski & Pavlova (2015), whereas Blake & Arnofsky (1999), Blake (2006) and Williams (2007) treated *Scolelepis* and *Parascolelepis* as two full genera. Of the 86 currently recognized species of *Scolelepis*, Sikorski & Pavlova (2015: Table 1) referred 74 species to *S.* (*Scolelepis*) and 12 species to *S.* (*Parascolelepis*).

The different characters used by different authors for generic breakdown of the Spionidae, and the practice of establishing new genera without designation of type species in the past have resulted in confusing placement of the same species within different generic taxa. The unstable taxonomic position of some old species, especially within such genera as *Spio*, *Scolelepis*, *Malacoceros* and *Nerine* complicates links to the old literature and often results in missing important morphological information obtained in the past.

In agreement with Blake & Kudenov's (1978) conclusion summarised above, and in the absence of an explanatory phylogenetic hypothesis for the diverse morphological characters exhibited by *Scolelepis* members, I suggest dispensing with subgenera and referring all the spionids with pointed snouts (at least at larval stage) and branchiae from chaetiger 2 at least partially fused to notopodial postchaetal lamellae to *Scolelepis sensu lato*.

The morphology and the taxonomy of the European *Scolelepis* were summarized by McIntosh (1915a,b) and then redescribed and discussed by Pettibone (1963), Maciolek (1987), Sikorski (2001), Sikorski & Pavlova (2015) and Surugiu (2016). The identification key presented below is mainly based on their descriptions. Despite these descriptions, the morphology of many European *Scolelepis* remains poorly known. Therefore, the key presented below is very provisional. The ranges of variable characters shown in the key can be useful for species distinguishing but should be taken with caution because they hardly cover real variability of the species. A revision of the European *Scolelepis* is urgently needed; such a revision, however, should be based on the detailed description of the morphology of the species, comprising different ontogenetic stages, and using a complete set of taxonomic characters. Needles to say that molecular data would be very helpful, but, unfortunately, this kind of information remains unknown for this difficult group of spionids.

Key to *Scolelepis* from the continental shelf of northern Europe

(to follow)

Spio Fabricius, 1785

Spio Fabricius, 1785: 264. Cuvier 1817a: 525. Savigny 1822: 45. Fauvel 1927: 43. Blake & Kudenov 1978: 226-227. Maciolek 1990: 1111. Blake 1996a: 157. Bick & Meißner 2011: 41. Meißner *et al.* 2011: 6-7.

Type species. *Nereis filicornis* O.F. Müller, 1776. By Söderström 1920: 245.

Synopsis.

Remarks. *Spio* Fabricius, 1785 is one of the largest and most problematic groups of spionid polychaetes currently comprising about 35 species.

Pigmentation could be a good character but color pigment, distinct and species specific in life, especially on palps, often becomes invisible after fixation (white, yellow or other colorful pigment), and palps are usually missing in specimens in sample.

Arrangement and dentition of hooks could be another set of important characters, but such kind of information is often lacking. Quite common for *Spio*, same as for many other spionids, that hooks develop first in larvae from a species-specific chaetiger but then are lost from anterior neuropodia in one or more chaetigers which number is also oduced less and less species-specific. Larvae or recently settled juveniles have been investigated in a very few species and arrangement of hooks is usually described from bid individuals. Dentition of hooks may also be confusing. It seems that in some species, tridentate hooks first develop in larvae in neuropodia but adults produce bidentate hooks. Whether switch from tridentate to bidentate hooks occurs gradually, with superior tooth in hooks becoming produced less developed, or drastically, when distinctly bidentate hooks replace tridentate hooks, remains uncertain.

Morphology and taxonomy of some European *Spio* was described and discussed by Bick *et al.* (2010), Meißner and Bick (2011). The identification key presented below is mainly based on their descriptions.

Key to *Spio* from the continental shelf of northern Europe

(to follow)

Spiophanes Grube, 1860

Spiophanes Grube, 1860: 88. Pettibone 1962: 77. Foster 1971: 40. Blake & Kudenov 1978: 224. Imajima 1991b: 115. Maciolek 2000: 539-540. Meißner & Hutchings 2003: 118-120. Meißner 2005: 6. Meißner & Blank 2009: 6-7.

Type species. *Spiophanes kroyeri* Grube, 1860. By monotypy.

Synopsis.

Remarks. *Spiophanes* Grube, 1860 is one of the largest groups of spionid polychaetes currently comprising about 31 species. The adult morphology of many species was redescribed and the taxonomy clarified by Meißner & Hutchings (2003), Meißner (2005), Meißner & Blank (2009) and Meißner *et al.* (2012), but uncertainties still remain. In northern European waters, two species of *Spiophanes* have been reported frequently: *S. bombyx* (Claparède, 1870), originally described from the Gulf of Naples, Italy, and *S. kroyeri* Grube, 1860 originally described from the Greenland Sea. *Spiophanes urceolata* Imajima, 1991, originally described from Japan and reported from Europe by Hartmann-Schröder (1996) and Sikorski (2001), was placed by Meißner & Hutchings (2003) into synonymy with *S. wigleyi* Pettibone, 1962. Analysis of two gene fragments by Meißner & Blank (2009: fig. 10) suggested the presence of two species within the samples from the North Sea identified as *S. kroyeri*, but the authors did not comment on this.

The main taxonomic characters to identify adult *Spiophanes* include the shape of the prostomium, nuchal organs, glandular organs and fiber spreaders, dentition and arrangement of hooks and sabre chaetae, and the presence of lateral interneuropodial pouches. These characters are briefly discussed below.

Fronto-lateral horns on prostomium. Various spionids have processes (referred to as appendages, extensions, projections and horns) on the antero-lateral parts of prostomium. The degree of the development of the processes varies a great deal and the terminology used to describe them is often confusing. Adults of many *Spiophanes* species have an inverted bell-shaped prostomium, with the anterior part expanded laterally. In some species, *e.g.*, *S. kroyeri* Grube, 1860 and *S. japonicum* Imajima, 1991, the anterior extensions are well developed and are often referred to as short antero-lateral projections or horns, and the whole prostomium is referred to as T-shaped. It may be difficult to separate antero-lateral horns from a bell- or T-shaped prostomium. The decisive information can be obtained from the observations on transformation of the prostomium in ontogenesis. For example, young pelagic larvae of *S. bombyx* have rounded prostomium (Hannerz 1956: fig. 9B); the horns appear in larva before settlement and metamorphosis as distinct appendages arising from the antero-lateral sides of the prostomium (Hannerz 1956: fig. 9A). In *S. kroyeri*, paired processes develop as expansions of the whole fronto-lateral sides of the prostomium (Hannerz 1956: fig. 11). Unfortunately, the ontogenetic transformations are described only for a very few *Spiophanes* species.

The length/width ratio of the antero-lateral processes can be used as a criterion to separate a bell-shaped prostomium from a prostomium with horns: ≤ 1:1 for the antero-lateral projections of the bell-shaped prostomium, > 1:1 < 2:1 for a prostomium with short antero-lateral horns, and ≥ 2 for a prostomium with long antero-lateral horns. This criterion should however be used with caution because of possible changes in ratio during ontogenesis and changes due to fixation. Adults of *S. bombyx* have antero-lateral horns more than twice as long as wide.

Nuchal organs. Various kinds of entire and metameric nuchal organs have been distinguished in adult spionids (Jelsing 2003; Radashevsky 2012), and three kinds of organs were described in adult *Spiophanes*: 1) entire straight longitudinal ciliary bands, as in *S. kroyeri*, 2) entire U-shaped ciliary bands, as in *S. wigleyi* Pettibone, 1962, and 3) metameric ciliary bands, as in *S. bombyx*. As conservative morphological structures, the nuchal organs can mark monophyletic clades within the Spionidae and *Spiophanes*, but this has never been tested in a corresponding phylogenetic analysis. It may be difficult to recognize the type of organ under a light microscope, especially on poorly fixed specimens, but observations of live individuals and various kinds of staining and scanning electron microscopy are usually revealing (*e.g.*, Meißner & Hutchings 2003: fig. 2A, C). Adults of *S. bombyx* have metameric nuchal organs, comprising the first pair of oblique metamers extending from the posterior part of prostomium to the middle (to nototroch) of chaetiger 3, and a series of short metamers on successive chaetigers, each extending over the posterior half of a chaetiger (Jelsing 2003: fig. 2E, F).

Glandular organs and fiber spreaders. Large paired glandular organs in the base of neuropodia from chaetiger 5 to chaetigers 13-14 were first described by Claparède (1870) in *S. bombyx* and represent one of the apomorphies shared by all *Spiophanes* members. The complex composition and histology of the organs were described by Söderström (1920) who referred to them as "Drüsensackes" (glandular sacs) and "Drüsenorgane" (glandular organs). The posterior walls of the openings of glandular organs are ornamented with epithelial grooves and ridges running from the inner proximal base to the outer distal part of the wall and are used to guide out long fiber-like chaetae that originate in the wall of the glandular organ. In *S. kroyeri* examined by Söderström (1920), each glandular organ of chaetigers 5–7 opened to the exterior via a semicircular slit, which posterior wall appeared as a club-shaped structure. Söderström (1920) called the long fiber-like chaetae "Drüsenborsten" (glandular chaetae) due to their association with glands and the club-shaped posterior walls of the openings "Drüsenborstenspreiter" (chaetal spreaders). He suggested that these structures were used to spread the secretion of the glandular organs over the tube wall, while the glandular chaetae were used to evenly distribute this secretion and, thus, the glandular organs were involved in tube construction. The anatomy and ultrastructure of the glands were described in detail by Meißner *et al.* (2012), who confirmed the crucial role of the glands in tube construction.

Meißner & Hutchings (2003) described five different types of opening for gandular organs within *Spiophanes* and suggested their use as a diagnostic character. They did not define the character explicitly, however, and introduced it as "the appearance of gland openings exhibiting a chaetal spreader" (Meißner & Hutchings 2003: 117). Meißner (2005) and Meißner & Blank (2009) used the term "chaetal spreader" as a synonym for the openings ("openings = chaetal spreader"). Radashevsky (2012) noticed the ambiguities in the definitions of the types of spreaders provided by Meißner & Hutchings (2003) and proposed alternative typology for the openings. Herein, I suggest use of the term "spreader" as originally applied by Söderström (1920), in reference to the posterior wall of the opening of a glandular organ, but not to the opening itself. Furthermore, I suggest use of the term "fiber spreader" instead of "chaetal spreader" to avoid confusion with chaetae associated with parapodia, even though the gland-associated fibers are produced in the same way and have the same ultrastructure and composition as chaetae (Meißner *et al.* 2012; Guggolz *et al.* 2015). Meißner *et al.* (2012) noted an overall similarity in the histological architecture and ultrastructure of the large anterior and small posterior glandular organs, and described gland-associated fibers and cuticular ridges on the posterior walls of the openings in both kinds of organs. For some reason, however, they repeatedly stated that the spreaders were absent in small posterior glandular organs (from chaetiger 9) which opened to the exterior via vertical slits. I consider the posterior walls of the slit-like openings of the posterior organs to be fiber spreaders. They fulfill the same function as spreaders in the anterior organs and differ only in shape, being flat or concaved instead of convex, club-shaped, *etc.*

Meißner & Blank (2009) noted that, in *S. bombyx*, the openings of the glandular organs on chaetigers 5, 7 and 8 were usually undulate, "0+1 type", according to their typology (the numbers refer to the lobes arising from the anterior and posterior margins of the opening slits). In specimens of *S. bombyx* from northern Europe, I observed individual variation in the shape of the openings and fiber spreaders on chaetigers 5, 7 and 8. The openings were semicircular to semioval or gradually transformed from Type 3 on chaetiger 5 to Type 4 on chaetiger 8, according to the typology of Radashevsky (2012). The fiber spreaders, respectively, appeared as one lobe with a rounded to straight frontal edge on chaetiger 5. They had a variously developed middle depression on the frontal edge and appeared as two rounded lobes on chaetiger 8.

Hooks. The hooks are similar in different *Spiophanes* species and have a unique outline; thus fragments of worms can be identified to generic level according to hook morphology. The short upper part of the hook shaft, protruding from the body, is thinner than the long lower part, embedded into the body wall, so the lower manubrium can be distinguished. Three main hook characters of taxonomic value are: the arrangement (first appearance of hooks in neuropodia, i.e., the first chaetiger where they replace two vertical rows of capillaries present in preceding chaetigers), dentition, and the presence of a hood.

The first appearance of hooks in the neuropodia is usually known for adult individuals and reported as starting from chaetigers 14-16. In late larvae and early juveniles, however, hooks appear from more anterior chaetigers (e.g., chaetiger 11 in *S. bombyx*, as reported by Mesnil

1896; Hannerz 1956; Cazaux 1970; Blake 2006). It may be a common pattern of hook "ontogenetic behavior" when juvenile hooks are replaced by capillaries in anterior chaetigers and the start of hooks shifts posteriorly with age, as also occurs in many other spionids, e.g., *Aonides*, *Dispio*, *Laonice*, *Prionospio*, *etc*. *Spiophanes* differ, however, in that the anterior hooks are lost quickly in early juveniles, in a very few chaetigers, and then retain their anterior position; in other spionids, hooks fall out throughout life and their anterior starting point is age (size)-dependent. Unfortunately, studies on the larval development of *Spiophanes* are very few and data about the arrangement of hooks in ontogenesis are rare.

The dentition of hooks in *Spiophanes* is also problematic. Earlier studies with light microscopy reported bi- or tridentate hooks (*e.g.*, Mesnil 1896; McIntosh 1915; Pettibone 1962), while SEM examinations found hooks to be basically quadridentate, with the main fang surmounted by a single median upper tooth and a pair of smaller superior teeth, with additional small superior teeth sometimes also present (Meißner 2005). Unfortunately, SEM studies are rare and usually limited to certain neuropodia; thus, the exact dentition and its variability in many *Spiophanes* remains uncertain. In *S. bombyx*, the number of small superior teeth was shown to vary from three to four even in a series of hooks in one neuropodium (Meißner & Blank 2009: fig. 4B).

The hood in the subdistal part of hooks (Radashevsky 2012: fig. 7B) is an important diagnostic character. It is easily observed under a light microscope and, when present, appears the same in different species. This is the only kind of hood in the hooks of *Spiophanes*. It is often referred to as a reduced hood implying its evolutionary reduction. Similar hoods are also present in hooks of many *Prionospio* species, which differ from *Spiophanes*, however, in having an additional external hood covering the whole distal end of the hook. Whether the subdistal hoods in these taxa are homologous, and whether the small hood in *Spiophanes* resulted from an evolutionary reduction of large external hood, remains unknown. In the absence of a phylogenetic hypothesis explaining this character, I suggest that we call it a subterminal hood, to refer to its position, rather than to an unknown evolutionary event.

Sabre chaetae. In juveniles and adults of *Spiophanes*, the inferior capillary chaetae arranged in the anterior neuropodia are completely replaced by sabre chaetae from a species-specific chaetiger. In adults of *S. kroyeri* and some other species, the sabre chaetae are large in chaetiger 4 and then gradually diminish in size to chaetiger 15 (the first hook-bearing chaetiger); in chaetiger 15, they are large again and then gradually diminish again on successive chaetigers. In some species, however, the sabre chaetae are not easy to distinguish from the thickened inferior capillaries in preceding chaetigers. The arrangement of sabre chaetae is not always correlated with that of hooks. Meißner & Blank (2009) noted that in *S. bombyx*, hooks started from chaetigers 14-15 and sabre chaetae were present only in hook-bearing chaetigers. The earlier start of hooks in juveniles of this species, from chaetiger 11, was reported by Mesnil (1896) and other authors (see above) but the exact arrangement of sabre chaetae in juveniles remains unknown. In northern European specimens of *S. bombyx* examined in the present study (specimens more than 0.3 mm wide on chaetiger 4), sabre chaetae appeared invariably from chaetiger 15.

Lateral pouches. Thin membranes joining adjacent neuropodia are characteristically present in adults of some species of different genera of Spionidae. The pouches have been assumed to be linked to reproduction and are, therefore, often called genital pouches. This assumption has not been confirmed; although spawning of eggs into the pouches has been reported for some spionids, brooding has never been observed. It is also notable that, when the pouches are present, both sexes have them. Radashevsky & Lana (2009) discussed ontogenetic changes in the arrangement of lateral pouches in adults of *Laonice*. Such information is not available for *Spiophanes* species. The statement below: "lateral interneuropodial pouches present from chaetiger 15" means that the first pair of pouches is present between the neuropodia of chaetigers 15 and 16.

Key to *Spiophanes* from the continental shelf of northern Europe

1 Prostomium with long fronto-lateral horns. Occipital antenna absent. Nuchal organs metameric (first pair of metamers oblique ciliary bands extending from posterior of prostomium to middle of chaetiger 3, and a series of short metamers on successive chaetigers). Sabre chaetae and hooks in neuropodia from chaetiger 15; hooks with small subterminal hood. Lateral interneuropodial pouches absent. Glandular organs in chaetigers 5-8 large, with long coiled fibers, in chaetigers 9-14 small, with short fibers; organs opened to the exterior through semicircular to semioval slits on chaetigers 5, 7 and 8, small hole or slit on chaetiger 6, and large vertical slits on chaetigers 9-14 .... ***S. bombyx***

– Prostomium without fronto-lateral horns, bell-shaped, broad anteriorly to subtriangular, almost oval. Occipital antenna present or absent. Nuchal organs entire, not metameric **2**

2 Occipital antenna present. Nuchal organs two parallel ciliary bands extending to chaetigers 14-16. Sabre chaetae in neuropodia from chaetiger 4. Hooks in neuropodia from chaetiger 15; hooks without hood. Lateral interneuropodial pouches present from chaetiger 15. Glandular organs in chaetigers 5-7 large, with long coiled fibers, in chaetigers 8-14 small, with short fibers; organs opened to the exterior through semicircular to semioval slits on chaetigers 5-7, small indistinct hole on chaetiger 8, and large vertical slits on chaetigers 9-14 ....
.... ***S. kroyeri***

– Occipital antenna absent. Nuchal organs U-shaped ciliary bands extending to end of chaetiger 3. Sabre chaetae and hooks in neuropodia from chaetiger 15; hooks with small subterminal hood. Lateral interneuropodial pouches absent. Glandular organs opened to the exterior through indistinct, crescent-shaped, horizontal openings on chaetigers 5–8, and large vertical slits on chaetigers 9-14 .... ***S. wigleyi***

32. *Spiophanes bombyx* (Claparède, 1870: 485–487, pl. XII, fig. 2, as *Spio bombyx*). Gulf of Naples, Mediterranean, Italy. Mesnil 1896: 249-257, pl. XV, figs 1-22; 1897: 91–92, pl. III, figs 17, 20, 21. Söderström 1920: 243–244, fig. 135. Fauvel 1927: 41, figs 14a–i.

Hartmann-Schröder 1971: 327-329, fig. 112; 1996: 341-342, fig. 156. Meißner 2005: 54-58, figs 33-35 (*Part.*). Meißner & Blank 2009: 7-11, figs 2-4. Common in shallow water sand and mixed substrata; ubiquitous.

33. *Spiophanes kroyeri* Grube, 1860: 88-89, pl. V, fig. 1. Greenland Sea. Hartmann-Schröder 1971: 326-327, fig. 111; 1996: 342-343, fig. 157. Meißner 2005: 7-14, figs 1-3. Common in offshore and stable muddy habitats; ubiquitous.
34. *Spiophanes wigleyi* Pettibone, 1962: 83–85, figs 5–6. Georges Bank, off Massachusetts, USA. Meißner 2005: 61. Uncommon, offshore.

Streblospio Webster, 1879

Streblospio Webster, 1879: 120. Foster 1971a: 112. Rice & Levin 1998: 694.

Type species. *Streblospio benedicti* Webster, 1879. By monotypy.

Synopsis.

Remarks. *Streblospio* Webster, 1879 currently comprises three species which usually occur in shallow water with reduced salinity. *Streblospio benedicti* and *S. gynobranchiata* are probably native to the western Atlantic, the former in shallow waters of the North America from Nova Scotia, Canada, south to Florida (Berkeley & Berkeley 1954; Schulze *et al.* 2000), the latter in Central and South America from the Gulf of Mexico south to Paraná, Brazil (Omena *et al.* 2012). *Streblospio shrubsolii* is probably native in the eastern Atlantic, originally distributed in shallow waters all around Europe. *Streblospio benedicti* on the Pacific coast of North America has been considered to be an introduction through ballast water release (Carlton 1975; Schulze *et al.* 2000). *Streblospio benedicti japonica* Imajima, 1990 from Yatsu tidelands in Tokyo Bay, Japan, is possibly also an introduction of the same species. *Streblospio benedicti* has also been introduced to northern Europe and is spreading widely, probably with ballast waters (Fonsêca-Genevois & Cazaux 1987; Dauvin *et al.* 2003; García-Arberas & Rallo 2004; Kocheshkova & Matviy 2009), while *S. gynobranchiata* has been introduced and is spreading in the eastern Mediterranean basin: Aegean Sea and Bosphorus Strait, Turkey (Çinar *et al.* 2005a, b, 2009, 2014), Black Sea, Russia and Ukraine (Boltacheva 2008; Radashevsky & Selifonova 2013; Boltachova *et al.* 2015), and southern part of the Caspian Sea, Iran (Taheri *et al.* 2009; Taheri & Foshtomi 2011).

Streblospio dekhuyzeni Horst, 1909 was described from Zuiderzee, North Sea, Holland, but Hartman (1959) treated it as a junior synonym of *S. shrubsolii*.

Adults of *S. benedicti* and *S. gynobranchiata* exhibit sexual dimorphism: gravid females have midventral seminal receptacles in certain fertile segments and special structures to brood the developing larvae: dorsal pouches in the former species (Levin 1984), and finger-like extensions of the lateral body wall in the latter species (Rice & Levin 1998). Females of *S. shrubsolii* have no seminal receptacles and lay a few large eggs on the inner surface of their tube where entirely benthic lecithotrophic larval development occurs (Cazaux 1985). The juveniles and males appear similar in all three *Streblospio* species and can hardly be distinguished.

Identification difficulties resulted in the late recognition of *Streblospio* invasions in European waters.

The only morphological character to distinguish immature European *S. shrubsolii* from the non-native American *S. benedicti* and *S. gynobranchiata* is the starting point of the hooded hooks: in the neuropodia from chaetigers 8-10 in adults of the former species and from chaetiger 7 in the two latter species. This character should be observed with caution, however. The hooks in *Streblospio* worms are very fragile and easily broken, thus their anteriormost position should be checked on intact specimens.

Key to *Streblospio* from the continental shelf of northern Europe

1 Hooks in neuropodia from chaetigers 8-10. No epithelial brooding structures in females – gametes released directly into water .... ***S. shrubsolii***

– Hooks in neuropodia from chaetiger 7 2

2 Oocytes from chaetigers 9-11; sperm from chaetigers 8-9. Females brooding larvae in epithelial pouches on dorsal side from chaetigers 18-23 to chaetigers 23-38 .... ***S. benedicti***

– Oocytes from chaetiger 8; sperm from chaetiger 7. Females with dorso-lateral digitiform epithelial extensions from chaetigers 19-21 to chaetigers 26-32 .... ***S. gynobranchiata***

35. *Streblospio benedicti* Webster, 1879b: 120-121; 1886: pl. (V)8, figs 48-50. Wellfleet Harbor, Cape Cod Bay, Massachusetts, USA. Fonsêca-Genevois & Cazaux 1987: 236-256, figs 2-4. Dauer *et al.* 2003: 208-212, fig 1A, B. Zakas & Wares 2012: 5447-5457.
36. *Streblospio gynobranchiata* Rice & Levin, 1998: 694-707, figs 1-13. Courtney Campbell Causeway, Tampa Bay, Florida, USA. Radashevsky & Selifonova 2013: 265-266, figs 2, 3. Boltachova *et al.* 2015: 23-27, figs 4, 5. Common in many UK estuaries in variable salinity. Non-native, possibly invasive, and probably still most likely near ports and harbours.
37. *Streblospio shrubsolii* (Buchanan, 1890: 175-200, figs 1-14, as *Hekaterobranchus shrubsolii*). Sheppey, Thames River mouth, England. Cazaux 1985: 209-220, figs 1-7 (larval morphology). Dauer *et al.* 2003: 208-212, figs 1C, 2, 3. Common in estuaries and lagoons; ubiquitous. Possibly declining in areas colonised by *S. benedicti*.

Trochochaeta Levinsen, 1883

Disoma Örsted, 1843, preoccupied by *Disoma* Ehrenberg, 1831. *Fide* Chamberlin 1919a: 369.

Trochochaeta Levinsen, 1883: 129. Pettibone 1963: 308-309; 1976: 3-4, as a replacement name for *Disoma* Örsted, 1843 preoccupied by *Disoma* Ehrenberg, 1831. Rouse 2001: 273-275.

Disomides Chamberlin, 1919a: 369, as a replacement name for *Disoma* Örsted, 1843 preoccupied by *Disoma* Ehrenberg, 1831. *Fide* Pettibone 1963a: 309.

Thaumastoma Webster & Benedict, 1884: 737. *Fide* Mesnil 1897: 94-95. Pettibone 1963a: 309.

Nevaya McIntosh, 1911: 149-151. *Fide* Pettibone 1963a: 309.

Type species. *Disoma multisetosum* Örsted, 1843. By monotypy.

Nominal species. *Trochochaeta sarsi* Levinsen, 1883 (= posterior end of *Disoma multisetosum* Örsted, 1843). *Fide* Pettibone 1963a: 309.

Synopsis.

Remarks. Örsted (1843) established a new genus for a new species, *Disoma multisetosum* Örsted, 1843, and placed it together with the genera *Leucodorum* (=*Polydora*), *Nerine* (=*Scolelepis*) and *Spio* within the group **Ariciae naidinae** (=Spionidae) in the family Ariciae Audouin & Milne Edwards, 1829. Claparède (1869: 77) noted similarity between *Polydora* Bosc, *Disoma* Örsted and the chaetopterids and concluded "Les affinities de ces Annélides entre elles sont si grandes, qu'on pourrait désirer une nouvelle étude des *Disoma*, avant d'être parfaitement certain qu'il s'agit de Spiodiens et pas de Chétoptériens." Levinsen (1883) was the first to place *Disoma* Örsted within the Spionidae and to suggest affinity between *Disoma* Örsted and *Poecilochaetus*. Levinsen (1883) also established a new genus for a new species, *Trochochaeta sarsi* Levinsen, 1883, and placed it within the family Amphinomidae Lamarck, 1818. Michaelsen (1897) showed the identity of *Disoma multisetosum* Örsted (based on anterior fragments) with *Trochochaeta sarsi* Levinsen (based on a posterior fragment), treated the latter name as a junior synonym of the former, and placed the species within the family Spionidae. Mesnil (1897) suggested affinity between *Disoma* Örsted and *Poecilochaetus* and established a new family Disomidae Mesnil, 1897 to encompass the two genera. Chamberlin (1919a: 370) noted "Since *Disoma* Örsted was preoccupied by *Disoma* Ehrenberg (Polyg., 1844), it is here replaced by *Disomides* and the family name is altered accordingly to Disomididae." In a revision of the Spionidae, Söderström (1920) placed *Disoma* Örsted and *Poecilochaetus* in a new subfamily Disominae within the Spionidae. Based on the morphology of the larvae, Hannerz (1956) established a new family Poecilochaetidae for *Poecilochaetus*, and placed *Disoma* Örsted within the family Disomidae. Pettibone (1963a: 308) confirmed the identity of *Disoma multisetosum* Örsted, 1843 with *Trochochaeta sarsi* Levinsen, 1883 and, because *Disoma* Örsted, 1843 was preoccupied by *Disoma* Ehrenberg, 1831, recognized *Trochochaeta* Levinsen, 1883 as the type genus and established a new family name Trochochaetidae Pettibone, 1963 to replace the family names Disomidae Mesnil, 1897 and Disomididae Chamberlin, 1919. Söderström (1920), Hartman (1947), Dales (1962), Orrhage (1964) and Pettibone (1976b) discussed the taxonomy of disomids/trochochaetids. Studies on the morphology, biology and phylogenetic relationships of *Trochochaeta* with other spionids were reviewed by Rouse (2001c). Rouse (2001c: 275) noted that "In containing only *Trochochaeta*, the name Trochochaetidae is empty and redundant" and placed *Trochochaeta* as an individual taxon within the Spionida Dales, 1962. There is more on the taxonomy of *Trochochaeta* in the introduction section above.

Trochochaeta currently comprises 13 valid species and one unnamed species. Hartman (1947), Pettibone (1976b), Hernández-Alcántara & Solís-Weiss (2011) and Bochert & Zettler (2013) provided identification keys to the *Trochochaeta* species described up to 2013.

In north European waters, only *T. multisetosa* (Örsted, 1843) has been reported by various authors. Pettibone (1963a) and Weitbrecht (1984) described details of adult morphology, while Thorson (1946) and Hannerz (1956) described the gametes and pelagic larvae of *T. multisetosa*.

38. *Trochochaeta multisetosa* (Örsted, 1843: 41-42, as *Disoma multisetosum*). Near Hveen (Ven) island in the Øresund strait, Sweden. Rare.

Polydorini Benham, 1896

Polydoridae Benham, 1896: 323.
Polydorini: Radashevsky 2012: 13.
Polydorinae: Kerckhof & Faasse 2014: 1.

Type genus. *Polydora* Bosc, 1802.

Synopsis.

Remarks. Benham (1896) established a family **Polydoridae** to encompass spionids with heavy spines in chaetiger 5. The family rank of this taxon was not accepted by later authors and, although being called **polydorids,** ***Polydora*** species were considered as members of the family Spionidae. *Pseudopolydora* Czerniavsky, 1881, *Boccardia* Carazzi, 1893 and *Carazzia* Mesnil, 1896 were established to distinguish different groups of polydorids but used mainly as subgenera of *Polydora* until Blake & Kudenov (1978) revised the group and assigned former *Polydora* species to six genera of the ***Polydora*** **complex**: *Boccardia* Carazzi, 1893, *Boccardiella* Blake & Kudenov, 1978, *Carazziella* Blake & Kudenov, 1978, *Polydora* Bosc, 1802, *Pseudopolydora* Czerniavsky, 1881 and *Tripolydora* Woodwick, 1964. Radashevsky (2012) emended the diagnosis of the group to encompass only spionids with heavy falcate spines in the posterior row of notochaetae on chaetiger 5 and referred them to a tribe, **Polydorini** Benham, 1896, using the family-group name established by Benham (1896). The monophyly of this tribe requires further investigation, however, and the membership of some previously-defined *Polydora*-complex taxa within the Polydorini requires validation. Remarkably, in contrast to Polydorini members (**polydorins**) with the falcate spines in the posterior row of notochaetae on chaetiger 5, adults of *Tripolydora* have heavy spines in the anterior row of notochaetae on chaetiger 5 (Blake & Woodwick 1981; Radashevsky & Fauchald 2000: fig. 4I; Radashevsky 2015), and adults of *Atherospio* have heavy spines in the neuropodia of chaetiger 5. *Tripolydora* and *Atherospio* are considered herein not to be members of the Polydorini.

Some polydorins inhabit silty or sandy tubes in soft sediments or on the surfaces of stones and rocks, while others bore into sponges, mollusc and barnacle shells, corals and other biogenic calcareous structures or into non-biogenic hard substrata such as lime-, mud- and sandstones. Remarkably, boring polydorins are also able to construct tubes and use them to extend their burrows. Nevertheless, most of the species practice only one mode of life that can be used as an additional character for their identification. There is no structural adaptation to distinguish boring from non-boring worms and the lifestyle of an individual cannot be ascertained from its morphology. Conspecificity of individuals living in tubes in sediment and boring into shells was reported for several polydorins but has been proven only for *Boccardia proboscidea* Hartman, 1940 and *Dipolydora carunculata* (Radashevsky, 1993) (see Radashevsky & Pankova 2013). The boring is mainly chemical, probably with the acid mucopolysaccharides secreted by the glandular pouches regularly arranged in the neuropodia of anterior segments. The pouches are present in all polydorins and also in some other tube-building spionids and likely appeared once within the Spionidae in association with the evolution of tube-building mode of life. Polydorins are the only borers within the family Spionidae. Both tube-building and shell-boring species occur in different genera, thus, the ability to bore has likely evolved independently several times within the Polydorini. The heavy spines in notopodia of segment 5 are present both in tube-building and shell-boring polydorins and are likely not related to the boring activity, although may facilitate the boring process. Segment 5 spines of polydorins as well as spines in anterior segments of other spionids are likely used to fix body within the tube when the worm protrudes outside and also to maintain the diameter of the tube.

Boccardia Carazzi, 1893

Polydora (*Boccardia*) Carazzi, 1893: 15. Fauvel 1927: 48. Hartmann-Schröder 1971: 314.

Boccardia: Mesnil 1893: 645. Chamberlin 1919a: 369. Blake & Woodwick 1971: 31. Blake & Kudenov 1978: 235. Light 1978: 133-134. Blake 1996a: 203.

Type species. *Boccardia polybranchia* (Haswell, 1885). By monotypy.

Synopsis.

Remarks. *Boccardia* Carazzi, 1893 currently comprises about 24 valid species. In the notopodia of chaetiger 5, adult *Boccardia* have heavy spines, with bristles on their expanded distal ends in an anterior row, and simple falcate spines in a posterior row; the superior capillaries are shorter and less numerous than those on chaetigers 4 and 6, absent in some species. The branchiae begin on chaetiger 2 in adults (chaetiger 7 in small juveniles). Adults of most species live in tubes in soft sediments and have rather limited distributions. In contrast to their congeners, adults of *B. proboscidea* inhabit tubes in soft sediments and also bore into mollusc and barnacle shells, other non-biogenic hard substrata such as lime-, mud- and sandstones, and are distributed widely due to human mediated activities. Three species of *Boccardia* have been reported from European waters: *B. polybranchia* (Haswell, 1885), *B. semibranchiata* Guérin, 1990, and *B. proboscidea*. Their taxonomy is briefly discussed below.

Polydora polybranchia (=*B. polybranchia*), the type species of *Boccardia*, was originally briefly described by Haswell (1885) based only on an anterior fragment from New South Wales, Australia. Later attempts to find and re-describe the worms from the type locality in the Hunter River by Blake & Kudenov (1978) and myself in 2013 (see Radashevsky 2015) were unsuccessful and the species remains one of the most enigmatic and poorly defined spionids, which has nevertheless been reported all over the world. In Europe, *P. polybranchia* / *B. polybranchia* was reported from the Mediterranean, Italy and Greece (Lo Bianco 1893; Laubier

1962a; Simboura & Nicolaidou 2001), the Straight of Gibraltar (Sardá 1986), Bay of Biscay, Spain (Rioja 1931), northern France (Mesnil 1896; Dauvin *et al.* 2003; Lejart & Hily 2011), and the Isle of Man, Irish Sea (Moore 1937). No material from those studies has been deposited in a public colection and their identity cannot be verified at present. It is most likely that the worms were misidentified and actualy belong to one of the species discussed below.

Boccardia semibranchiata was originally described from the Gulf of Lion, Mediterranean France (Guérin 1990, 1991), and later reported from Normandy, northern France (Ruellet 2004), and San Sebastián, Bay of Biscay, Spain (Martínez *et al.* 2006). Comparison of specimens from Arcachon Bay, France, identified as *B. semibranchiata* with specimens of *B. pseudonatrix* Day, 1961 from South Africa showed them to be conspecific (Radashevsky unpublished). Consequently, the former species is herein treated as a junior synonym of the latter.

Boccardia proboscidea was originally described from California, USA (see Radashevsky & Harris 2010; Fauchald *et al.* 2011), and later reported from the Asian Pacific, Australia, Argentina, and South Africa. In Europe, *B. proboscidea* was first collected in 1996 on the rocky intertidal near sewage outfall of San Sebastián, Bay of Biscay, Spain (Martínez *et al.* 2006). In 2001, adults were found near the port of Harwich, Essex, south-eastern England (Tim Worsfold, pers. comm.), and also in Galway Bay on the west coast of Ireland (Brendan O'Connor, pers. comm.). In 2008, *B. proboscidea* was present in King Edwards Bay, Tynemouth, and Cullercoats Bay, north-eastern England (Radashevsky unpublished) and the Clyde Sea, Scotland (Myles O'Reilly, pers. comm.); and in 2016 it was present in Kent and Sussex (Robin Shrubsole, pers. comm.) and found in Great Cumbrae Island, western Scotland (Radashevsky unpublished). In 2011 and 2013, worms were collected on the intertidal of the Isle of Skye, northern Scotland (Hatton & Pierce 2013), and in 2011 they were found in the North Sea, on groynes along the Belgian coast and among the Pacific oysters *Magallana gigas* (previously *Crassostrea*) (Thunberg, 1793) in the south-western Dutch delta (Kerckhof & Faasse 2014). In 2014, worms were found on the intertidal rocky reef in Wimereux, Opal Coast, La Manche, France (Spilmont *et al.* 2016). Spilmont *et al.* (2016) also reported *B. proboscidea* from La Rochelle, French coast of the Bay of Biscay. *Boccardia proboscidea* is an aggressive invasive species, widely distributed throughout the world through human activities (see Kerckhof & Faasse 2014; Elías *et al.* 2015; Jaubet *et al.* 2015). It appears that the species has established itself throughout the British Isles and is spreading through northern Europe. The reproductive biology of *B. proboscidea* has been described in California and British Columbia (Hartman 1941; Woodwick 1977; Gibson 1997; Gibson *et al.* 1999; Smith & Gibson 1999; Gibson & Smith 2004; Gibson & Carver 2013), Australia (Blake & Kudenov 1981), South Africa (David & Simon 2014), and Argentina (Jaubet *et al.* 2015).

Key to *Boccardia* from the continental shelf of northern Europe

1 Caruncle to end of chaetiger 1. Mid-dorsal longitudinal ridge present from chaetiger 5 to middle of chaetiger 8 .... ***B. pseudonatrix***

– Caruncle to end of chaetiger 3. Mid-dorsal ridge absent on anterior chaetigers ....
B. proboscidea

39. *Boccardia proboscidea* Hartman, 1940: 382–387, fig. 1; 1941: 299-304, pl. 46, figs 22-28, pl. 47, figs 30-37. California, USA. Woodwick 1963a: 133-137, figs 2-4; 1977: 348-352, figs 1-12 (larval morphology). Imajima & Hartman 1964: 279-280, pl. 36, figs a-f. Blake & Kudenov 1978: 238, fig. 33a-c. Light 1978: 147-149, textfig. 148. Petch 1995: 26-28. Gibson 1997: 215-220, figs 1-3. Gibson *et al.* 1999: 746-749, figs 3-6. Bailey-Brock 2000: 27-29, fig. 1. Sato-Okoshi 2000: 447-448. Gibson & Smith 2004: 136-145, figs 1-3. Martínez *et al.* 2006: 59-62, figs 4, 5. Sato-Okoshi *et al.* 2008: 498. Simon *et al.* 2009: 18-24; 2010: 594-596, figs 4, 5. Gibson & Carver 2013: 13-19, figs 1-6 (larval morphology). Hatton & Pearce 2013: 2-3, figs 2 & 3. Kerckhof & Faasse 2014: 3-4, figs 4-6. Jaubet *et al.* 2015: 613-617, figs 2-5 (adult & larval morphology).

Polydora (*Boccardia*) *proboscidea*: Hobson & Banse 1981: 38. Hartmann-Schröder 1982a: 85.

Polydora californica Treadwell, 1914, 203–204. California. LACM-AHF POLY 638 (type). Radashevsky & Harris 2010: 203-207. Fauchald *et al.* 2011: 134-136. *Fide* ICZN 2012: 232-234.

Locally common; in intertidal soft stone, clay, peat and stiff mud and amongst stones. Non-native, invasive, probably now ubiquitous.

40. *Boccardia pseudonatrix* Day, 1961: 493, fig. 5 e–j. The Heads, Knysna River estuary, Western Cape Province, South Africa. Simon *et al.* 2010a: 596-597.

Boccardia semibranchiata Guérin, 1990: 39-41, figs 1-2. 1991: 147-150, fig 1. Étang de Berre, Bouches-du-Rhône, Gulf of Lion, Mediterranean, France. From shell debris. Martínez *et al.* 2006: 55-59, figs 2, 3. New synonymy.

Rare, probably non-native. Boring into shells of the cultivated Pacific oyster *Magallana gigas* (previously *Crassostrea*).

Boccardiella **Blake & Kudenov, 1978**

Boccardiella Blake & Kudenov, 1978: 264–265. Blake 1996a: 202.

Polydora (*Boccardiella*): Hartmann-Schröder 1996: 320.

Type species. *Polydora hamata* Webster, 1879. By Blake & Kudenov 1978: 274.

Synopsis.

Remarks. *Boccardiella* Blake & Kudenov, 1978 currently comprises about five valid species. In the notopodia of chaetiger 5, adult *Boccardiella* have capillary companion chaetae in an anterior row and simple falcate spines in a posterior row; the superior capillaries are shorter and less numerous than those on chaetigers 4 and 6. The branchiae begin on chaetiger 2 in adults (chaetiger 7 in small juveniles). Various names had been used for worms with these characteristics from European waters (see below) until Blake & Woodwick (1971) showed that *Polydora* (*Boccardia*) *redeki* Horst, 1920 from Holland was a junior synonym of *Boccardia ligerica* Ferronnière, 1898 from France, and Blake & Kudenov (1978) established the genus *Boccardiella* and placed *B. ligerica* in it. *Boccardiella ligerica* has been reported from both Atlantic and Pacific coasts of North and South America and should be considered cryptogenic in European waters.

Boccardiella hamata (Webster, 1879) was originally described from Virginia, USA, and later reported around the world as boring into mollusk shells and also dwelling in tubes in soft sediments (see Kerckhof & Faasse 2014). The species was identified in samples collected in 2013 among Pacific oysters *Magallana gigas* (previously *Crassostrea*) in the southwestern Dutch delta, North Sea, Holland; this was the first record of the species from European waters, where it is considered non-indigenous (Kerckhof & Faasse 2014).

Key to *Boccardiella* from the continental shelf of northern Europe

1 Caruncle to end of chaetiger 2. Branchiae on chaetigers 2, 3 and from chaetiger 7 up to chaetiger 21, absent from posterior 1/2-2/3 of body. Pygidium flat, without a notch, with a pair of long postero-lateral anal cirri. Tube- dwelling; tubes usually attached to hard substrata ..... ***B. ligerica***

– Caruncle to middle of chaetiger 4. Branchiae on chaetigers 2, 3, 6 and following chaetigers, absent from posterior 1/3-1/2 of body. Pygidium with two broad ventral lappets, each having a short postero-lateral process. Boring into mollusc shells and also dwelling in tubes in soft sediments .... ***B. hamata***

41. *Boccardiella hamata* (Webster, 1879a: 51-52, pl. VIII, figs 111-116, pl. IX, figs 117-118, as *Polydora hamata*). Northampton County, Virginia, USA. Radashevsky 1993: 4-7, figs 2, 3. Reunov *et al.* 2010: 448-450, figs 1-5 (sperm ultrastructure). Kerckhof & Faasse 2014: 4, figs 7, 8. *Fide* Blake & Kudenov 1978: 265.

Boccardia uncata E. Berkeley, 1927: 418, pl. 1, figs 9–13. Piper's Lagoon, Nanaimo, Vancouver Island, British Columbia, Canada. Tubes in soft sediments. *Fide* Blake 1966: 177.

Boccardia hamata: Blake 1966: 177-182, figs 1-11. Dean & Blake 1966: 316-327, figs 1-7 (larval morphology).

Polydora (*Boccardia*) *hamata*: Hobson & Banse 1981: 38.

Rare, probably non-native. Recently recorded from among the Pacific oyster *Magallana gigas* (previously *Crassostrea*) in Holland.

42. *Boccardiella ligerica* (Ferronnière, 1898: 109-111, pl. 6, figs *a-i*, as *Boccardia ligerica*). Loire-Inférieure, northern France. *Fide* Blake & Kudenov 1978: 265.

Boccardia ligerica: Hartman 1959a: 375. Blake & Woodwick 1971: 32-34, fig. 1. Kudenov 1983: 144-145.

Polydora (*Boccardia*) *ligerica*: Fauvel 1927: 57-58, fig. 19 n-s.

Polydora (*Boccardiella*) *ligerica*: Hartmann-Schröder 1980b: 400.

Polydora ligerica: Rullier & Amoureux 1969: 110. Amoureux 1972: 62.

Polydora (*Boccardia*) *redeki* Horst, 1920: 111. Holland. Augener 1939, 141-142, fig. 2. Rullier 1960: 231-242, figs 1-31 (adult & larval morphology). Eliason & Haahtela 1969: 215-217, fig. 1. Bonsdorff 1981: 143. *Fide* Blake & Woodwick 1971: 32, 34.

Polydora redeki: Halsinaho 1984: 55-57.

Boccardia redeki: Amoureux & Calvário 1981: 150.

Polydora uncatiformis Monro, 1938: 311-313, figs 1-3. Arroyo de las Brujas, Canelones, Uruguay. *Fide* Blake & Kudenov 1978: 265.

Common on pilings, pontoons and in gravel in low salinity parts of tidal Thames.

***Dipolydora* Verrill, 1881**

Dipolydora Verrill, 1881: 320. Resurrected and redefined by Blake 1996: 181.

Type species. *Polydora concharum* Verrill, 1879. Designated by Verrill (1881), by monotypy.

Synopsis.

Remarks. *Dipolydora* Verrill, 1881 currently comprises about 50 species. The name *Dipolydora* was not in use after its designation by Verrill (1881) until Blake (1996) resurrected it and assigned to it a series of *Polydora* Bosc, 1802 species. Adults belonging to this genus have notochaetae on chaetiger 1, bilimbate-tipped capillaries in the anterior row and falcate spines in the posterior row of notochaetae of chaetiger 5, branchiae beginning after chaetiger 5, and neuropodial hooded hooks with slightly curved shafts without constrictions. They inhabit silty or sandy tubes in soft sediments and also bore into sponges, coralline algae, soft rock and shells of various molluscs and barnacles from the intertidal to deep water. Preliminary phylogenetic analysis of morphological and molecular characters suggested polyphyletic composition of *Dipolydora* as it is currently defined (Radashevsky unpublished).

Key to *Dipolydora* from the continental shelf of northern Europe

1 Branchiae from chaetiger 7, basally fused to notopodial postchaetal lamellae. Posterior notopodia with more than four awl-like spines in addition to capillaries **2**

– Branchiae from chaetigers 7-10, free from notopodial postchaetal lamellae. Posterior notopodia with only capillaries or with additional awl-like spines (up to four in a tuft) or numerous needle-like spines **5**

2(1) Heavy spines of chaetiger 5 falcate, with central main fang, large lateral tooth and apical structure appearing as wide hood or third tooth on convex side of main fang. Pygidium cup-shaped to bilobed .... ***D. armata***

– Heavy spines of chaetiger 5 without apical transverse structure; lateral tooth present or absent. Pygidium with four lobes **3**

3(2) Heavy spines of chaetiger 5 distally bifurcated, with two short massive unequal teeth and fine bristles between them .... ***D. quadrilobata***

– Heavy spines of chaetiger 5 falcate, with a long pointed main fang bearing dense bristles on convex side **4**

4(3) Pygidium with four almost equal lobes .... ***D. caulleryi***

– Pygidium small, disc-like with dorsal gap .... ***Dipolydora* sp. A**

5(1) Prominent finger-like occipital antenna present on prostomium between palp bases. Posterior notopodia each with up to eight awl-like spines loosely grouped in a tuft in addition to 1-5 capillaries. Pygidium large and fleshy, cup-shaped with dorsal incision or three-lobed with two small dorsal lobes and a bigger ventral lobe .... ***Dipolydora* sp. B**

– Occipital antenna absent. Posterior notopodia with or without modified spines in addition to capillaries. Pygidium cup-shaped or lobate **6**

6(5) Caruncle to end of chaetiger 3. Posterior notopodia with only capillaries. Falcate spines of chaetiger 5 with additional structures on lateral or convex sides. Boring into mollusc shells and coralline algae 7

– Caruncle to end of chaetiger 4 or 5. Posterior notopodia with modified spines in addition to capillaries. Falcate spines of chaetiger 5 with smooth lateral and convex sides. Inhabiting tubes in soft and coarse sediments **8**

7(6) Branchiae from chaetiger 7. Falcate spines of chaetiger 5 with low transverse subdistal collar or shelf on convex side. Pygidium small, cup-shaped to disc-like with dorsal gap ....

....

D. langerhansi

– Branchiae from chaetigers 8-10. Falcate spines of chaetiger 5 with lateral tooth on one side and fine spur or protuberance on another side. Pygidium three-lobed .... ***D. giardi***

8(6) Posterior notopodia with loose fascicles of long needle-like capillaries protruding out of body wall. Falcate spines of chaetiger 5 ten or more in a series, straight, without subdistal spoon-like hollow on concave side .... ***D. coeca***

– Modified spines in posterior notopodia embedded into body wall. Falcate spines of chaetiger 5 up to seven in a series, with subdistal spoon-like hollow on concave side **9**

9(8) Notopodia from chaetigers 8-9 with tight packets of needle-like spines in addition to capillaries. .... ***D. flava***

– Posterior notopodia with 2-4 awl-like spines in addition to capillaries ....

....

D. saintjosephi

43. *Dipolydora armata* (Langerhans, 1880: 93–94, pl. 4, fig. 5 *a–c*, as *Polydora armata*). Madeira Island, Portugal. Blake 1996 (*Part.*): 196–198, fig. 4.36. Bick 2001: 178–186, figs 1–7. Williams 2001: 438–442, figs 5, 6. Radashevsky & Nogueira 2003: 377–381, figs 1–7. Sato-Okoshi *et al.* 2008: 495–496, fig. 4. Radashevsky 2015: 643-645, fig. 5. *Polydora armata*: Blake & Kudenov 1978: 255–258, fig. 43a–e.

Polydora (*Polydora*) *armata*: Hartmann-Schröder 1979: 134, figs 299-302; 1987: 55. Hobson & Banse 1981: 41.

Polydora monilaris Ehlers, 1905: 43–44, pl. VI, figs 5–14. French Pass, Elmslie Bay, New Zealand. *Fide* Day 1954: 24.

Polydora rogeri Martin, 1996: 161–167, figs 1–5. Bay of Blanes, Mediterranean, Spain. Boring into calcareous algae. *Fide* Radashevsky & Nogueira 2003: 377.

Rarely found in samples, when present forming numerous colonies due to asexual reproduction by architomy. Boring into mollusc shells and calcareous algae.

44. *Dipolydora caulleryi* (Mesnil, 1897a: 88-89, figs 12-16, as *Polydora caulleryi*). Hague, Netherlands, North Sea. Blake 1996: 194, 198.

Polydora caulleryi: McIntosh 1915b: 210-212, pl. 100, fig. 8, pl. 106, fig. 5.

Polydora (*Polydora*) *caulleryi*: Hartmann-Schröder 1971: 310-311, fig. 105 a-c; 1996: 312-313, fig. 141.

Widespread; tubes in gravel and soft sediments.

45. *Dipolydora coeca* (Örsted, 1843: 39, as *Leucodorum coecum*). Öresund, Denmark. Blake 1996: 188.

Leucodore caecus: Malmgren 1867: 95.

Leucodore coecus Quatrefages, 1865: 302.

Leucodore coeca: Willemoes-Suhm 1873: 348, pl. XVIII, figs 4-5.

Polydora coeca: Ditlevsen 1929: 30-31.

Polydora sp.: Mesnil 1897: 86-87, pl. III, figs 6-8.

Polydora caeca: Eliason 1920: 46-49, fig. 12. Söderström 1920: 259-260 (*Part.*).

? *Polydora socialis*: Ramberg & Schram 1983: 242-243 (*Part.*), fig. 6. Not *Leucodore socialis* Schmarda, 1861.

Leipoceras uviferum Möbius, 1874: 200-201, pl. XI, figs 4-14. *Fide* Hartman 1959: 378.

Not *Polydora caeca*: Saint-Joseph 1894: 59-61, pl. III, figs 65-70. Annenkova 1952: 126. Uschakov 1955: 274.

Not *Polydora coeca*: Mesnil 1896: 191-193, pl. XII, figs 23-29.

Probably common but true abundance unknown due to previous confusion with related species; tubes in sediments.

46. *Dipolydora flava* (Claparède, 1870: 487–488, as *Polydora flava*). Gulf of Naples, Mediterranean, Italy. Blake 1996: 189.

Polydora flava: Mesnil 1896: 182-191, pl. 11, figs 18-26, pl. 12, figs 1-22. Fauvel 1927: 52-54, figs 17 n-u. Day 1967: 468-469, fig. 18.3.a-d. Sardá 1986: 72, 75, fig. 1.

Polydora (*Polydora*) *flava*: Hartmann-Schröder 1971: 305; 1996: 317.

Polydora pusilla Saint-Joseph, 1894: 65–66, pl. III, figs 74–77. Golfe de St.-Malo, Dinard, Bretagne, northern France. *Fide* Hartman 1959: 385.

Occasional; tubes in gravel and soft sediments.

47. *Dipolydora giardi* (Mesnil, 1893: 643, as *Polydora giardi*). St. Martin Bay, La Manche, France. Blake 1996: 186. Radashevsky & Petersen 2005: 28-33, fig. 2.

Polydora giardi: Mesnil 1896: 195-202, pl. XIII. figs 1-12.

Polydora (*Polydora*) *giardi*: Hartmann-Schröder 1971: 306; 1996: 317. Hobson & Banse 1981: 41, fig. 5a.

Abundance unknown due to previous confusion with related species; when present forming numerous colonies due to asexual reproduction by architomy. Boring into mollusc shells and calcareous algae.

48. *Dipolydora langerhansi* (Mesnil, 1896: 202-203, textfigs 1, 2, as *Polydora langerhansi*). Madeira Island, Portugal. *Fide* Blake 1996: 193.

Polydora ciliata minuta: Langerhans, 1880: 91-92. Possibly not *Leucodore ciliata minuta* Grube, 1855. *Fide* Mesnil 1896: 202.

Abundance unknown due to previous confusion with related species; when present forming numerous colonies probably due to asexual reproduction by architomy. Boring into mollusc shells and calcareous algae.

49. *Dipolydora quadrilobata* (Jacobi, 1883: 1-87, 2 pls, as *Polydora quadrilobata*). Bay of Kiel, Germany. Blake 1996: 194, 198, fig. 4.32 I-N.

Polydora quadrilobata: McIntosh 1915b: 209-210, pl. 98, fig. 13, 17, pl. 100, fig. 9, pl. 106, fig. 4. Blake 1971: 13-15, fig. 9. Radashevsky 1993: 18-21, fig. 9.

Polydora (*Polydora*) *quadrilobata* Hartmann-Schröder 1971: 308-310, fig. 104; 1996: 319-320, fig. 144. Hobson & Banse 1981: 40.

Common in shallow waters; tubes in soft sediments.

50. *Dipolydora saintjosephi* (Eliason, 1920: 49, as *Polydora Saint Josephi*). Golfe de St.-Malo, Dinard, Bretagne, northern France. Blake 1996a: 189.

Polydora caeca: Saint-Joseph 1894: 59-61. pl. III, figs 65-70. *Fide* Eliason 1920: 49. Söderström 1920: 259-260 (*Part.*). Fauvel 1927: 52, fig. 18, a-k. Friedrich 1938: 133, fig. 86 e-g. Day 1967: 469, fig. 18.3.e-h. Hartmann-Schröder 1971: 307-308, fig. 103 (*Part.*). Bick & Gosselck 1985: 240, pls 29/6, 30/4 (*Part.*). Acero & San Martín, 1986: 17. Sardá 1986: 72, 75, fig. 1. Bick & Burckhardt 1989: 241. Not *Leucodorum coecum* Örsted 1843: 39.

Polydora coeca: Mesnil 1896: 191-193, pl. XII, figs 23-29. Fauvel 1900: 314. Rioja 1917: 18; 1931: 70-71, pl. 18, figs 1-9. Not *Leucodorum coecum* Örsted 1843: 39.

Abundance unknown due to previous confusion with related species; tubes in gravel and soft sediments.

51. *Dipolydora* sp. A. Northern France. Adults appear very similar to those of *D. caulleryi* but differ from them in having disc-like pygidium with dorsal gap instead of quadrilobate pygidium with four well separated lobes. Rare, boring into mollusc shells.

52. *Dipolydora* sp. B. Common in some places; boring into mollusc shells, coralline algae, and also inhabiting tubes in gravel and soft sediments.

Polydora Bosc, 1802

Polydora Bosc, 1802: 150. Savigny 1822: 45. Blake & Kudenov 1978: 245–247. Blake 1996: 167.

Polydora (*Polydora*): Fauvel 1927: 48. Hartmann-Schröder 1971: 304; 1996: 310.

Type species. *Polydora cornuta* Bosc, 1802. By monotypy.

Synopsis.

Remarks. *Polydora* Bosc, 1802 is one of the largest genera of Spionidae; it currently comprises about sixty species occupying diverse habitats from the intertidal to deep water. Five species of *Polydora* have been reported from European waters. Their taxonomy is briefly discussed below.

Polydora cornuta Bosc, 1802 was originally briefly described based on small individuals from intertidal sites in Charleston Harbor, South Carolina, USA. The type material was lost and the species considered indeterminable until Blake & Maciolek (1987) designated a neotype and demonstrated that *P. cornuta* is a senior synonym of *P. ligni* Webster, 1879 described from New Jersey, USA. The worms were reported from temperate and subtropical zones worldwide mainly under the name *P. ligni*. Rice & Simon (1980), Rice (1991), Rice *et al.* (2008) and Rice & Rice (2009) suggested that two or more sibling species might be involved. Radashevsky (2005) and Radashevsky & Selifonova (2013) described ontogenetic variability of *P. cornuta*, showed that the worms are easily transported with ballast water and as fouling of ocean-going vessels and, contrary to Rice *et al.* (2008), explained the wide distribution of the species as due to transportations with human activities. These transportations obscured the native distribution of the species, which remains uncertain.

Polydora ciliata (Johnston, 1838) was described from Berwick Bay, Berwick-Upon-Tweed, Northumberland, England, as living "between the seams of slaty rocks near low-water mark, burrowing in the fine soft mud which lines the fissures" (Johnston 1838: 68, as *Leucodore ciliatus*). Spionids morphologically similar to *P. ciliata* but boring into calcareous substrata were described before and after Johnston's (1838) publication, but Mesnil (1896) synonymized them with *P. ciliata*, and later descriptions of the species were based on boring individuals (Söderström 1920; Fauvel 1927; Annenkova 1938; Hartman 1941; Uschakov 1955; Imajima & Hartman, 1964; Hartmann-Schröder 1971; Blake 1983). Ultimately, *P. ciliata* has been widely reported in Europe and around the world as living both in silty tubes in soft sediments, on stones and rocks, and also boring into mollusc shells, coralline algae and other hard substrata. Radashevsky & Pankova (2006) highlighted ambiguity in the original description of the habitat of *P. ciliata*, resurrected shell-boring *P. calcarea* (Templeton, 1836) as a valid species, and redescribed it based on material from the Sea of Japan. Molecular analysis of shell-boring *P. calcarea* from the Sea of Japan, Russia, and Scotland showed their conspecificity (Radashevsky unpublished). Careful re-examination of the morphology, ecology and molecular characteristics of *P. ciliata* from Berwick Bay is urgently needed to clarify the taxonomy of this species and its relationships with *P. limicola* Annenkova, 1934 and *P. aggregata* Blake, 1969 (see Manchenko & Radashevsky 1993). At this point, in northern Europe, I suggest naming similarly appearing shell-boring worms as *P. calcarea* and tube-dwelling worms in soft sediments and on rock surfaces as *P. ciliata*.

Polydora hoplura Claparède, 1868 was originally described from the Gulf of Naples, Italy, and later reported worldwide as boring into shells of cultivated oysters and abalone (see Sato-Okoshi *et al.* 2016; Radashevsky & Migotto 2017; Radashevsky *et al.* 2017). The species was erronously re-described as *P. uncinata* in Japan by Sato-Okoshi (1998) and reported as such from Chile, to where it was accidentally transported with abalone brood stock from Japan (Radashevsky & Olivares 2005). Attaining 6 cm in length and 2 mm in width for more than 200 chaetigers (Carazzi 1893; Lo Bianco 1893), adults of *P. hoplura* are among the largest congeners. The larval development of *P. hoplura* boring into oyster shells in the River Yealm, south-west England, was described by Wilson (1928). The worldwide transportation of *P. hoplura* with aquaculture materials has obscured the native distribution of this species, which remains uncertain.

Polydora hermaphroditica Hannerz, 1956 was described based on larvae collected in the plankton in Gullmar Fjord, Sweden, and on juveniles and adults grown from those larvae in the laboratory. Hannerz (1956) noticed that the new species was very similar to *P. ciliata* but differed in having more hooks in the neuropodia of adults (up to 11 per neuropodium instead of 9 - usually 5-7), different pigmentation patterns in larvae, and in the development of both female and male gametes in one individual instead of separate female and male individuals. For the first time for polydorins, Hannerz (1956) described the early development of sperm in larvae (neoteny) and later development of oocytes in the same individual (simultaneous hermaphroditism), which he reflected in the name of the species. Since the original description, the species has been mentioned in various lists and keys but never redescribed or recorded.

Key to *Polydora* from the continental shelf of northern Europe

1 Occipital antenna present on prostomium (in *P. hoplura* in individuals with more than 90 chaetigers). Caruncle to end of chaetiger 3 .... **2**

– Occipital antenna absent on prostomium. Caruncle to end of chaetiger 2 .... **3**

2(1) Tube dwelling. Prostomium anteriorly bifurcated and flaring laterally. Fine continuous black line often present on palps, along edges of frontal longitudinal groove; worms with up to 60 chaetigers usually having black spots on lateral sides from chaetigers 7–10 to chaetigers 10–19. Chaetiger 5 with only falcate spines alternating with companion chaetae; dorsal superior and ventral capillaries absent; falcate spines with lateral tooth and narrow thin subdistal longitudinal flange or keel; companion chaetae closely adhering to convex side of falcate spines, with feathery, dishevelled tip appearing bifurcated. Posterior notopodia with only capillary chaetae **P. cornuta**

– Boring into shells. Prostomium anteriorly with shallow incision, often seen only in ventral view. Pigmentation absent on body; up to 25 black paired bands usually present on each palp in individuals with more than 50 chaetigers; occasionally bands on palps absent. Chaetiger 5 with dorsal superior and ventral capillaries, and falcate spines alternating with bilimbate-tipped companion chaetae; falcate spines with lateral subdistal flange. Posterior notopodia with heavy recurved spines in addition to capillary chaetae .... ***P. hoplura***

3(1) Posterior notopodia with needle-like spines in addition to capillary chaetae; spines loosely held in tufts and greatly protruding out of body wall. Intense dark pigment diffused (not forming distinct patches or spots) on prostomium, peristomium, dorsal and ventral sides of 5-9 anterior chaetigers. Hermaphrodites with sperm from chaetigers 7-14 to chaetigers 15-19, and oocytes from chaetigers 17-20 to about chaetiger 40 .... ***P. hermaphroditica***

– Posterior notopodia with only few slender capillary chaetae. Black pigment diffused or forming distinct patches or blotches on dorsal side of peristomium and some anterior and posterior. Gonochorists **4**

4(3) Boring into shells and coralline algae .... ***P. calcarea***

– Tube dwelling in soft sediments and on stones and rocks .... ***P. ciliata***

53. *Polydora calcarea* (Templeton, 1836: 234: fig. 27, as *Spio calcarea*). Whitehead, Belfast Lough, Ireland, Irish Sea. Radashevsky & Pankova 2006: 247-249, figs 2-3.

    Common; boring into mollusc shells and calcareous algae in the intertidal and in shallow waters.

54. *Polydora ciliata* (Johnston, 1838: 67, pl. III, figs 1-6, as *Leucodore ciliatus*). Berwick Bay, England.

    Taxonomic status uncertain; possibly junior synonym of *Polydora calcarea* (Templeton, 1836). Inhabiting tubes in soft sediments and on rock surfaces in the intertidal and in shallow waters.

55. *Polydora cornuta* Bosc, 1802: 150–153, pl. 12, figs 7–8. Charleston, South Carolina, USA. Blake & Maciolek 1987: 12-14, fig. 1. Radashevsky 2005: 3-19, figs 1-4 (adult and larval morphology).

    Common, cryptogenic. Inhabiting tubes in soft sediments in the intertidal and in shallow waters, including estuaries.

56. *Polydora hermaphroditica* Hannerz, 1956: 111-117, fig. 39. Gullmar Fjord, Sweden. Abundance and habitat uncertain.

57. *Polydora hoplura* Claparède, 1868: 58–59, pl. XXII, fig. 2. Gulf of Naples, Mediterranean, Italy. Sato-Okoshi *et al.* 2016: 3–6, figs 6, 7. Radashevsky & Migotto 2017: 860–865, figs 2–5 (adult and larval morphology). Radashevsky *et al.* 2017: 545-551, figs 2-4.

    Common, cryptogenic; boring into mollusc shells and calcareous algae.

Pseudopolydora Czerniavsky, 1881

Pseudopolydora Czerniavsky, 1881: 362. Blake & Kudenov 1978: 267. Blake 1996: 202.

Polydora (*Carazzia*): Fauvel 1927: 48.

Polydora (*Pseudopolydora*): Hartmann-Schröder 1971: 317; 1996: 322.

Type species. *Polydora antennata* Claparède, 1868, by monotypy.

Synopsis.

Remarks. *Pseudopolydora* Czerniavsky, 1881 currently comprises 23 valid species. Adults usually inhabit tubes and live in dense populations in the intertidal and in shallow waters, often in estuarine environments. Larvae easily survive in ballast waters, can be transported worldwide and, after settlement in an appropriate environment, establish new populations in remote places (Junqueira *et al.* 2009).

Pseudopolydora paucibranchiata (Okuda, 1937) originally described from Japan and widely distributed in the northern Pacific (Radashevsky 1993), was reported in Europe from Oslofjord, Norway (Ramberg & Schram 1983), the Netherlands (Faasse 2016), and the Mediterranean (Dagli & Çinar 2008; Simboura *et al.* 2010). The identity of the Mediterranean, Dutch and North Pacific specimens has been confirmed by molecular analysis, whereas most other north European specimens were found to be different (Radashevsky unpublished) and referred to a new species provisionally named herein as *Pseudopolydora* sp. A.

Key to *Pseudopolydora* from the continental shelf of northern Europe

1 Prostomium narrow and rounded anteriorly. Occipital antenna present or absent on prostomium. Notopodia of chaetigers 7-10 with anterior-row capillaries having flag-like limbation **2**

– Prostomium bilobed anteriorly. Occipital antenna present on prostomium. Notopodia of chaetigers 7-10 with anterior-row capillaries having narrow limbation **3**

2(1) Caruncle to end of chaetigper 2. Occipital antenna absent on prostomium .... ***Pseudopolydora* sp. A**

– Caruncle to middle of chaetiger 4. Occipital antenna present on prostomium .... ***P. paucibranchiata***

3(1) Prostomium weakly incised. Caruncle to end of chaetiger 1. Small individuals without pigmentation; large individuals with black pigment diffused on dorso-lateral sides of prostomium, peristomium and 5-7 anterior chaetigers. Up to 50 narrow transverse black bands regularly arranged on each palp, fewer bands in small individuals. Pygidium large thin disc to cup with wide dorsal gap .... ***P. pulchra***

– Prostomium deeply incised. Caruncle to end of chaetiger 6. Pigmentation absent. Pygidium with two fleshy lateral lobes separated by distinct dorsal and ventral incisions .... ***P. antennata***

58. *Pseudopolydora antennata* (Claparède, 1868: 60–61, pl. XXI, fig. 3, as *Polydora antennata*). Gulf of Naples, Mediterranean, Italy. No confirmed UK records; inhabiting tubes in soft sediments.
59. *Pseudopolydora paucibranchiata* (Okuda, 1937a: 231-233, figs 11, 12, as *Polydora (Carazzia) paucibranchiata*). Onomichi, Hiroshima Prefecture, Inland Sea, Japan.

Common where established, invasive; inhabiting tubes in muddy sediments. In northern Europe, first collected in 2015 in the Netherlands (Faasse 2016); could be expected in UK; often estuarine, shallow water.

60. *Pseudopolydora pulchra* (Carazzi, 1893: 26-27, as *Polydora* (*Polydora*) *antennata* var. *pulchra*). Gulf of Naples, Mediterranean, Italy. Common; inhabiting tubes in muddy and mixed sediments; mainly infralittoral, full salinity.
61. *Pseudopolydora* sp. A. Common; inhabiting tubes in muddy sediments; circalittoral, full salinity.