Handbook of Zoology
Annelida

Volume 2:
Pleistoannelida, Sedentaria II

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Edited by Günter Purschke, Markus Böggemann
and Wilfried Westheide

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Preface

Annelida, the segmented worms, comprise one of the most important taxa of invertebrates. The majority of annelid species occur in marine environments but they can also be found in freshwater and terrestrial realms. In particular, the marine forms are one of the most widespread, abundant, and diverse elements of the world's benthic fauna. Although comprising just approximately 21,000 described species, annelids show a remarkable diversity comparable, for instance, with that observed in crustaceans. This diversity could only be achieved by the plasticity of their bauplan constituting the prostomium, followed by a number of primarily identical modules, the segments, and the pygidium. Species are usually of median size and do not exceed a few centimeters in length. However, their range is much wider; some interstitial annelids of the smallest adult metazoans are known with body lengths of 300 to 400 µm such as certain Nerillidae, as well as species exceeding body lengths of more than 3 m such as *Eunice aphroditois*. The number of segments varies accordingly from less than ten to several hundred. The marine forms often show broadcast spawning and their life cycle is primarily comprised of a planktonic larval stage, the trochophore, and a benthic adult stage. However, there are many deviations from this pattern that, *inter alia*, are correlated with life style and body size. Thus, their reproductive biology is highly diverse as well.

The traditional classification and subdivision of Annelida into Polychaeta and Clitellata comprising Oligochaeta and Hirudinea does not reflect their phylogenetic systematization, but the names *polychaetes* and *oligochaetes* are still in use for practical reasons. Recent phylogenetic analyses have confirmed that polychaetes constitute nothing else but a paraphyletic assemblage of the more or less plesiomorphic Annelida. The same applies for the oligochaetes representing a basal grade of Clitellata. Therefore, polychaetes are those annelids that do not possess a clitellum, a view that is followed in the *Handbook of Zoology*. Annelid phylogeny now sees a so-called basal grade only comprising a few taxa but the majority of Annelida, termed Pleistoannelida, are now classified into two large monophyletic groups: Errantia and Sedentaria. In a highly derived position, the latter also comprise Clitellata, earthworms and leeches. Thus, phylogenomic analyses led to the resurrection of two traditional taxa albeit with somewhat different taxon compositions that, for a long time, were not thought to represent monophyletic groups. In addition, some taxa that were once regarded to represent separate phyla turned out to be nothing else but true Annelida, although being morphologically highly derived especially with respect to one of the so-called key characters, segmentation. These taxa are Sipuncula, Myzostoma, Pogonophora, and Echiura, which are now placed in different positions in the phylogenetic tree of Annelida. This fact impressively demonstrates the adaptive capacity and potential of the annelid bauplan. It is hoped that these former phyla will be reduced in rank to the family level; this already happened to Pogonophora, which are now known as Siboglinidae, and the next candidate may be Echiura, which in the future may be known simply as Echiuridae, or for priority reasons, Thalassematidae.

The vast majority of polychaete species is marine; here, they are dominant members of the epi- and endobenthos but there are also a few holopelagic species. Polychaetes comprise one of the most important groups of invertebrates in the marine food web, where they can be found in almost every habitat, often in high abundance. In addition, a few polychaete species managed to colonize even freshwater and terrestrial realms. Moreover, certain polychaetes occur in comparatively extreme environments—from hydrothermal vents at the ocean floor spreading centers to terrestrial ground water. Most polychaete species are microphagous or predatory but a number of species are symbionts or commensals. In contrast, the mainly terrestrial forms or clitellate oligochaetes are structurally more uniform but also have representatives in limnetic and marine habitats. Nevertheless, oligochaete Clitellata is a comparatively speciose taxon and many species are extraordinarily important members in terrestrial decomposer communities often occurring in high abundances. Surprisingly enough, one group of these oligochaetes is closely related to parasitic or carnivorous forms, the leeches. With global human activities and climate change, the distribution patterns of many species have been subjected to dramatic changes; as a consequence, certain introduced species turned out to become pests with often fatal effects for the original ecosystems.

The Annelid volume of the first edition of the *Handbook of Zoology* appeared in the years between 1928 and 1934, edited by W. Kükenthal and T. Krumbach. In particular, the anatomical part still serves as a valuable resource of knowledge. However, since then, our knowledge on annelids has broadly increased. The amount of information on annelids has not only expanded in the number of investigated and described as well as revised taxa but the details of observations, quality of data, and numbers

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of different approaches have increased. Moreover, in morphological and taxonomic research, new methods have become available such as electron microscopy and confocal laser scanning microscopy as well as molecular tools that currently allow us to sequence and analyze whole genomes. Although several reviews on annelids have been published, they usually cover only special topics in this group of invertebrates. Therefore, around the year 2010, the idea was born that a new edition of this very successful work would be urgently needed. Very soon thereafter, it turned out to be impossible to write a handbook in its strict sense treating morphology, anatomy, reproduction, development, ecology, phylogeny, and taxonomy on this group of animals in a single volume. Now, more than ever, such a task could not be achieved by a single person or by just a few authorities, and so we began looking for authors who could contribute to such a big effort. Unfortunately, we had to learn that for many annelid groups, specialists did not exist in the scientific zoological community or were not available for various reasons. Therefore, it took much longer than originally planned to compile the manuscripts and despite our efforts, there will remain a few gaps of missing chapters. This is the reason why currently only the polychaetes will be treated in the handbook. Because all the authors have many other duties and the writing of handbook chapters is rather time-consuming, it took some time to compile the manuscripts from our authors. It was a great advantage that each chapter ready for publication was published electronically in *Zoology Online* so that the chapters were available for the scientific community quite soon after acceptance. All contributions were peer-reviewed and revised prior to publication.

We were very happy and proud that it was possible to publish the first volume on annelids at the beginning of 2019 and now, within a comparatively short time after this date, the second volume appears in the same year. In the meantime, the Annelida series in the *Handbook of Zoology* will comprise four volumes. Because we try to keep as up-to-date as possible with scientific progress, we roughly follow the new phylogeny in the arrangement of the taxa treated in the various chapters, each of which is generally devoted to a single family. We are well aware of the fact that such a phylogeny is nothing else but a hypothesis which, with our current knowledge, best explains the phylogeny or evolution of a certain group. Therefore, it cannot be excluded that this system would need to be revised somehow in the future resulting in a different order of taxa. Moreover, there are more than 100 families of annelids and the systematic position has not been solved for every taxon and there are still many open questions in their relationships. Therefore, some taxa may now seem to be in a position that is predisposed to changes; however, this does not interfere with the information contained in those chapters. Furthermore, because there are still several aspects of annelid phylogeny under discussion, not all of our colleagues and authors who contributed to this handbook accept this new phylogeny completely.

This second volume covers the second part of Sedentaria comprising the clades Sabellida/Spionida and Opheliida/Capitellida. The latter also includes Echiura, a taxon that was among the first of the former annelid-like phyla to group constantly within the sedentary polychaetes in molecular phylogenetic analyses. Unfortunately, we still have a few gaps, which means a few families are missing, and it is hoped that we can add them in the forthcoming volume. Accordingly, the third volume will be devoted to the remaining Sedentaria with the exception of Clitellata and the first part of Errantia, whereas the final volume will treat the rest of Errantia.

At this point, we would like to thank all the authors that contributed to this volume of the *Handbook of Zoology*; they have done an excellent job. The work of the various reviewers is gratefully acknowledged; reviewing scientific manuscripts always takes a considerable amount of working time, especially because some chapters on larger groups are voluminous. Nonetheless, their helpful suggestions for improvements helped in keeping the scientific standards as high as possible. Last but not least, we thank the lectors and employees of our publisher, De Gruyter, for their endless help and fruitful discussions during the publishing process.

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7.4 Sedentaria: Sabellida/Spionida

7.4.1 Spionidae Grube, 1850

Introduction

The Spionidae represent one of the largest and most common polychaete families in marine benthic invertebrate communities; it currently includes approximately 590 species grouped into 38 genera. They are readily recognized by their general body shape, especially the anterior end, which carries a pair of long prehensile palps; the posterior extension of the prostomium, which is termed the caruncle; the form of the parapodia, which often have foliose postchaetal lamellae; dorsally flattened branchiae; and the presence of specialized chaetae including neuropodial and sometimes notopodial hooks, which are typically hooded. However, there is no single synapomorphy that distinguishes the Spionidae; instead, a suite of characters, some homoplasic, are used together to define the family.

The Spionidae and five other morphologically similar family-level taxa have typically been grouped into the order Spionida (Blake 1996; Rouse and Fauchald 1997; Rouse and Pleijel 2001, 2006). Currently, these additional families include the Poecilochaetidae, Trochochaetidae, Uncispionidae, Apistobranchidae, and Longosomatidae (genus *Heterospio*). The Poecilochaetidae, Trochochaetidae, and Uncispionidae are sister taxa to Spionidae and are treated in separate chapters in this handbook (Blake and Maciolek 2019a,b,c). Despite the presence of paired palps or tentacles, the last two families are not closely allied with the Spionidae (Fauchald and Rouse 1997) and are also treated separately (see Blake and Petti 2019 for Apistobranchidae). The genus *Heterospio* (Longosomatidae) is treated with the cirratuliform polychaetes (Blake and Maciolek 2019d).

Spionids occur in a wide variety of habitats from the intertidal to the deep sea, sometimes forming dense benthic assemblages. Individuals may extend their palps from burrows or tubes to filter particles from the water; in other situations, the worms are surface deposit feeders and use their palps to sweep the sediment surface. Some spionids, such as *Polydora* and related genera, bore into calcareous substrates and are sometimes considered pests by the shellfish industry. Other polydorids are known to form tubes within or on sponges. A few species are opportunistic, occupying environments that are disturbed or organically enriched; such species have life history patterns that allow them to populate available areas rapidly. Details and references to these activities are provided in the Biology sections.

Because so many spionids occur in shallow waters and are readily accessible for collection and study, the literature concerning their morphology, biology, ecology, and systematics is extensive. Several articles have treated the reproduction and larval development of multiple species (Hannerz 1956; Blake 1969, 2006; Blake and Arnofsky 1999) and elucidated the different types of gametes, spawning patterns, larval life, and larval morphology found in this family. Reproductive and larval data have recently been incorporated into phylogenetic analyses (Blake and Arnofsky 1999).

In the sections that follow, we describe the morphology of adult and larval spionids, their biology and behavior, phylogenetic relationships, taxonomy, and current classification. The majority of illustrations have been taken from the works of three of the chapter authors and, where possible, our original plates or photographs have been used and reimaged, modified, or updated to better illustrate the topics in a manner different from that originally intended. Numerous new, original figures have also been incorporated. Every effort has been made to include abbreviations on the figures to identify key morphology. We expect that this chapter will serve to introduce new students of polychaetes to this large and interesting family.

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Morphology

External morphology

Body shape. The bodies of spionids are elongate and subcylindrical in cross-section. Although lacking any distinctive division into abdomen and thorax, they are divided as in other types of polychaetes into (1) a presegmental region consisting of the prostomium and peristomium, (2) a long segmental region, and (3) a postsegmental region consisting of the pygidium and a growth zone that produces new segments. Anterior segments are usually widest, with the body tapering posteriorly to a pygidium that consists of lobes, cirri, or discs (Figs. 7.4.1.1 B; 7.4.1.2 B). The anterior end bears a pair of long prehensile palps (Figs. 7.4.1.1 A–C, F–H; 7.4.1.2 A, B). Segments are numerous, short, and similar; the fifth segment is modified in some genera (e.g., *Dipolydora* and *Polydora*; Fig. 7.4.1.2 B). Branchiae are present on all genera (Fig. 7.4.1.1 B, F, G) except *Amphipolydora*, *Glyphochaeta*, and *Spiophanes* (Fig. 7.4.1.1 A)

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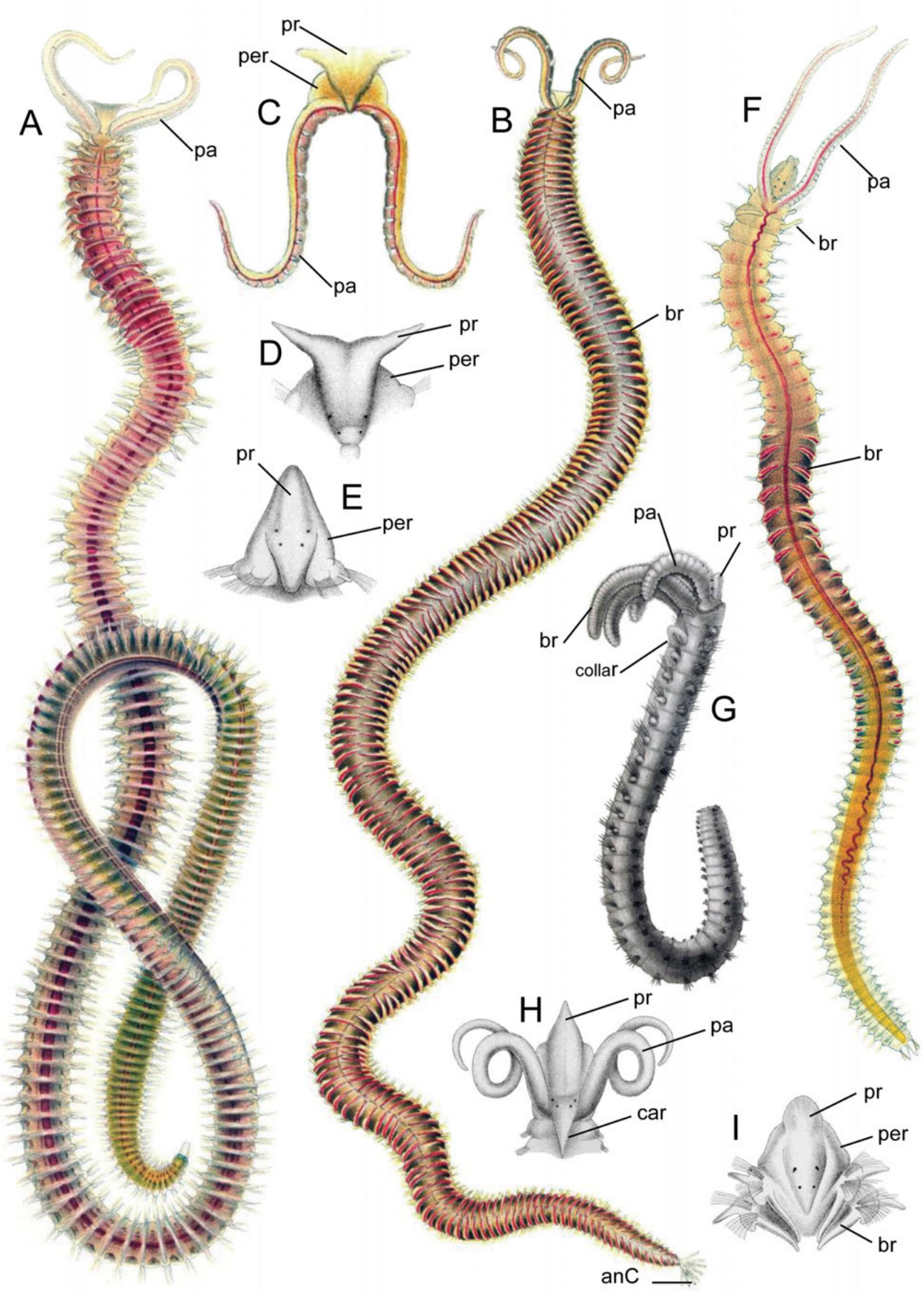
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and, when present, are limited to a few anterior chaetigers (Fig. 7.4.1.1 G), middle segments (Fig. 7.4.1.1 F), or continues for numerous segments (Figs. 7.4.1.1 B; 7.4.1.2 A, B) but are usually absent from far posterior segments. Dorsal membranous transverse crests are present on some species (Fig. 7.4.1.2 F). Transverse and/or longitudinal ciliary bands are usually present on some body segments and often form distinctive patterns (Fig. 7.4.1.3 C, G, I, J). Some genera have rows of pits or glands, usually on the venter (Fig. 7.4.1.3 H).

Spionids generally have relatively narrow, elongate bodies ranging from 8 to 20 mm long and 0.5 to 1.0 mm wide, with 50 to 150 chaetigers; however, as noted subsequently, size differences can be extreme. *Polydorella kamakamai* is only 1.3 mm long and 0.3 mm wide with 14 chaetigers (Williams 2004), whereas the largest spionid recorded seems to be *Lindaspio southwardorum* from hydrothermal vents on the Juan de Fuca Ridge with the holotype 15.9 cm long, and 7 mm wide for 304 chaetigers; fragments of an even larger specimen were observed in the same collection (Blake and Maciolek 1992). *Spio aequalis* from New Zealand is reported to be approximately 15 cm long and 7 mm wide, only slightly smaller than *L. southwardorum* (Read 1999). Some species of *Scolelepis* such as *S. foliosus* can also be in the 14 to 15 cm range. *Dipolydora concharum* is also large, up to 14.0 cm long with 300 chaetigers (Blake 1971); however, this species is a shell borer and its burrows are curved and twisted, making extraction of complete specimens and measurements difficult.

Spionid bodies are typically widest anteriorly due to well-developed parapodia, branchiae, and long capillary chaetae; posteriorly the parapodia are reduced, branchiae are shorter or absent, and capillaries are often replaced at least in part by hooks and short spines.

Color. The larvae and postlarvae of some spionids are often characterized by distinct melanophores or bands and spots of black pigment and these are sometimes retained or carried over to the adults. The pigment pattern of adult *Dipolydora socialis* is a good example of this, having distinct bands of melanin on the dorsal and ventral surfaces of adults that are similar to the larval pigment pattern (Blake 1969, 1971).

The bodies of adult spionids are generally tan or light brown in color when alive, with red blood visible especially in the branchiae and palps (Figs. 7.4.1.1 B, F; 7.4.1.2 A, B); preserved specimens are often tan to opaque white. Adults are generally not heavily pigmented but some species have reflective yellow or white pigment or various colors that may be in bands or patterns on the body and along the palps (Fig. 7.4.1.3 G, I); such patterns are best observed when the worm is alive because, after preservation, this pigment either disappears or appears brown or black.

External details of the integument. A general classification of annelid epidermal glands distinguishes between secretory cells loosely spread in the epidermis ("unicellular glands" *sensu* Storch 1988), and the condensed occurrence of secretory cells forming glandular fields and multicellular glands (Hausen 2005; Rößger *et al.* 2015). This classification is also applicable to secretory cells present in Spionidae. As in many polychaetes, isolated secretory cells are present in the epidermis of Spionidae (Söderström 1920; Radashevsky 2012). They are of different shapes, open externally and are present in different parts of the body, in particular on the prostomium, pygidium, parapodia, branchiae, and the venter. The function of these cells has not been demonstrated, but is usually suggested to be involved in mucus production. The occurrence of multicellular glands has been reported repeatedly. Claparède (1870) observed "poches glanduleuses" or glandular pouches in *Polydora*. Later, the presence of large multicellular glands was also confirmed for other genera, for example, *Spio*, *Microspio*, *Pygospio*, and the *Polydora* complex (Mesnil 1896; Söderström 1920; Fauvel 1927). Glandular organs discovered more recently are those associated with grooved neuropodial spines in *Glyphochaeta* (Bick 2005a) and the large glandular organs present in some anterior segments of *Glandulospio* that open in the region of neuropodial chaetae (Meißner *et al.* 2014). Today, it is accepted that complex multicellular glands are rather common and diverse among Spionidae, and in particular among the Spioninae, and their comparison requires the consideration of all available information (Meißner *et al.* 2012; Rößger *et al.* 2015). However, except for the parapodial glandular organs of *Spiophanes* (Meißner *et al.* 2012) and the ventral epidermal glands of *Spio* and *Microspio* (Rößger *et al.* 2015), multicellular glands of Spionidae have not been studied using the techniques of modern histology and complementary anatomical data are lacking. Based on current knowledge, the

◂ **Fig. 7.4.1.1**: Examples of Spionidae, entire worms and prechaetiger morphology. A, *Spiophanes bombyx*, entire worm, dorsal view; B, *Malacoceros vulgaris*, entire worm, dorsal view; C, same, anterior end, dorsal view; D. *Malacoceros fuliginosus*, anterior, dorsal view; E, *Aonides oxycephala*, anterior end, dorsal view; F, *Pygospio elegans*, entire worm, dorsal view; G, *Streblospio shrubsolii*, entire worm, right lateral view; H, *Scolelepis squamata*, anterior end, dorsal view; I, *Spio* sp. (as *S. filicornis*), anterior end, dorsal view. A–F, H, I, after McIntosh (1915); G, after Buchanan (1890). Abbreviations: anC, anal cirrus; br, branchiae; car, caruncle; pa, palp; per, peristomium; pr, prostomium.

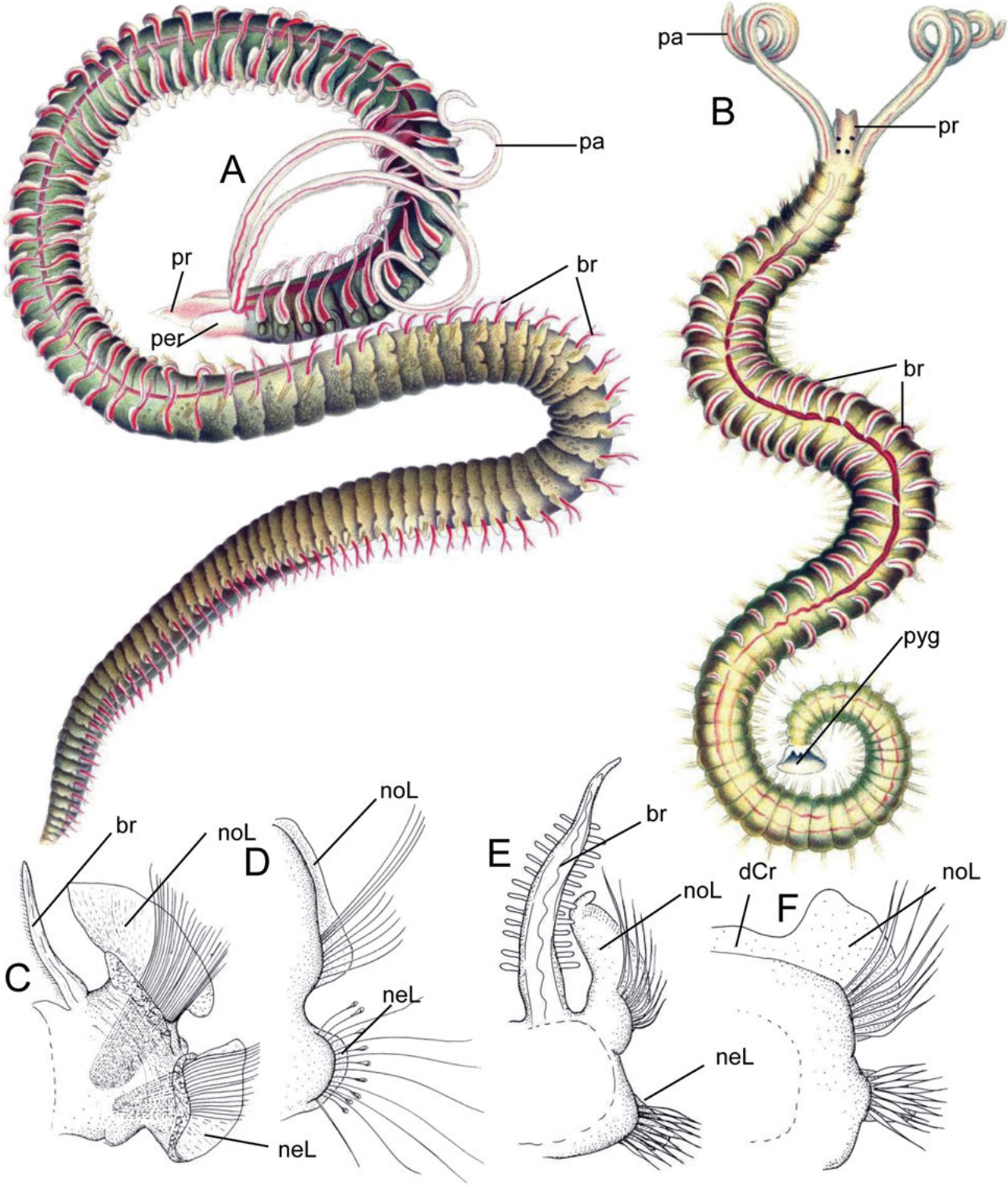


Fig. 7.4.1.2: Examples of Spionidae, entire worms and parapodia. A, *Scolelepis squamata*; B, *Polydora ciliata*; C, *Laonice antarcticae*, chaetiger 5, anterior view; D, *Prionospio fauchaldi*, chaetiger 21, anterior view; E–F, *Prionospio orensanzi*: E, chaetiger 5, anterior view; F, chaetiger 7, anterior view. A, B, after McIntosh (1915); C, E, F, after Blake (1983); D, after Maciolek (1985). Abbreviations: br, branchiae; dCr, dorsal crest; neL, neuropodial lamella; noL, notopodial lamella; pa, palp; per, peristomium; pr, prostomium; pyg, pygidium.

ventral epidermal glands of *Spio* and *Microspio* stand out by being intraepidermal, meaning they are strictly limited to the epidermal layer and by their position away from the parapodia, whereas other multicellular epidermal glands of Spionidae are located subepidermally, and are usually associated with the parapodia.

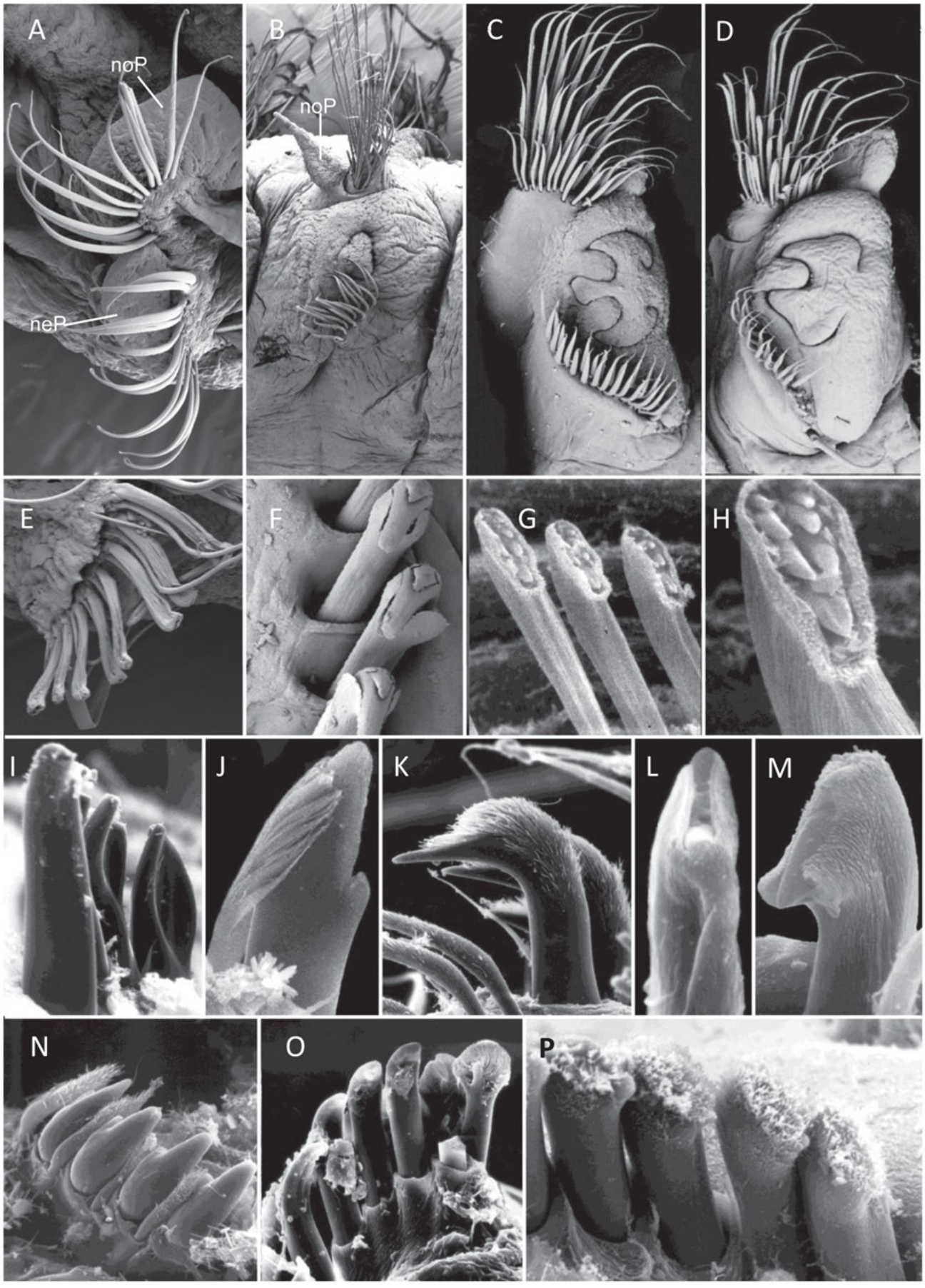
Glandular pouches are comprised of epidermal glandular cells grouped together in a single envelope, and hence are multicellular epidermal glands. Individual cells are grouped into an array of cells with large and rounded expanded ends that then taper to a thin point where several arise (Fig. 7.4.1.6 C). The entire structure containing the individual cells is the glandular pouch. The term "glandular pouch" or segmental mucus gland is commonly but not exclusively used for glands present in the *Polydora* complex (e.g., Dorsett 1961a,b). These glands secrete acid mucopolysaccharides that are believed to play a role in tube building and boring into calcareous structures. Much of the early literature associated with boring was reviewed by Blake and Evans (1973). Details of the potential role of these glands in boring are presented in the tube-building section later in this chapter.

The parapodial glandular organs (PGO) present in all *Spiophanes* are an excellent example of highly derived compound multicellular glands. They were first described by Claparède (1870) as "organes trop exceptionnels" in his original description of *Spiophanes bombyx*. These organs are of conspicuous size, and they bulge deeply below the epidermis invading the coelomic sac. The PGOs are directly associated with the parapodia of the middle body region, comprising chaetigers 5 to 14 or 5 to 15. Large PGOs, usually present in chaetigers 5 to 7 (rarely 5–8), display different species-specific types of openings termed "chaetal spreaders" (Fig. 7.4.1.4 C, D) whereas small PGOs, present from chaetiger 9, always open in a simple vertical slit (Meißner and Hutchings 2003; Meißner 2005; Radashevsky 2012). Meißner *et al*. (2012) conducted a detailed study regarding the functional anatomy and ultrastructure of PGOs in *Spiophanes* together with a three-dimensional reconstruction based on semi-thin section series. The authors distinguished three main complexes: (1) a glandular sac with several distinct epithelia of secretory cells and secretory cell complexes and a reservoir filled with fibrous material, (2) a gland-associated chaetal complex, and (3) a bilayered musculature surrounding the gland. It was determined that both large and small PGOs have the same general composition, but that small PGOs lack the "chaetal spreader", which is part of the gland-associated chaetal complex in large PGOs. Very fine gland-associated chaetae (called "bacillary chaetae" in the taxonomic literature) emerge from inside the PGOs guided by the "chaetal spreader". It was documented that these chaetae are typical annelid chaetae formed by chaetoblasts and follicle cells (Meißner *et al*. 2012). Among the different cell types involved in secretory activity, guidance of the gland-associated chaetae, and final expulsion of the fibrous secretion in PGOs, the secretory cells with cup-shaped microvilli located in the proximal glandular complex are the most interesting from a phylogenetic perspective (for additional information and an extended discussion on this subject, see, e.g., Southward *et al*. 2005; Meißner *et al*. 2012; Guggolz *et al*. 2015; Müller *et al*. 2015). It has been shown that β-chitin is produced by the secretory cells with cup-shaped microvilli in both the pyriform glands of Siboglinidae and the PGOs of *Spiophanes*, and is used for tube-building (Shillito *et al*. 1995; Guggolz *et al*. 2015).

The term "ventral pores", sometimes used in the literature, refers to the presence of small openings on the venter on several anterior and middle segments in *Spio* and *Microspio*. They are easily detected in well-preserved specimens using scanning electron microscope (SEM) or in live specimens, and also become apparent after methyl green staining as white dots against the surrounding blue-stained tissue or in a blue ring-shaped pattern (Fig. 7.4.1.3 H). The ventral pores are openings of ventral epidermal glands, which are supposedly involved in tube construction. The ventral epidermal glands were studied in detail and three-dimensionally reconstructed based on semi-thin section series by Rößger *et al*. (2015). Acinar and tubular ventral epidermal glands were found and the authors suggested that the acinar type stains in a ring-shaped pattern, whereas the tubular type becomes apparent as a white dot. This hypothesis still needs support from additional data. Nonetheless, information on the types and distribution patterns of the ventral epidermal glands along the body is of taxonomic significance at the species level (see Maciolek 1990; Bick and Meißner 2011; Meißner *et al*. 2011; Meißner and Götting 2015).

Rows of dorsal holes or openings have been observed on the branchiate region of *Aonidella* cf. *dayi* (Meißner *et al*. 2014). These are only observed with SEM and their function is unknown. Some, however, are observed with cilia protruding from their openings, suggesting a sensory function (see Fig. 7.4.1.13 C, D in the taxonomic section).

Bacillary glands are elongate striated cells that occur on the dorsum and on the pygidium of some spionid larvae (Hannerz 1956) and adults. The tips of these cells protrude through the cuticle and are collectively called bacillary glands. Groups of bacillary glands occur on the dorsal surface of some segments in species of *Amphipolydora*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(see Fig. 7.4.1.31 A in the taxonomic section; Blake 1983; Paterson and Gibson 2003).

Head. The prostomium is longer than wide and overlies the peristomium; it is narrow and more or less wedge-shaped, with an anterior end that may be entire (Figs. 7.4.1.1 E, I; 7.4.1.3 D), incised, or bilobed (Fig. 7.4.1.2 B); rounded (Figs. 7.4.1.1 I; 7.4.1.3 J), pointed (Figs. 7.4.1.1 H; 7.4.1.2 A), or expanded laterally into prominent frontal horns (Figs. 7.4.1.1 A, B; 7.4.1.3 A–D). It is typically widest in the middle where eyespots are present and narrows as it continues posteriorly as a caruncle over one or more anterior chaetigers (Fig. 7.4.1.3 D). The caruncle may bear an occipital antenna (sometimes called a nuchal tentacle), which is usually a single short digitiform projection that appears at about the level of the palps. The presence or absence of an occipital antenna is an important taxonomic character. *Polydora bioccipitalis* has two such antennae on the caruncle (Blake and Woodwick 1972). In *Streblospio*, a similar structure is separate from the prostomium but it is uncertain whether this is homologous to the antenna found in other spionids (Dauer 1984; Dauer *et al*. 2003).

Prostomial eyes may be present (Fig. 7.4.1.1 E, F, H, I) or absent. These may be black or red. Comparatively small they are usually refered to as eyespots. In spionid larvae, there are typically one or two pairs of larger lateral eyespots and a single pair of medial eyespots. These usually persist in adults in more or less the same arrangement, but are dependent on the final form of the prostomium. In some instances, larval eyespots merge into a single one in adults; in other cases, additional eyespots develop in adults. Fixation may alter the color of eyespots from black to red as they fade in preservative. The eyespots have been described in *Scolelepis squamata* as consisting of only two cells each, a pigment cell and rhabdomeric receptor cell (Rhode 1991).

Prostomial papillae have been described in species of *Paraprionospio* (Ehlers 1901; Dauer 1985), *Marenzelleria* (Verrill 1873; Dauer 1997), *Prionospio* (Maciolek 1985, as prostomial "peaks"), and *Streblospio* (Dauer *et al*. 2003). These papillae are eversible and may be sensory in nature with a role in selecting or rejecting sediment particles (Dauer 1997; Dauer *et al*. 2003). They may be randomly scattered over the prostomial surface or confined to certain locations, and they may be smooth or irregular in appearance. Although considered to be of taxonomic value, the eversible nature of the structure results in some difficulty in ascertaining patterns after fixation.

Nuchal cilia are developed to varying degrees lateral to the caruncle. These first appear in larval stages as rounded to oval-shaped ciliary patches. In adults, they appear as paired longitudinal bands of cilia on either side of the caruncle, but also appear in spionids such as *Spiophanes* that lack a caruncle (Fig. 7.4.1.3 B). Nuchal organs vary considerably in size and appearance. They may be short, extending only as far as the end of the caruncle, or may continue posteriorly along the body for many segments. These elongate nuchal organs may occur as a continuous pair along the dorsum or may be interrupted segmentally; they may be straight, curved, or diagonal. Their ultrastructure has been investigated in *Pygospio elegans* by Schlötzer-Schrehardt (1986, 1987) and in a number of additional species by Jelsing (2002, 2003) and Jelsing and Eibye-Jacobsen (2010). The segmental continuation of the nuchal ciliation is often accompanied by transverse ciliary bands (Fig. 7.4.1.3 C, G, I, J), which are likely derived from the larval nototrochs. In addition, other ciliary bands may form longitudinal groups along the body (Fig. 7.4.1.3 C, G, I). These various types of segmental or metameric ciliary bands were termed "dorsale Sinnesorgane" by Söderström (1920). The arrangement and organization of these dorsal sense organs with or without accompanying nuchal cilia are highly diagnostic and important taxonomic characters.

The peristomium is achaetous and surrounds the mouth ventrally and the prostomium dorsally, and often forms a pair of lateral lobes that in some species of *Prionospio*, *Paraprionospio*, and *Streblospio* are enlarged to form erect, membranous wings. In *Streblospio*, the peristomium extends anteroventrally to encompass the mouth and laterally forms a transverse hood that surrounds the bases of the palps dorsally (Dauer 1984; Dauer *et al*. 2003); in *Paraprionospio*, this hood continues dorsally, forming wings that encompass and cover part of the prostomium.

◂ **Fig. 7.4.1.3**: Spionidae parapodia and chaetae. A, *Paraprionospio* sp. (Gulf of Mexico), chaetiger 4, parapodium, anterior view; B, *Spiophanes* cf. *bombyx* (Massachusetts Bay), chaetiger 7, right lateral view; C, *Spiophanes duplex*, chaetal spreader; D, *Spiophanes berkeleyorum*, chaetal spreader; E, *Paraprionospio* sp. (Gulf of Mexico), midbody neuropodial hooded hooks and capillaries; F, *Spiophanes* cf. *bombyx* (Massachusetts Bay), neuropodial hooded hooks; G, H, *Streblospio benedicti* (California), neuropodial hooded hooks; I, *Dipolydora commensalis*, major spines from chaetiger 5; J, *Polydora cornuta*, major spine and companion chaeta from chaetiger 5; K, *Dipolydora blakei*, major spine from chaetiger 5; L, *Dipolydora commensalis*, neuropodial hooded hook; M, *Tripolydora spinosa*, neuropodial hooded hook; N, *Dipolydora giardi*, major spines and companion chaetae from chaetiger 5; O, *Boccardia berkeleyorum*, major spines from chaetiger 5; P, *Dipolydora quadrilobata*, major spines from chaetiger 5. A, B, E–J, L, O, P, originals; C, D, after Meißner and Hutchings (2003); K, after Maciolek (1984a); M, after Blake and Woodwick (1981); N, after Blake (1981). Abbreviations: neP, neuropodium; noP, notopodium.

In both *Paraprionospio* and *Streblospio*, the peristomium and first segment are entirely fused ventrolaterally. This segment has chaetae that are lost during metamorphosis from the larval form to the adult. In contrast, adults of *Prionospio* retain chaetae on segment 1, which is not fused or only partially fused to the peristomium.

The paired palps arise dorsolaterally at the posterior end of the peristomium in all spionids (Figs. 7.4.1.1 A–C, F, G, H; 7.4.1.2 A, B; 7.4.1.3 G, I). The palps are elongate prehensile organs that are actively used to collect particles from either the water column or sediment surface; they are used in tube construction and/or feeding (Dorsett 1961a). A ciliated ventral groove acts as a channel to carry particles to the mouth where they are either ingested or manipulated and placed on tubes. Species of *Scolelepis* lack grooves on their palps and captured particles are carried to the everted proboscis by contraction of the palp into a coil (Dauer 1983).

Polydora commensalis lives in shells occupied by hermit crabs and its palps appear unusually short compared with other spionids. The worms extend their palps to retrieve food particles brought in by the crab. Dualan and Williams (2011) determined that palp length was negatively influenced by the hermit crab host, which can cut or damage them during its movements. Worms experimentally removed from the shells developed palps that were of a length typical for other species of *Polydora*.

Lindsay and Woodin (1992) investigated the effect of palp loss on feeding behavior and exposure to predation for two infaunal species: *Rhynchospio glutaea* and *Pseudopolydora kempi*, both of which extend their palps from tubes to feed. Additionally, *R. glutaea* extends several anterior segments during feeding whereas *P. kempi* does not. Therefore, loss of feeding palps resulted in a greater exposure to predation for *R. glutaea* than *P. kempi*. Palp loss also reduces the potential area that the worms can access during feeding because the feeding area is a circle around the tube opening. Without palps, this area was reduced by 90% for *R. glutaea* and by nearly 100% in *P. kempi* (Lindsay and Woodin 1992).

Worsaae (2001, 2003) and Williams (2007) suggested that palp morphology was of taxonomic significance within the genera *Dipolydora, Polydora, Prionospio*, and *Scolelepis*. The morphology of palp cilia and their arrangement are complex and differ among spionid genera, but are generally similar among species of individual genera (Dauer 1987; Worsaae 2001). According to Worsaae (2003: 259), 13 palp characters are present in 10 genera of Spionidae: (1) motile frontal cilia, (2) nonmotile cilia, (3) basal transverse cilia, (4) lateral cilia, (5) latero-frontal cirri, (6) randomly scattered motile cirri, (7) randomly scattered nonmotile cilia, (8) nonmotile cirri on papillae, (9) ciliary sensory organs, (10) mucus glands, (11) glandular holes, (12) single transverse ciliary bandlets, and (13) transverse ciliary bands. The two latter characters were identified by Worsaae (2003) for two species of *Prionospio* that, unlike related species, exhibit considerable morphological differences in palp morphology. Williams (2007) identified four distinct palp ciliation patterns in species of *Scolelepis* where palp morphology has been reported. Meißner and Götting (2015) found a notably elevated number of mucus-secreting cells compared to accompanying cilia on palps of *Scolelepis inversa*. To date, however, these diverse ciliary patterns have not been applied to phylogenetic analyses or used widely as taxonomic characters.

In *Paraprionospio*, a basal sheath surrounds the base of the paired palps (Dauer 1985). A similar sheath is present in *Scolelepis* but it is typically fused with the palp and is difficult to discern. The edge of this sheath may be papillated in some species of *Scolelepis* (Blake 1996).

Segmentation and parapodia. The parapodia of spionids are biramous and lack aciculae. Podial lobes are generally reduced but prechaetal and postchaetal lamellae may be developed to varying degrees (Figs. 7.4.1.2 C–F; 7.4.1.4 A, B); these decrease in size and complexity posteriorly. In some genera, such as *Prionospio*, transverse dorsal crests sometimes connect the parapodia (Fig. 7.4.1.2 F). Interramal membranes or pouches, also called genital pouches, may be present between successive parapodia in genera such as *Laonice, Prionospio*, and *Spiophanes*. Dorsal and ventral cirri are absent.

Prechaetal lamellae are rare in spionids, whereas postchaetal lamellae occur in all genera. These lamellae are usually best developed in anterior segments (Fig. 7.4.1.2 C, D), becoming reduced and inconspicuous posteriorly. Prechaetal notopodial lamellae in some species of *Prionospio* are merged with postchaetal lamellae to form a kind of hood from which the notochaetae emerge (Blake 1996). The shape or form of postchaetal lamellae varies, but is highly diagnostic in some genera and species. For example, in species of *Laonice* and *Prionospio*, the postchaetal lamellae are often large and foliaceous (Figs. 7.4.1.2 C–E; 7.4.1.4 A) and sometimes merge with dorsal crests to form a continuous membrane from one side to the other (Fig. 7.4.1.2 F).

Dorsal crests extend across the dorsum of some species of *Prionospio* and *Laonice* and connect with the postchaetal notopodial lamellae (Fig. 7.4.1.2 F). These crests may be large and high, appearing membranous, or may be simple low elevations. Typically, dorsal crests are highest on the segment where they first appear, becoming lower and less prominent on following segments. Ventral crests are known only for *Laubierellus* and extend from the

ventral postchaetal lamellae (Maciolek 1981b; Erickson and Wilson 2018). The presence and form of these crests are of taxonomic significance. Membranous transverse dorsal ridges occur on chaetiger 1 in *Paraprionospio*, on chaetiger 2 in *Streblospio*, and on middle body chaetigers in some species of *Spiophanes* (Blake 1996).

Ventrolateral interparapodial pouches are thin membranes that occur between adjacent neuropodia on either side of the body; these form pockets that open dorsally. They are best known in species of *Laonice*, but also occur in certain species of *Prionospio* (e.g., *P. ehlersi*), *Aonidella*, and *Spiophanes*. The first presence of these pouches and their extent along the body are taxonomic characters. There are reports that these pouches, often called "genital pouches", have a role in reproduction. Much of the information regarding this subject is anecdotal and not well supported; further study is needed to clarify their role. Similarly, dorsal interparapodial membranes that form pockets that open ventrally have been reported for *Prionospio steenstrupi* (Sigvaldadóttir and Mackie 1993) and are known to occur in at least one other undescribed species of *Prionospio* (Maciolek unpublished). Sigvaldadóttir and Mackie (1993) note that the dorsal folds in *P. steenstrupi* are not as well developed as the ventrolateral pouches of other species; their function is also unknown.

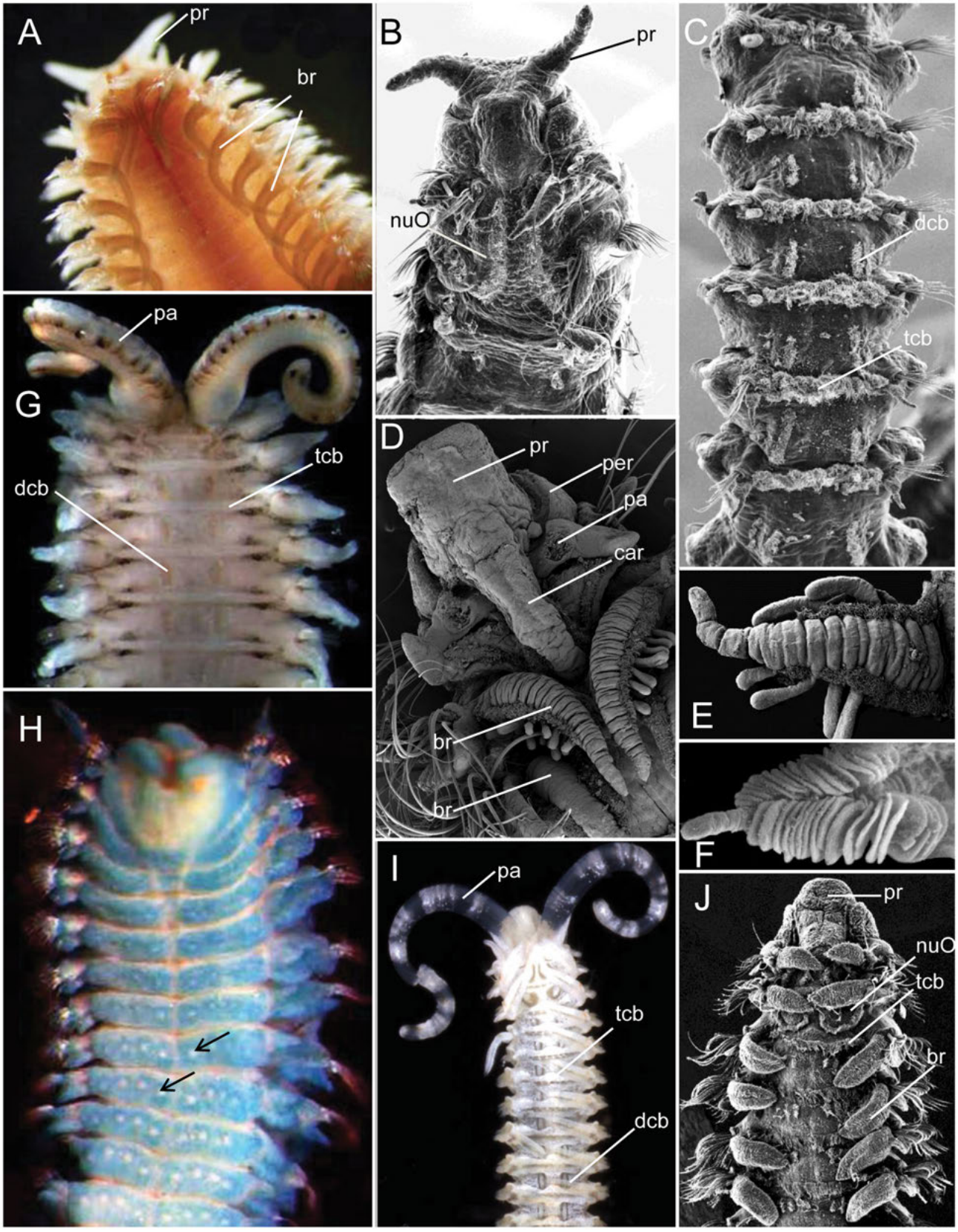
Chaetae. Spionid chaetae are all simple and include smooth and winged (limbate) capillaries, hooded and nonhooded hooks with one to several teeth, and curved inferior sabre chaetae in some neuropodia. Modified spines of various types, some with a bristled apex, occur in the fifth chaetiger of *Polydora* and related genera (Fig. 7.4.1.4 I–K, N–P). A recurved crooklike chaeta occurs in the first chaetiger of *Spiophanes* species; modified posterior notopodial spines, needles, or recurved spines occur in species of *Microspio, Polydora,* and *Boccardia*. Unusual spoonlike neurochaetae occur in some chaetigers instead of hooded hooks in species of *Pygospio*. The distribution and morphology of these numerous chaetal types are of major taxonomic significance for genera and species of Spionidae and will be discussed in the taxonomic section.

The arrangement of noto- and neurochaetae in spionid parapodia was originally described by Mesnil (1896) and updated and refined by Radashevsky and Fauchald (2000) and Radashevsky (2012). The basic patterns are (1) anterior notochaetae include two rows of capillaries and a dorsal superior tuft; (2) anterior neurochaetae include two rows of capillaries and a ventral tuft; (3) posterior notochaetae are reduced in number, with rows or groups becoming indistinct; and (4) posterior neurochaetae include the replacement of capillaries by hooded hooks and the presence or absence of an inferior sabre chaeta.

Within these basic patterns are many modifications, additions, and subtractions. For example, (1) *Spiophanes* species have long, thin capillaries in anterior notopodia and crooklike spines in the neuropodia of chaetiger 1; (2) species of *Lindaspio* have groups of up to 10 large heavy spines in the notopodia of chaetigers 2 to 4; (3) acicular spines of different types occur in the posterior notopodia of several of the polydorid species and other genera; these may be rosettes of awl-shaped spines, bundles of needles, or strongly curved boat hooks; (4) all of the polydorids have a modified chaetiger 5 typically with one or two rows of modified chaetae of different types; a dorsal tuft of capillaries is usually present as well as a tuft of ventral neurochaetae. The modified spines of polydorids include curved falcate spines with or without apical teeth or flanges (Fig. 7.4.1.4 I, J, N). Some spines have an expanded apex covered with a cloak of fine bristles (Fig. 7.4.1.4 K, O, P).

Hooded hooks or crotchets. The presence of hooded hooks in the neuropodia is a characteristic feature of Spionidae. Rarely, hooks are also present in the notopodia, but never in notopodia only. The number of teeth or dentition of the hooks is an important taxonomic character. There is typically a large main fang surmounted by one, two, three, or more apical teeth (Fig. 7.4.1.4 E–H, L, M). Apical teeth are typically in sequential pairs that, when numerous, are difficult to count, as in the multidentate hooks of species of *Prionospio*. Hooks of *Spiophanes* are usually quadridentate with one single apical tooth surmounted by two smaller teeth (Fig. 7.4.1.4 F). Unhooded neuropodial hooks of *Pygospiopsis* species are curved spines with or without a subapical tooth or cusp on the concave side and may have a bristled apex and no hood (Blake 1983, 1996; Blake and Maciolek 2018). The hood that covers most spionid hooks is thin and transparent in light microscopy and is termed an outer hood; the dentition of the teeth is readily visible. With SEM, apart from a narrow opening in the hood from which the main fang projects, the smaller apical teeth are often not fully visible (Fig. 7.4.1.4 E, L). Species of *Prionospio* and *Paraprionospio* have a separate secondary hood that covers the subdistal part of the hook. Secondary hoods also occur in some species of *Spiophanes*; many species of *Spiophanes* have half-hoods that extend from the tip of the main fang to the shaft (Fig. 7.4.1.4 F), but do not cover the apex of the chaeta and some species lack a hood entirely. *P. elegans* has a unique hooded hook with a spoonlike distal end in addition to more typical bidentate hooks (Light 1978).

Branchiae. Dorsal paired branchiae occur along the body of most spionids (Fig. 7.4.1.1 B, F); these are either entirely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separate from the postchaetal lamellae (Figs. 7.4.1.2 C, E; 7.4.1.3 D, J), or fused with them to varying degrees. Ventral branchiae that originate below the neuropodia as well as dorsal branchiae have been reported for *Lindaspio* (Blake and Maciolek 1992). A separate kind of branchia, often called a lateral or accessory branchia, is palmately branched and arises directly from the body wall posterior to the dorsal lamellae in species of *Dispio*.

Dorsal branchiae of most spionids are typically smooth, ciliated, and either flat and straplike or thin and tapered. Those without lateral appendages are considered to be simple branchiae and are termed apinnate (Figs. 7.4.1.2 C; 7.4.1.3 A, J). When lateral pinnules are present, the branchiae are termed pinnate; the pinnules may be either digitiform, which are cylindrical (Figs. 7.4.1.2 E; 7.4.1.3 D, E), or platelike, which are flattened and stacked (Fig. 7.4.1.3 F). Pinnate branchiae are characteristic of some species of *Prionospio*; platelike branchiae occur in species of *Apoprionospio* and *Paraprionospio*. In some species of *Prionospio*, both apinnate and pinnate branchiae occur together in various combinations that are of taxonomic significance. In *Apoprionospio*, anterior apinnate branchiae are followed by a pair of platelike branchiae, whereas *Paraprionospio* species have only platelike branchiae. An additional form of branchia was described by Maciolek (1985) for two species of deep-sea *Prionospio*. These branchiae were neither smooth nor pinnate, so were best described as "wrinkled;" however, the taxonomic value of this form is unclear.

Dorsal branchiae are relatively flat structures typically oriented parallel with the dorsal surface and directed at the branchia on the opposite side (Figs. 7.4.1.1 B, F; 7.4.1.2 A, B; 7.4.1.3 A, I, J). In some instances where branchiae are long, a pair will meet or overlap at the dorsal midline. In several genera, such as *Malacoceros* and *Scolelepis*, the branchiae are fused to the dorsal postchaetal lamellae to varying degrees. The two small pairs of branchiae on *Aurospio dibranchiata* are fused basally to the dorsal lamellae of chaetigers 3 to 4 (Maciolek 1981a). In contrast, the branchiae of *Prionospio* species are generally free from the dorsal lamellae. This distinction has not been recognized by recent authors and a few species of *Prionospio* may have been erroneously referred to *Aurospio* (Sigvaldadóttir 2002; Mincks *et al*. 2009; Patterson *et al*. 2016).

On most spionids, branchiae are added continuously along the body with growth and with the addition of new segments. In species with a fixed number of branchiae as in some species of *Prionospio*, *Laonice*, *Aurospio*, *Aonides*, and some polydorids, branchiae will be added as juveniles develop up to the point where the adult arrangement is attained. In these instances, branchiae are limited to a few anterior segments. In late planktic larvae of the polydorid genera *Boccardia* and *Boccardiella*, branchiae develop on chaetiger 7 and subsequent segments; the development of branchiae on anterior chaetigers 2 to 4 and 6 is delayed until postlarval development (Rullier 1960; Dean and Blake 1966; Woodwick 1977; Blake and Kudenov 1981). However, as part of a recent study on the development of *Boccardia berkeleyorum*, branchiae both anterior and posterior to chaetiger 5 were already developed in late planktic larvae (Blake 2017). Branchiae of *P. dubia* occur on chaetigers 2 to 3 and 7 to about chaetiger 16; branchiae of chaetigers 2 to 3 are free from the dorsal lamellae, whereas those from chaetiger 7 are basally fused to the notopodial lamellae (Blake 1983). In species of *Pygospio*, branchiae are fused to the notopodial lamellae and occur from chaetiger 10 or posterior (Fig. 7.4.1.1 F). However, males may have a separate pair of branchiae on chaetiger 2 that is not fused to dorsal lamellae (Fig. 7.4.1.1 F).

Pygidium. The pygidial segment takes on several distinctive forms in spionids, including the presence of additional accessory lobes, cirri, cushions, discs, collars, and combinations of these forms. The number and length of anal cirri are of taxonomic significance, but they are often lost or damaged in preservation. In *Prionospio* species, there are typically three anal cirri, one long and dorsal, two short and ventral. *Spiophanes* species have a pair of cirri arising from a small ventral lobe, or up to 11 cirri in dorsal or lateral position. Four anal cirri, two dorsal and two ventral, are typical for *Microspio*, *Pygospio*, and *Spio*. Species of *Aonides*, *Malacoceros*, *Marenzelleria*, and *Rhynchospio* may have anywhere from 5 to 15 or more anal cirri (Fig. 7.4.1.1 B). However, these numbers are likely age dependent, with fewer cirri in juveniles. Species of *Scolelepis* have a cushionlike pygidium with thick, fleshy, and rounded pads surrounding the anal opening.

◂ **Fig. 7.4.1.4**: Spionidae external morphology. A, *Malacoceros jennicus*, anterior end, dorsal view; B, C, *Spiophanes bombyx* (SEM): B, anterior end, dorsal view; C, middle body segments, dorsal view; D, E, *Prionospio* cf. *steenstrupi*: D, anterior end, dorsal view; E, pinnate branchia; F, *Apoprionospio pygmaea*, platelike branchia; G, *Spio filicornis*, anterior end, dorsal view; H, *Spio arndti*, anterior end, ventral view; I, J, *Spio blakei*: I, anterior end, dorsal view from life; J, anterior end, SEM. A, after Graff *et al*. (2008); B, C, after Meißner and Blank (2009); D–F, originals; G, H, after Meißner *et al*. (2011); I, J, after Meißner and Götting (2015). Abbreviations: br, branchiae; car, caruncle; dcb, dorsal ciliary band; nuO, nuchal organ; pa, palp; per, peristomium; pr, prostomium; tcb, transverse ciliary band.

The polydorids exhibit a wide range of pygidial morphologies. *Boccardiella* species have a pair of rounded lobes bearing short cirri. Some *Boccardia* species have the anus surrounded by multiple lobes. Species of *Dipolydora* and *Polydora* often have the anal opening surrounded by a thin disclike structure that is either entire with a dorsal gap (Fig. 7.4.1.2 B) or divided into three or four partitions. The shape and size of these pygidia are of taxonomic significance. Pygidial lobes may also contain large reflective bacillary glands.

Anatomy

Musculature. The musculature of Spionids as described by Buchanan (1890) for *Streblospio shrubsolii* consists of a thin circular layer that is best developed in the ventral region just over the nerve cord and can be seen in transverse thin sections (Fig. 7.4.1.5 C). Longitudinal muscles are well developed with one dorsal and two ventral bands. A delicate layer of coelomic epithelium, forming the outer wall of the coelom and consisting of a few nuclei on the extremities of the muscle fibers, occurs below and above the dorsal and ventral longitudinal muscles, respectively. Dorsoventral muscles divide the dorsal longitudinal muscles on either side, and vertically become attached close to the thickened portion of the ventral epidermis. Dorsoventral muscles divide the cavity of each of these segments more or less completely into three longitudinal chambers. In addition, there are segmental muscles along the ventral body wall on each side to the corresponding two chaetal bundles.

Digestive system. The digestive system of spionids consists of a pharynx and a simple intestinal track consisting of a short foregut or esophagus followed by a hindgut (Fig. 7.4.1.5 A). The pharynx is unarmed, and is either a soft, ciliated, or slightly eversible axial proboscis as in *Streblospio* and *Scolelepis* (Buchanan 1890; Dales 1962) or a muscular ventral pharyngeal organ with a mouth that opens into a pharynx with dorsolateral folds and muscular ventral pharyngeal organ as in *Prionospio cirrifera* (Purschke and Tzetlin 1996). Orrhage (1964) had earlier reported a simple ventral buccal organ in *Prionospio* and *Spiophanes*. The intestine is lined by ciliated columnar cells and may have lobes or folds that presumably increase surface area (Figs. 7.4.1.5 A; 7.4.1.6 B). In some species, the intestine has been found to be infested with gregarine parasites that are attached to the cellular lining (Fig. 7.4.1.6 B).

As part of a study of five spionid species, Penry and Jumars (1990) determined that they all belonged to a group of deposit feeders having simple ciliated tubular guts consisting of a short foregut and a longer hindgut. In some species of *Carazziella*, *Dipolydora*, and *Spiophanes*, there is a muscular gizzardlike structure on the posterior part of the foregut (Blake 1969, 1971, 1979a; Radashevsky 1993; Meißner 2005). In *Carazziella* species where a gizzard occurs, there are four symmetrically arranged muscles that encircle the gizzard and presumably crush or otherwise treat the incoming food particles (Fig. 7.4.1.6 E) (Blake 1979a). In *D. socialis*, there are four embedded chitinous plates, teeth, or inclusions that are associated with the muscles (Fig. 7.4.1.6 A, D) (Blake 1969, 1971) and that presumably assist in the same function. Gizzardlike structures are also present in other spionids such as *Paraprionospio* and *Spiophanes*, but these are entirely muscular (Radashevsky 2012).

Excretory system and nephridia. Both protonephridia and metanephridia are described for Spionidae (Bartolomaeus and Quast 2005). Protonephridia generally develop first and are found in the anterior chaetigers of larvae. In adults, paired metanephridia or segmental organs occur throughout the body (Figs. 7.4.1.5 A; 7.4.1.7 A–C). The metanephridial system functions both for filtration by special cells termed podocytes and in reproduction with gonoducts. A nephrostome or ciliated funnel serves as an entrance to a ciliated nephridial canal (Fig. 7.4.1.7 A) through which gametes are transported to a nephridiopore from which they are released or spawned (Söderström 1920; Rice and Reish 1976). Details of the role of nephridia in the reproduction of spionids in presented in the following section.

Blood vascular system. A closed circulatory system with dorsal and ventral vessels connected by lateral vessels with capillaries is present in most spionids. Buchanan (1890) described the anatomy and function of the circulation in *Streblospio shrubsolii*. Blood flows anteriorly in the dorsal vessel and posteriorly in the ventral vessel. The dorsal and ventral vessels connect to blood loops in the palps and branchiae where blood is oxygenated; the ventral vessel connects to sinuses that run along most of the intestine (Fig. 7.4.1.5 A). Buchanan (1890) also identified a heart body as being present in *Streblospio*; this has been confirmed by Radashevsky (2012) in the closely related *Prionospio*, but not in other genera. Blood is red in color due to the respiratory pigment erythrocruorin; however, there are no erythrocytes.

Nervous system and sensory organs. The nervous system of several spionids was well described by Orrhage (1964) and more recently reviewed by Orrhage and Müller (2005).

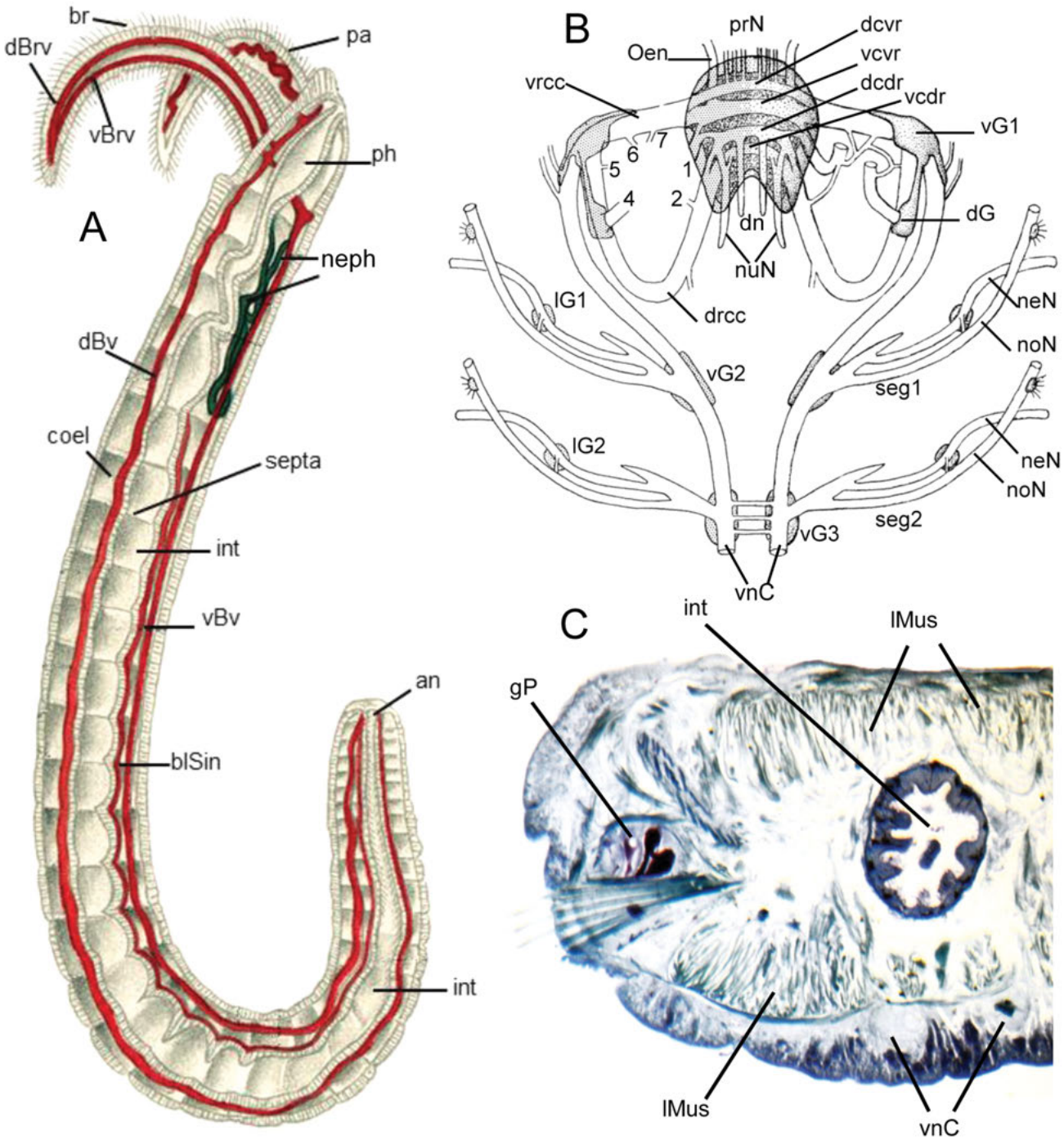


Fig. 7.4.1.5: Spionidae internal morphology. A, *Streblospio shrubsolii*, circulatory system, nephridium, intestine; B, *Scolelepis* spp., diagram of nervous system; C, *Boccardiella hamata* (California), cross-section of middle body segment with muscles, intestine, ventral nerve cord, and glandular pouch. A, after Buchanan (1890); B, modified after Orrhage (1964); C, original. Abbreviations: A, an, anus; blSin, blood sinus; br, branchia; coel, coelom; dBrv, dorsal branchial vessel; dBv, dorsal blood vessel; int, intestine; neph, nephridium; pa, palp; ph, pharynx; vBrv, ventral branchial vessel; vBv, ventral blood vessel. B, dcvr, dorsal commissure of the ventral root; dcdr, dorsal commissure of the dorsal root; dG, dorsal ganglion of dorsal nerves; dn, dorsal nerves; drcc, posterior (dorsal) root (drcc); neN, neuropodial nerves; noN, notopodial nerves; nuN, nuchal nerves; Oen, esophageal nerve; Palp nerves (numbered: 1, 2, 4, 5, 6, 7); prN, prostomial; vcdr, ventral commissure of the dorsal root; vcvr, ventral commissure of the ventral root; vnc, ventral nerve cords; vrcc, anterior (ventral) circumesophageal root. C, gP, glandular pouch; lMus, longitudinal muscles; int, intestine; vnC, ventral nerve cord.

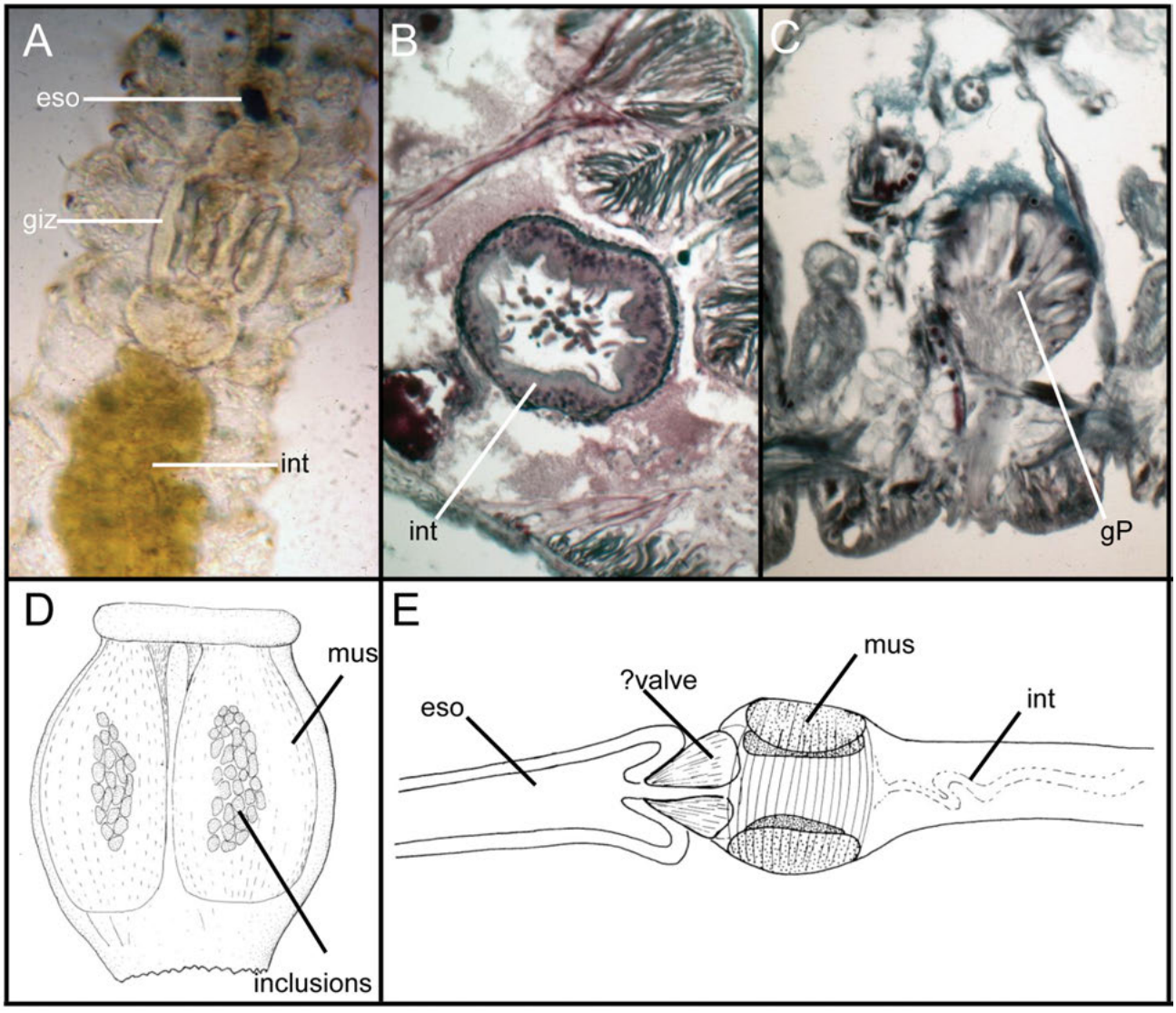
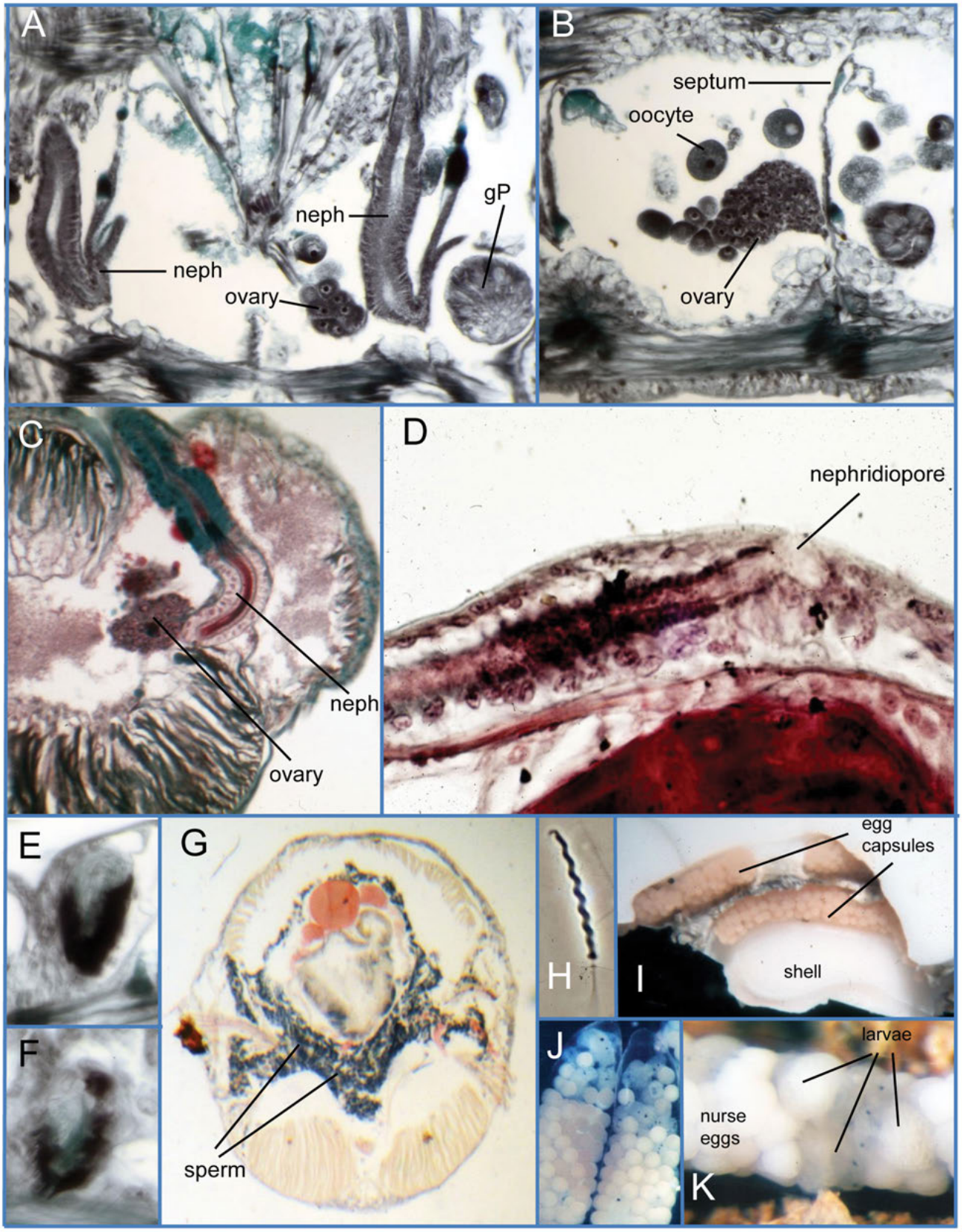


Fig. 7.4.1.6: Spionidae internal morphology. A, *Dipolydora socialis*, juvenile, digestive tract with gizzard; B, *Boccardiella hamata*, cross-section of middle body with intestine infested with gregarine parasites; C, *Polydora cornuta*, sagittal section showing large glandular pouch; D, *Dipolydora socialis*, gizzard of adult; E, *Carazziella hobsonae*, gizzard. A–C, originals; D, after Blake (1971); E, after Blake (1979). Abbreviations: eso, esophagus; gP, glandular pouch; giz, gizzard; mus, muscle; int, intestine.

The example shown in Fig. 7.4.1.5 B for *S. squamata* (as *Nerine cirratulus*) is modified and updated from Orrhage (1964). The brain or supraesophageal ganglion of spionids, like that of many polychaetes, consists of four transverse commissures: dorsal commissure of the ventral root (dcvr); ventral commissure of the ventral root (vcvr); dorsal commissure of the dorsal root (dcdr); and ventral commissure of the dorsal root (vcdr) (Fig. 7.4.1.5 B). Two of these (dorsal and ventral) connect with an anterior (ventral) circumesophageal root (vrcc); the other two connect to a posterior (dorsal) root (drcc). Prostomial nerves arise directly from the dcvr; esophageal nerves arise from vcvr. Palp nerves (1, 2, 4, 5, 6, 7) arise from both the vrcc and drcc (Fig. 7.4.1.5 B). Dorsal nerves arise from the dcdr whereas the nuchal nerves arise from both the dcdr and vcdr or the posterior brain. The drcc and vrcc on each side form

▸ **Fig. 7.4.1.7**: Spionidae reproductive morphology. A, B, *Polydora cornuta* (California), sagittal section of female with ovaries and nephridia; C, D, *Boccardiella hamata* (California): C, cross-section of female with ovary and nephridia; D, detail of nephridiopore; E, F, *P. cornuta* (California), female with seminal receptacle and spermatophores; G, *B. hamata* (California), cross-section of male with sperm masses; H, *Spio setosa* (Maine), mature sperm with spiral nucleus; I, *Dipolydora concharum* (Maine), egg capsules in burrows in shells of *Placopecten magellanicus*; J, *Boccardia proboscidea* (California), egg capsules with larvae and nurse eggs; K, *Polydora quadrilobata* (Maine), detail of egg capsule with nurse eggs and larvae. All originals. Abbreviations: gP, glandular pouch; neph, nephridium.


A
neph
gP
neph
ovary
B
septum
oocyte
ovary
C
neph
ovary
D
nephridiopore
E
F
G
sperm
H
I
egg
capsules
shell
J
K
larvae
nurse
eggs

the circumeophageal connectives which continue as the ventral nerve cord (Fig. 7.4.1.5 B, C) that extends along the body, giving off branches to each segment with additional branches to the noto- and neuropodia.

The overall morphology of the spionid nervous system is most similar to that of *Trochochaeta* and *Poecilochaetus* (Orrhage 1964). Among spionids, Orrhage (1964) provided descriptions of six species of *Scolelepis* (as *Nerine* and *Nerinides*), *Spio, Laonice*, *Spiophanes*, and *Prionospio*. The overall arrangement of the nerves as described for the example in Fig. 7.4.1.5 B is nearly identical with that of the other spionids described by Orrhage (1964).

Reproductive organs and gametes. All spionids have paired ovaries. However, there are two patterns of ovary structure and oogenesis: intraovarian and extraovarian (Eckelbarger 1983, 1988, 1992). In species with intraovarian oogenesis, a single pair of ovaries is located in each segment, associated with nephridial blood vessels and covered by a thin layer of peritoneal cells. Oocytes are retained in the ovary and derive nutrition from associated blood vessels. Intraovarian oogenesis has been described for *Streblospio benedicti*, *Marenzellaria viridis* and *Spiophanes uschakowi* (Eckelbarger 1980, Bochert 1996a, Radashevsky *et al*. 2018). In species with extraovarian oogenesis, the paired ovaries are attached to muscles near the ventral midline (Fig. 7.4.1.7 A, B); oocytes are released into the coelom where they continue to develop in association with coelomocytes (Fig. 7.4.1.7 B). This pattern of gamete production and spawning was described by Dorsett (1961a) for *Polydora ciliata* and by Blake (2006) for *Polydora cornuta*. The gonads of *P. ciliata* and *P. cornuta* arise from the medial border of the ventral longitudinal muscle in a few anterior chaetigers. The ovaries appear as pairs of club-shaped sacs that project into the coelom (Fig. 7.4.1.7 A–C). In *P. ciliata*, the oocytes remain in the ovaries until they reach a diameter of 25 to 30 µm, at which time they are released into the coelomic cavity; this pattern seems to be the same for *P. cornuta* (Fig. 7.4.1.7 B). After release from the ovaries, oocytes move toward middle body segments where they accumulate in the parapodia and continue to grow and mature to a maximal size of approximately 130 µm (Dorsett 1961a). At the time of spawning, mature eggs are transported through nephridial canals to the nephridiopores where they are released into egg capsules as they are formed. At the same time, sperm that are stored in seminal receptacles are also released into the capsules. The same pattern was observed for *Boccardia proboscidea* by Woodwick (1977).

Two different types of vitellogenesis have been reported in spionids (Eckelbarger 1992). *S. benedicti* has intraovarian oogenesis and accumulates yolk outside the oocyte by a process termed heterosynthesis. In *P. cornuta,* which has extraovarian oogenesis, yolk is produced by the oocyte, a process called autosynthesis (Eckelbarger 1992).

Three different types of eggs have been reported in spionids (Blake and Arnofsky 1999; Blake 2006): (1) eggs with thick, highly ornamented egg envelopes (= membranes) that are honeycombed externally (Fig. 7.4.1.8 J) and may contain prominent and numerous cortical alveoli (= membrane vesicles) (Fig. 7.4.1.8 I); (2) eggs with thick egg envelopes formed of several layers that have a reticulated, but not honeycombed surface and lack cortical alveoli; and (3) eggs with thin envelopes consisting of a single layer that is never ornamented and lacks cortical alveoli (Fig. 7.4.1.8 K). The first type of egg occurs in the genera *Aonidella, Aonides, Dispio, Laonice, Lindaspio, Malacoceros, Marenzelleria*, *Parascolelepis, Rhynchospio* (in part), *Scolelepis, Scolecolepides,* and *Spiophanes* (Fig. 7.4.1.8 I, J). The second egg type occurs in the *Prionospio* complex, including *Streblospio*, which has a three-layered egg envelope and seems to be intermediate between the highly ornamented types and those with thin, single-layered egg envelopes (Blake 2006). The third egg type occurs in *Microspio,* the *Polydora* complex, *Pygospio, Pygospiopsis*, *Rhynchospio* (in part), and *Spio* (Figs. 7.4.1.7 B; 7.4.1.8 K). Detailed observations of the ultrastructure of spionid eggs and oogenesis are available for five species: *P. cornuta, Spio setosa, S. benedicti*, *M. viridis*, and (Eckelbarger 1980, 1984, 1992, 1994; Bochert 1996a, Radashevsky *et al*. 2018).

In optical sections using light microscopy, the honeycombed envelope of type 1 eggs appears to be perforated by pores that connect cytoplasmically to the cortical alveoli (George 1966; Blake 2006). The number of pores and alveoli varies among genera. The alveoli of eggs of *Aonides* and *Dispio* are few but large and arranged in two rows. In spionids having this type of egg, the cytoplasm concentrates in the center after fertilization (Hannerz 1956; George 1966; Blake and Arnofsky 1999; Blake 2006). Hannerz (1956) speculated that pores in the envelope allow water to enter and exert a constant pressure on the cytoplasm. As development of the embryo continues, the original egg envelope becomes incorporated into the larval cuticle. Cilia and chaetae protrude, probably through the pores. This process was demonstrated for *M. viridis* by George (1966). Bochert (1996a) described the ultrastructure of the thick honeycombed egg envelopes and large cortical alveoli of *M. viridis*. Ten to 18 large cortical alveoli or vesicles occur just below the surface and are connected cytoplasmically to pores in the envelope. The surficial honeycomb appearance is due to furrows that extend 4 µm below the surface of the egg envelope. Individual microvilli are single structures that become elongate and branch irregularly as oocyte development proceeds. The tips of the microvilli extend

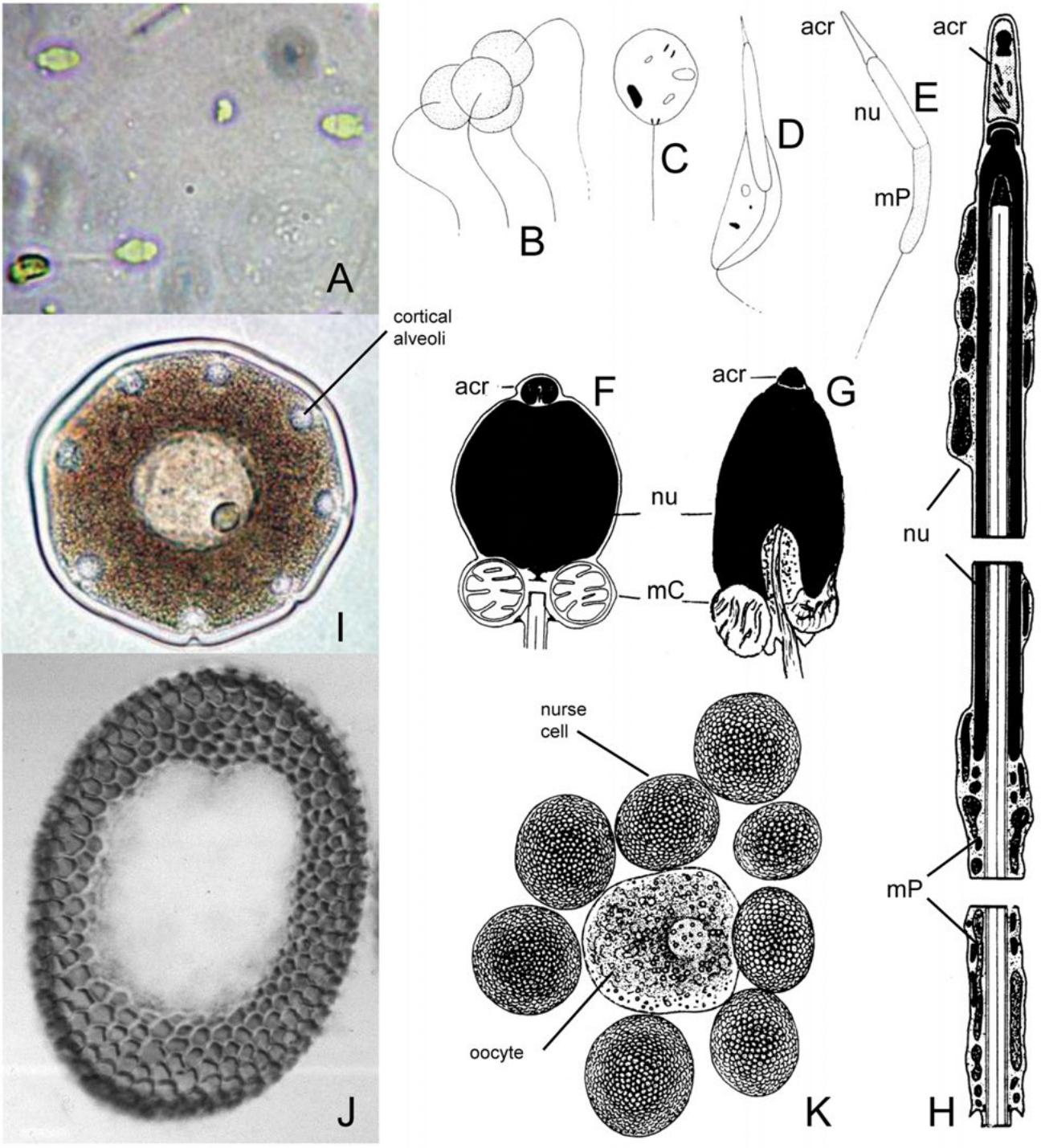


Fig. 7.4.1.8: Spionidae eggs and sperm. A, *Malacoceros jennicus*, mature sperm; B–E, *Dipolydora concharum* spermiogenesis: B, tetrad of four spermatids, C, early spermatid, D, late spermatid; E, mature sperm; F, *Prionospio* sp., ect-aquasperm; G, *Marenzelleria viridis*, ect-aquasperm; H, *Tripolydora* sp., introsperm; I, *M. jennicus*, mature egg with membrane vesicles; J, *Scolelepis* sp., mature egg with honeycombed membrane; K, *Pygospio elegans*, nurse eggs and oocyte. A, I, after Graff *et al*. (2008); B–E, after Blake (1996); F, H, after Rouse (1988) and Blake (2006); G, after Bochert (1996b); J, original; K, after Rasmussen (1973). Abbreviations: acr, acrosome; mC, mitochondria; mP, middle piece; nu, nucleus.

through the egg envelope where they terminate in spherical granules. According to Bochert (1996a), the high density of the microvillar tips (50–60 per μm^2) increases the available surface area of the oocytes, suggesting that increased surface area might facilitate movement of molecules across the membrane during development. Radashevsky (2018) described the newly released oocytes of *Spiophanes uschakowi* as being flattened or lentiform.

The egg envelope (type 2) of *S. benedicti* consists of three layers having digitiform microvilli that bifurcate basally and lie nearly parallel to the surface (Eckelbarger 1980). The microvilli produce glycocalyx strands that form the outer layer of the egg envelope. The inner and middle layers of the egg envelope consist of filamentous, electron-dense material; cortical alveoli are absent. *S. setosa* and *P. cornuta* have thin, single-layered egg envelopes (type 3) with no cortical alveoli (Eckelbarger 1984, 1992, 1994). In *S. setosa*, the microvilli are elongate, thin, double V-shaped structures; whereas in *P. cornuta*, the individual microvilli are shorter, solitary, and bulbous structures. The tips of the microvilli project through the egg envelope and therefore are in direct contact with fluid in the coelomic cavity or fluid within egg capsules.

The male reproductive system in spionids is best described for species of *Polydora, Dipolydora,* and *Streblospio* (Rice 1978, 1980, 1981). In *Polydora*, paired spermatogonia are suspended in the coelom between individual intersegmental septa and a nephridium. Each gonad is associated with an efferent parapodial blood vessel and surrounded by simple cuboidal cells (Rice 1981). Each gonad contains approximately 1000 spermatogonial cells. For the three polydorids studied by Rice (1981), gonads were first present in middle body segments.

Spermatogonial cells of polydorids are released into the coelom in pairs connected by a cytoplasmic bridge (Rice 1981). The first meiotic division results in four secondary spermatocytes attached by cytoplasmic bridges. Following the second meiotic division, eight spermatids are formed, also connected by cytoplasmic bridges. Dense masses of sperm accumulate in the coelom (Fig. 7.4.1.7 G). Using light microscopy, Blake (1969) diagrammed spermiogenesis for several polydorids. An example for *D. concharum* is shown in Fig. 7.4.1.8 B–E where individual spermatogonia develop into mature introsperm. The morphological changes in the maturation of spermatids into mature sperm including the elaboration of the acrosome, nucleus, and middle piece are described by Rice (1981).

In addition to the spermatogonia, sperm production, and maturation, the male reproductive system consists of a nephridium with a ciliated nephrostome or funnel that is located on the anterior border of intersegmental septa. In polydorids and some other genera, this leads through the septa to the nephridium and an elongated nephridial canal that terminates in a nephridiopore that opens on the dorsal surface (Rice 1978, 1981). In some spionids, sperm are concentrated into distinct spermatophores within the nephridial canal and these are in turn released from the nephridiopores where they are transferred in various manners to females. The biology of fertilization in spionids is further discussed in subsequent sections.

Retzius (1904) and Franzén (1956) defined two types of sperm: (1) primitive, referring to short-headed sperm (e.g., Fig. 7.4.1.8 A) that were spawned into seawater and (2) aberrant, referring to sperm that were modified and associated with copulation or a modified form of sperm transfer. Primitive sperm were subsequently referred to as aquatic sperm (Baccetti 1979) and aquasperm (Jamieson 1986a,b). Rouse and Jamieson (1987) and Jamieson and Rouse (1989) refined these definitions and introduced the terms ect-aquasperm and ent-aquasperm for the primitive types. Ect-aquasperm are freely spawned into seawater where eggs are fertilized. Ent-aquasperm are released and swim in seawater but are drawn into the tube or burrow of the female by inhalant feeding currents. For the aberrant sperm, Rouse and Jamieson (1987) introduced the term introsperm. Both ect-aquasperm and introsperm are found among spionids. The morphology of spionid sperm has now been documented for more than 30 species (see table 2 in Blake and Arnofsky 1999). The ultrastructure of ect-aquasperm has been described for *Prionospio* cf. *queenslandica* (Fig. 7.4.1.8 F) by Rouse (1988), *P. japonica* by Radashevsky *et al.* (2010), *Aonides oxycephala* by Radashevsky *et al.* (2011), *Marenzelleria neglecta* (as *M. viridis*) (Fig. 7.4.1.8 G) by Bochert (1996b), and *Spiophanes uschakowi* by Radashevsky (2018). The structure of spionid ect-aquasperm includes a spherical or ovoid nucleus, a midpiece consisting of four large, rounded mitochondria that surround two centrioles, and a free flagellum or tail (Rouse 1988; Bochert 1996b). The acrosome is typically a small, cylindrical structure that rests in a depression on the anterior end of the nucleus (see Fig. 7.4.1.8 F, G). Radashevsky *et al.* (2018) described the acrosome of *S. uschakowi* as being flattened and platelike. The reproductive biology and light microscopy investigations of the sperm of species of the genera *Scolelepis, Aonides, Laonice, Malacoceros, Parascolelepis,* and *Spiophanes* suggest that they also have ect-aquasperm.

Introsperm are found in *Microspio, Polydora, Dipolydora, Pygospio, Spio, Streblospio*, and some species of *Rhynchospio*. The morphology of introsperm includes modifications of the nucleus and midpiece. Mature sperm of polydorids have elongate heads (Fig. 7.4.1.8 H) and typically range from 59 to 74.5 µm long (Blake 1969, 2006). Sperm break away from aggregates of sperm plates when mature and lie free in the coelom. Ultrastructure details concerning spermatogenesis in *Polydora* and *Tripolydora* may be found in Rice (1981) and Rouse (1988).

In *Streblospio*, the nucleus is long and the midpiece is short; the acrosome is long and spiral (Rice 1981). Membrane-bound electron-dense bodies are present throughout the nucleus and midpiece of polydorid sperm and the nucleus of *Streblospio* sperm (Rice 1981; Rouse

1988). Other modifications include a spiral or coiled nucleus (Fig. 7.4.1.7 H) in *Spio setosa* (Simon 1967; Eckelbarger and Hodgson 2014) and an unusually long nucleus and midpiece with an unusually short flagellum or tail in *Boccardiella hamata* (Blake 1965; Rice 1992). The introsperm of dwarf males of *Scolelepis laonicola* have an elongated nucleus and middle pieces (Vortsepneva *et al.* 2006, as *Asetocalamyzas laonicola*). Rice (1981) suggested that females of polydorids and *S. benedicti* should be able to store sperm for prolonged periods without loss of viability. Such an adaptation would be ecologically important for species that produce multiple broods within a single season (= polytelic).

Reproduction and development

Reproduction

Sexual reproduction. Spionid polychaetes either spawn their gametes directly into seawater or males transfer sperm, usually in spermatophores, to females, which store the sperm in seminal receptacles until fertilization and spawning, usually into egg capsules. This topic was reviewed by Blake (2006).

Broadcast spawning is believed to occur in most of the genera referred to the subfamily Nerininae. These include the genera *Paraprionospio, Prionospio, Dispio, Aonides, Aonidella, Lindaspio, Spiophanes, Rhynchospio, Scolecolepides, Malacoceros, Marenzelleria, Scolelepis*, and *Laonice*. Unfortunately, there is little direct evidence that fertilization actually occurs in the water column. Available data were presented in Appendix 1 in Blake and Arnofsky (1999), but the authors noted that the absence of observations on spawning behavior in these genera is a major gap in an otherwise large and elaborate literature on reproduction and development. Based on that summary and more recent observations by Radashevsky (2007) and Radashevsky *et al.* (2014) on *Rhynchospio*, it would seem that three patterns of broadcast spawning occur: (1) dissemination of eggs and sperm into the water column where fertilized eggs develop freely into larvae; (2) discharge of eggs and sperm by paired males and females that result in an egg mass or cocoon within which fertilized eggs develop to a stage where they leave as planktic larvae; and (3) discharge of eggs and sperm into a dorsal posterior area on the abdomen, termed a "hatchery" by Radashevsky (2007) where gametes are discharged and held in place by long chaetae and where developing embryos and larvae are retained.

Observations of eggs and larvae taken from the plankton in Northern California strongly suggest that *Spiophanes bombyx, S. duplex*, and *Dispio uncinata* spawn their gametes directly into seawater where development proceeds in its entirety (Blake 2006). This was confirmed by observing that early planktic stages for these species ranged from fertilized eggs through pretrochophores. Radashevsky *et al.* (2006) reported that for *Prionospio patagonica*, small oocytes of 82 to 92 µm were spawned directly into seawater. Planktic larvae of the same species from small two-chaetiger stages to five- to six-chaetiger larvae settled and underwent metamorphosis in the laboratory. George (1966) observed broadcast spawning in *Marenzelleria viridis* (as *Scolecolepides*) and suggested that spawning was stimulated by changes in salinity. Bochert and Bick (1995), however, concluded that spawning of *M. viridis* in the Baltic Sea was related to decreasing water temperature because high densities of fertilized eggs were observed when the temperature decreased to 15°C. Blake (2006) supported George's (1966) observations based on high densities of *M. viridis* larvae in Penobscot Bay, Maine, USA where larvae were taken in plankton tows through lenses of low-salinity surface water. Larvae were rare or absent in deeper high-saline water.

Simple postspawning cocoons or egg masses are formed by some species of *Scolelepis* (subgenus *Parascolelepis*). For example, Imajima (1959) observed simple external cocoons for *Scolelepis yamaguchii* (as *Nerinides*). Blake and Arnofsky (1999) and Blake (2006) reported the same structures for *Scolelepis* cf. *tridentata* in California. Both species produce elongate, club-shaped cocoons that are anchored to the sediment by an elongate ribbon of mucous. Larvae are retained in the cocoons until three chaetigers have developed, after which they enter the plankton where they develop into large fusiform-shaped planktotrophic larvae. Larvae settle and metamorphose after approximately 18 chaetigers have developed. See Blake (2006) for details.

The formation of mucous egg masses after fertilization has also been reported. Guérin and Kerambrun (1984) identified such an egg mass in *Malacoceros fuliginosus*. The formation of any postspawning egg mass or cocoon would logically require pair formation among adults, but there are no observations to confirm this. Due to the lack of data on pair formation and spawning in species believed to be broadcast spawners, the number of species producing egg masses or cocoons may be underestimated.

Radashevsky (2007) described an unusual type of external brooding in *Rhynchospio nhatrangi* in which gametes, embryos, and larvae up to the four-chaetiger stage are held in place by long chaetae on the posterior dorsal surface of the abdomen prior to release of the larvae into the water column. In a later article, Radashevsky *et al.* (2014) reported a similar mode of brooding for *Rhynchospio asiatica*. These brooding species are hermaphroditic,

have thin-membraned eggs, and long-headed sperm. In contrast, *Rhynchospio* cf. *foliosa* reported by Radashevsky *et al.* (2016a) from Oregon, USA had thick-membraned eggs and short-headed sperm. These authors speculated that *R.* cf. *foliosa*, unlike other species of *Rhynchospio*, spawned gametes directly into the water column. The brooding of eggs and larvae on the surface of abdominal segments in some species of *Rhynchospio* is somewhat similar to that of *Streblospio gynobranchiata*, where eggs and larvae are held in place by branchiae-like structures.

In contrast to spionids that broadcast their gametes directly into the water column, a cocoon, or "hatchery", other spionids have been reported that package sperm into packets or spermatophores and variously discharge these in a manner that allows transmission to females. Spermatophores have been described for *Microspio mecznikowianus, Polydora cornuta, P. websteri, Tripolydora* sp., *Scolelepis* sp. (as *S. squamata*), *Spio filicornis, Streblospio benedicti, S. gynobranchiata,* and *Pygospio elegans* (Söderström 1920; Franzén 1956; Richards 1970; Greve 1974; Rice 1978, 1980; Rouse 1988; Rice and Levin 1998).

The nephridia become highly modified in segments where gametes mature and eventually serve as gonoducts for the passage of eggs and sperm out of the body (Fig. 7.4.1.7 D). Depending on the species, a pair of nephridia may join and have a common nephridiopore (Fig. 7.4.1.7 D), or there may be two separate nephridiopores. In species where spermatophores are formed, sperm are concentrated and enclosed in discrete packets that are discharged from the male nephridia. Rice (1980) investigated the formation of spermatophores in the nephridia of mature male *Polydora cornuta* (as *Polydora ligni*). The nephridia of this species are enlarged paired urogenital organs located in several segments; Rice divided the structure into seven morphological regions: (1) nephrostome, (2) descending nephridial canal, (3) dorsal curvature, (4) U-shaped depressions, (5) large urn-shaped depressions with long, thin microvilli, (6) U-shaped depressions as in region 4, and (7) ascending nephridial canal that terminates in the nephridiopore. Rice found that the spermatophores are composed of a central sperm mass surrounded by tubules that form a capsule.

Rice noticed that the tubules were identical to the microvilli found in areas 4, 5, and 6 of the nephridia and postulated that spermatophores were produced in the nephridia and derived from the same microvilli. The shape and size of spermatophores vary among species.

Rice (1978) demonstrated that spermatophores of *Polydora cornuta* were released from the male and deposited outside the tube. These were then picked up by the female using ciliary currents generated by the palps and carried into her tube. Sperm were then stored in seminal receptacles until egg spawning and capsule formation. This type of sperm transfer is a form of pseudocopulation because the male and female do not actually form pairs. In dense populations, this is a convenient manner in which males can disperse their gametes.

Richards (1970) observed spermatophores attached directly to the body of specimens of *Scolelepis* from Barbados. They were large, white-colored, and granular in appearance with a leaflike shape approximately the size of a parapodium. The sperm were bound together in a matrix and became active and were released when the spermatophores were manipulated in seawater. The author, however, was not able to observe how the spermatophores were produced or how the sperm were transferred to females.

The occurrence and morphology of seminal receptacles on female spionids has not been well documented. McEuen (1979) described seminal receptacle structures for several species including *Pseudopolydora paucibranchiata* and *Pygospio californica*. Similar appearing seminal receptacles are also found in *Polydora cornuta* (Fig. 7.4.1.7 E–F). These three species have dorsal seminal receptacles that are relatively small, but are found in all epitokous segments, whereas in *S. benedicti*, these same structures extend completely across the dorsum only of chaetigers 14 to 16 (McEuen 1979).

The unusual reproductive biology of *Scolelepis laonicola* was revealed by Vortsepneva *et al.* (2008), who discovered that a parasitic polychaete, *Asetocalamyzas laonicola*, previously described by Tzetlin (1985) from the White Sea, was actually a dwarf male of its host spionid polychaete, *Scolelepis* sp., a female. This type of sexual dimorphism is not known elsewhere in the Spionidae. The taxonomy required that both the host and parasitic male would be referred to the same species, which became *S. laonicola* (Tzetlin, 1985). The host had been previously described as *Scolelepis matsugae* Sikorski, 1994, which was officially recognized as a junior synonym of *S. laonicola* by Sikorski and Pavlova (2015).

Although the mode of fertilization and larval development of *S. laonicola* remain unknown, spermiogenesis, sperm ultrastructure, musculature, nervous system, and mode of attachment of the dwarf males have been described in detail (Vortsepneva *et al.* 2006, 2009a,b). All females observed by these authors had one to four attached males. The modified anterior end of the dwarf male is reduced, penetrates the female tissues and opens into its body cavity. The four main longitudinal muscle strands enter the female. These muscles are twisted 90° along the body of the male resulting in its dorsal side facing the dorsal side of the female with its ventral side turned up; the male is further oriented such that its posterior end faces the posterior end of

the female (Vortsepneva *et al*. 2009a). The septae of the host forms a chamber around the anterior region of the male (Vortsepneva *et al*. 2008). The males have a well-developed digestive track with the mouth opening inside the body cavity of the female where the male presumably derives nutrition (Vortsepneva *et al*. 2008).

Early and late spermatids are joined by cytoplasmic bridges into tetrads. Mature sperm have an elongated nucleus and middle piece (Vortsepneva *et al*. 2006), characteristic of spionids that have a modified type of fertilization *sensu* Franzén (1956) and an introsperm *sensu* Jamieson and Rouse (1989). Because no copulatory organs have been identified, Vortsepneva *et al*. (2008) suggest that sperm are transferred by pseudocopulation within the tube of the females.

The formation of egg capsules by spionids was first described by Söderström (1920) for *Pygospio elegans* and *Polydora* and later confirmed by Rice and Reish (1976) for *P. cornuta* (as *P. ligni*). Mucus is extruded from each nephridiopore and contacts the wall of the tube. Eggs are then squeezed through the same nephridiopores. The two adjacent streams of mucous and their eggs coalesce into a single chamber that fills with additional eggs. At the same time, sperm that are stored in seminal receptacles near the nephridiopores are discharged into the capsules. Capsules produced on adjacent segments merge with one another, forming a beadlike string. In some species, the individual capsules are so tightly joined to one another (Fig. 7.4.1.7 I) that the entire string appears to be one unit. Capsules of *P. cornuta* are attached to the tube by two thin extensions representing the paired nephridiopores. Species having only a single nephridiopore have a single attachment for the capsules. In *P. cornuta*, the individual capsules are loosely joined to one another, but sometimes individual capsules are separate. In *Dipolydora commensalis*, the individual capsules are tightly joined to one another. In *Boccardia proboscidea* and *Boccardia columbiana*, the individual capsules are not fused with adjacent ones and remain separate in a line attached to the wall of the tube (Figs. 7.4.1.7 J; 7.4.1.11 A). In *D. quadrilobata*, adjacent capsules fuse and form a single elongate cylinder (Blake 1969; Fig. 7.4.1.7 K). Gibson and Paterson (2003) reported that the egg capsules of *Amphipolydora vestalis* were smooth cylinders formed from seven fused capsules that lacked stalks and were attached to the tube wall by mucous.

Asexual reproduction. In a few species such as *Pygospio elegans* and several polydorids, asexual reproduction occurs as an additional form of reproduction. Two types of asexual reproduction occur in spionids: architomy and paratomy. Architomy is the simplest form and includes fragmentation of the body into individual segments or groups of segments, which then regenerate into new individuals (Fig. 7.4.1.9 G). Paratomy involves the division of the body into two distinct halves, with the reconstitution of missing parts by regeneration. Sometimes, the second half (stolon) remains attached to first half (stock) while regenerating. Additional divisions may also occur, resulting in chains of stolons being proliferated from the original stock parent. Spionids having paratomy tend to be very small, usually with a reduced and defined number of segments, whereas species having architomy are larger and have numerous segments.

To date, architomic asexual reproduction in Spionidae seems restricted to several species of the subfamily Spioninae. Architomy has been reported in the laboratory for *Dipolydora caulleryi* and *D. socialis* by Stock (1965), but has not been observed in the field. *P. elegans* has been widely reported as architomic (Rasmussen 1953, 1973; Bregenballe 1961; Muus 1967; Hobson and Green 1968; Armitage 1979; Wilson 1985; Anger 1984; Gibson and Harvey 2000; Thonig *et al*. 2016). Architomy also occurs in the closely related species *Pygospio californica* (Blake 2006). Blake (1983) reported architomy for *Amphipolydora abranchiata*, from off Argentina in 100 m. Gibson and Paterson (2003) reported architomy for *A. vestalis* from New Zealand. Radashevsky and Nogueira (2003) described architomic fragmentation in *Dipolydora armata*. David and Williams (2012b) report architomy for *Polydora colonia* from Long Island, New York, USA.

The best studied architomic species is *P. elegans*, in which the parent body divides into fragments through transverse fission. Each fragment regenerates into a separate individual (Fig. 7.4.1.9 G). Gibson and Harvey (2000) provided a defined sequence of events for regeneration following fragmentation: wound healing (day 1), development of a blastema to regenerate lost tissues and body regions (days 2–3), segmentation (days 3–6), and differentiation of regenerated segments into specific structures such as palps and pygidial cirri (days 4–8). This sequence was the same regardless of where on the body fission took place. Fragments having the original head had a higher survivorship than fragments containing the original posterior end. In most populations of *P. elegans* that have been studied, both sexual and asexual reproduction occurs. This strategy ensures that once colonized by settling larvae, populations could be expanded and maintained asexually. Armitage (1979), working with populations from two different localities in Tomales Bay, California, USA, found that both sexual and asexual phases of *P. elegans* were controlled primarily by seawater temperature with both forms of reproduction accelerated with increasing temperatures. These results support earlier observations by Rasmussen (1953) from Denmark that asexual reproduction in *P. elegans* increased during spring.

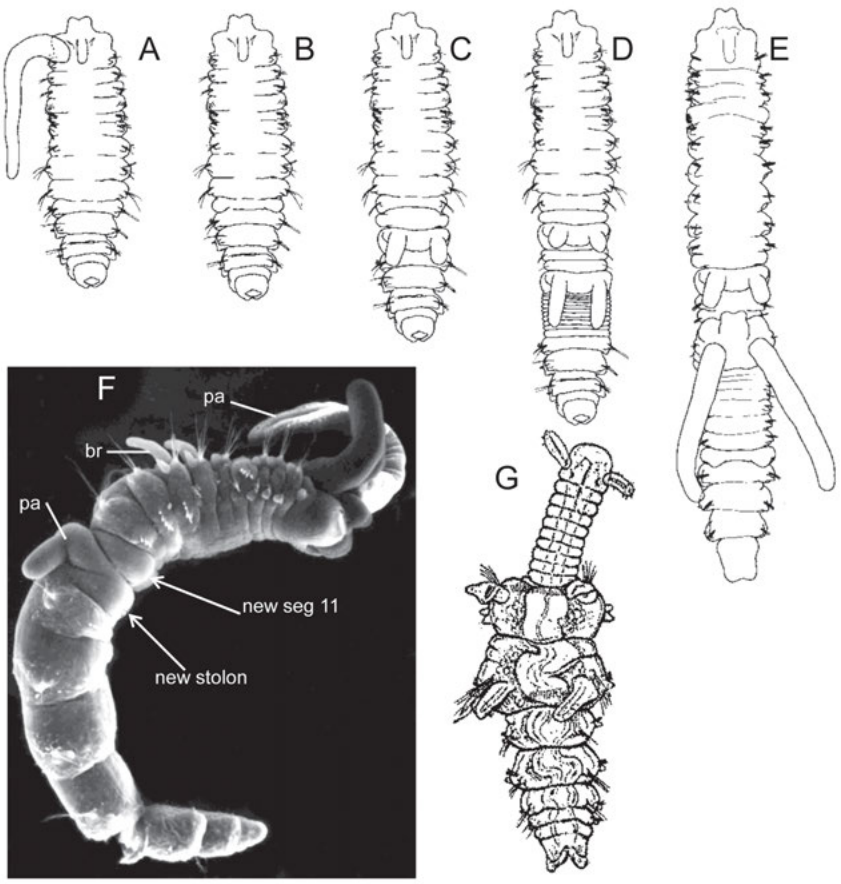


Fig. 7.4.1.9: Spionidae asexual reproduction. A–E, diagram of paratomic asexual reproduction in *Polydorella kamakamai*; F, stolonization in *Polydorella stolonifera*; G, architomic asexual fragmentation and anterior regeneration in *Pygospio elegans*. A–F, after Williams (2004); G, after Rasmussen (1953).

Recent observations on architomy in *Polydora colonia* by David and Williams (2012b) evaluated the effect of temperature on regeneration. These authors determined that temperature played an important role in the rate of regeneration after fragmentation, with regeneration being twice as fast at higher temperatures (24°C) than at low temperatures (14°C).

Paratomy has been reported for *Polydora tetrabranchia* and five closely related species of *Polydorella*: *P. prolifera, P. stolonifera, P. smurovi, P. dawydoffi*, and *P. kamakamai* (Campbell 1955; Blake and Kudenov 1978; Tzetlin and Britayev 1985; Radashevsky 1996; Williams 2004). *Polydora tetrabranchia* is a shell borer whereas the five *Polydorella* species construct tubes on the surfaces of sponges.

According to Campbell (1955), asexual reproduction in *P. tetrabranchia* occurs by transverse fission of the stock animal. Regeneration of new posterior and anterior ends proceeds while the separate stolons are still connected, providing the appearance of two joined individuals. A chain of three individuals was found in a laboratory experiment, but no more than two joined individuals were ever observed in the field. Asexual reproduction proceeded year-round and approximately one-third of all specimens collected were regenerating anterior or posterior ends.

Radashevsky (1996) and Williams (2004) reviewed the pattern of paratomy in *Polydorella* species. In *P. prolifera, P. stolonifera, P. kamakamai*, and *P. smurovi*, the fission and growth zone occurs between segments 10 and 11 (Fig. 7.4.1.9 A–F), whereas in *P. dawydoffi*, the growth zone appears between segments 11 and 12. The first three species have 15 segments; the latter two species have 16. Radashevsky (1996) has reported chains of five to six stolons for *P. dawydoffi*. In *P. stolonifera*, regeneration of a stolon begins with the development of a new anterior end with small palp buds that appear in the growth zone (Fig. 7.4.1.9 F). Eventually, the section of the worm anterior to the growth zone breaks away and regenerates a new posterior end, whereas the stolon differentiates into a fully functional and normal-appearing individual (Blake and Kudenov 1978). A similar pattern occurs in the other species (see Williams 2004). Sexual reproduction has been reported for *P. smurovi* and *P. kamakamai* but is likely to occur in all five species because a dispersive larval stage would be needed to colonize new sponges. Williams (2004), however, speculated that in lieu of sexually produced larval stages, adults of *Polydorella* species might leave their burrows and move to adjacent sponges, presumably by swimming or drifting.

Regeneration

The ability to regenerate lost or damaged body parts is widespread in marine invertebrates including annelids (Bely 2010; Bely and Nyberg 2010; Lindsay 2010). In spionid polychaetes, observations of anterior and/or posterior regeneration have been made on more than 25 species (Stock 1965; Lindsay *et al*. 2007; 2008; Whitford and Williams 2016).

The process of regeneration of the anterior ends was reviewed by Whitford and Williams (2016). After ablation of the anterior end, initial wound healing is followed by the formation of a blastema; this is followed by anterior extension of the blastema and differentiation of the prostomium. In addition, Whitford and Williams (2016) observed that in *Marenzelleria viridis*, intersegmental furrows representing the development of lost segments were formed at the posterior end of the regenerating section and progressed anteriorly as regeneration continued. This process had earlier been observed by Paterson and Gibson (2003) for *Amphipolydora vestalis* except that, for this species, the reappearance of missing segments was simultaneous rather than sequential. Whitford and Williams (2016), however, suggest that the sequential development of lost segments may occur in all spionids, but is too rapid and difficult to follow in light microscopy.

The number of segments that can be regenerated following ablation is somewhat limited by the number of segments that are lost. Whitford and Williams (2016) observed that for *M. viridis*, the number of segments replaced was equal to those lost by up to 10 segments; when 20 to 30 anterior segments were lost, regeneration replaced only 13 to 17 segments. These authors noted that other species replaced fewer segments.

There have been observations of spionids replacing both anterior and posterior ends from fragments (Stock 1965), but such extensive regeneration has not been well studied. It is similar, however, to asexual reproduction by fragmentation and regeneration that has been observed in species such as *Pygospio elegans*.

Life cycles

Spawning. In general, most species of Spionidae that have been studied to date seem to reproduce during periods when water temperature is highest (Blake 1969, 2017; Levin 1984a; Levin and Creed 1986; Sato-Okoshi *et al*. 1990). Typically, such species are polytelic, and capable of reproducing more than once during that interval. Many of these species are capable of establishing dense populations during the times they reproduce because sequential sets of gametes and spawnings can be produced by a single female. Blake (1969) found that at least two species of *Polydora* in Maine, *Dipolydora concharum* and *D. quadrilobata* type II, were species that likely reproduced during the winter months. Both species were found with egg capsules and larvae in the early spring months, suggesting that gametogenesis and spawning occurred during months when the water temperature was lower.

Larval development. An extensive literature exists on the larval development of spionids, largely because of their various types of development, elegant pelagic larvae, and the fact that so many species are available and accessible for study in nearshore habitats. Comprehensive accounts of spionid larval development that treat multiple species include those of Wilson (1928), Thorson (1946), Hannerz (1956), Blake (1969, 2006, 2017), Blake and Arnofsky (1999), and Blake and Woodwick (1975).

Spionid larvae are characterized by having long provisional serrated chaetae, and prominent ciliary bands including a prototroch, telotroch, neurotroch, nototroch, and gastrotroch. The degree of development, organization, and number of prototroch and gastrotroch bands are critical in the identification of larvae encountered in the plankton. Additionally, distinctive body shapes, as well as pigment patterns and colors are usually species-specific. Because of these characters, keys and pictorial guides to planktic spionid larvae have been produced that allow users to identify individual species after collection and removal from the samples (Hannerz 1956; Larink and Westheide 2011). In the following sections, examples are provided for the main types of larval development in spionids. Details of all species known as of 1999 were presented in Blake and Arnofsky (1999), followed by some updates in Blake (2006, 2017). A few additional references are noted subsequently.

Genera of Spionidae with species that spawn their eggs and sperm directly into the water column resulting in embryos that develop in the plankton include *Laonice, Malacoceros, Marenzelleria, Paraprionospio*, *Prionospio*, *Scolelepis,* and *Spiophanes* (Hannerz 1956; George 1966; Yokoyama 1981, 1996; Blake and Arnofsky 1999; Radashevsky *et al*. 2006). A complete list of studies through 1999 is included in Blake and Arnofsky (1999: appendix 1).

Radashevsky *et al*. (2006) reported that for *Prionospio patagonica* from Chile, small oocytes of 82 to 92 μm diameter were spawned directly into seawater. Planktic larvae of the same species were described from a small two-chaetiger stage to five- to six-chaetiger larvae, which settled and underwent metamorphosis in the laboratory; the presence of so few chaetigers in the planktic larvae of this species is unusual for the genus. The larvae of *Prionospio orensanzi* were described by Diaz-Jaramillo (2004). This species has eggs of approximately 110 μm diameter

and produces elongate, thin planktic larvae that settle and undergo metamorphosis at the 28-chaetiger stage.

The larvae of three species of *Paraprionospio* have been described from plankton*: Paraprionospio patiens* by Yokoyama (1981) (as *P. pinnata*) from Japan, *Paraprionospio cordifolia* (as *P*. sp. B) by Yokoyama (1996) from Japan, and *Paraprionospio alata* (as *P. pinnata*) by Blake and Arnofsky (1999) from Northern California. All reported larvae of *Paraprionospio* have elongate, narrow bodies. The species names and synonyms are based on Yokoyama (2007).

Examples of other well-described accounts of larval development of spionids that broadcast their gametes directly into seawater or in egg masses include the following: *M. viridis* from off Nova Scotia by George (1966 as *Scolecolepides viridis*); *Scolelepis* (*Scolelepis*) *foliosa* from Sweden by Hannerz (1956 as *Nerine foliosa*); *S.* (*Parascolelepis*) cf. *tridentata* from Northern California by Blake and Arnofsky (1999) and Blake (2006) as *Parascolelepis* cf. *tridentata*; and *Spiophanes duplex* from Northern California by Blake (2006). Examples of the larvae of these kinds of spionids are presented for *S.* (*Parascolelepis*) cf. *tridentata* (Fig. 7.4.1.10 A, B); *S. duplex* (Fig. 7.4.1.10 C, D), and *Laonice* sp. (Fig. 7.4.1.10 E, F).

The development of species of *Streblospio* includes brooding of larvae in dorsal pouches (*S. benedicti*) or

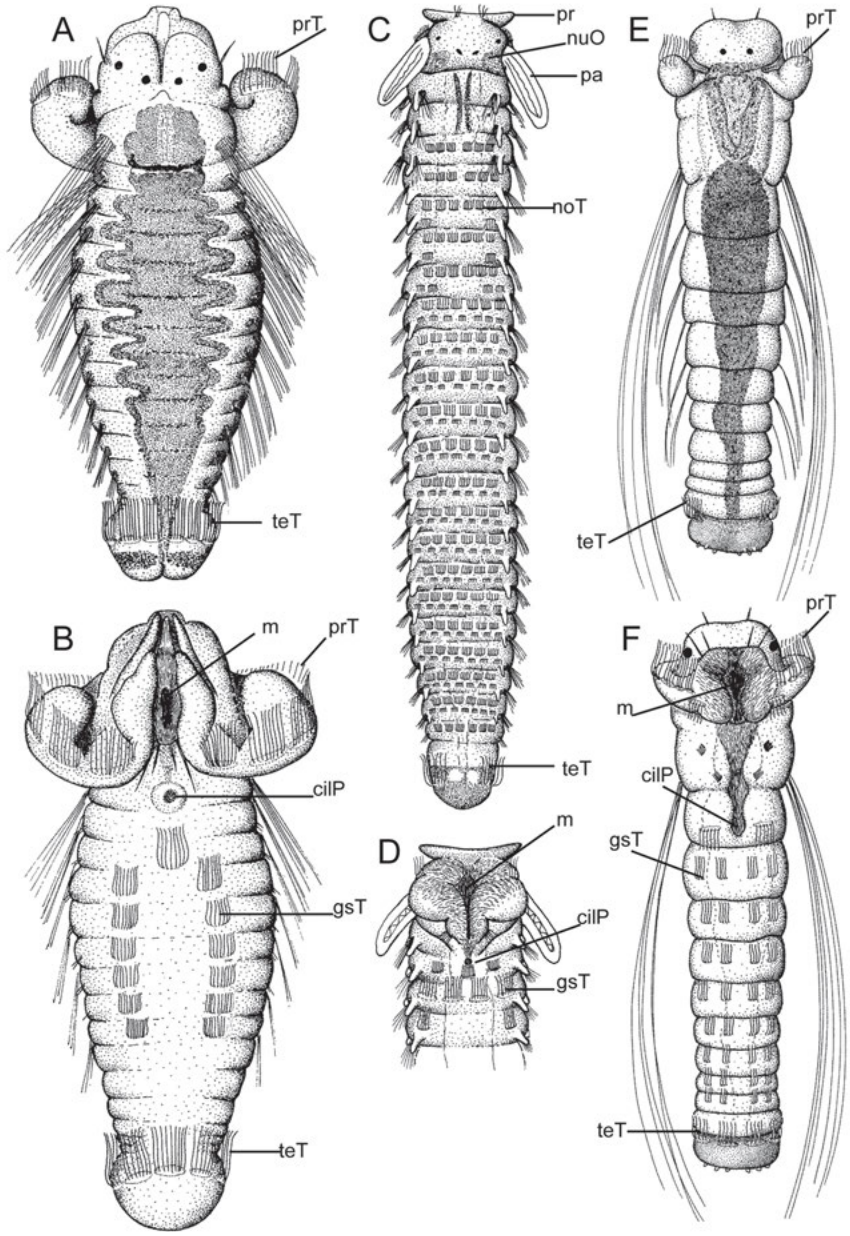


Fig. 7.4.1.10: Larvae of Nerininae. A, B, *Scolelepis* cf. *tridentata*: A, dorsal view; B, ventral view; C, D, *Spiophanes duplex*: C, dorsal view; D, ventral view, anterior end; E, F, *Laonice* sp.: E, dorsal view; F, ventral view. All after Blake (2006). Abbreviations: cilP, ciliated pit; gsT, gastrotroch; m, mouth; noT, nototroch; nuO, nuchal organ; pa, palp; pr, prostomium; prT, prototroch; teT, telotroch.

under specialized branchiae (*S. gynobranchiata*) prior to the release of larvae into the plankton. There is extensive literature on the larval development of *S. benedicti* (Dean 1965; Levin 1984b; Schulze *et al*. 2000; Pernet and McArthur 2006; Gibson *et al*. 2010). *S. gynobranchiata* development was described in detail by Rice and Levin (1998). Larvae of *S. shrubsolii* develop directly from eggs brooded in dorsal grooves on the body of the female until 14-chaetiger juveniles crawl off and burrow into the sediment (Cazaux 1985; Fonseca-Genevois and Cazaux 1987).

Females of *S. benedicti* brood their young in dorsal pouches (Fig. 7.4.1.11 A–C), with larvae eventually released into the plankton. Collier and Jones (1967) described the dorsal brood pouches as thin-walled, dorsolateral extensions of the coelom and explained how eggs were transported from the ovaries to those pouches. Males of both *S. benedicti* and *S. gynobranchiata* produce spermatophores that are transferred to ventral seminal receptacles on the females (Rice and Levin 1998). Blake and Arnofsky (1999) and Blake (2006) provided a summary of the literature on *S. benedicti*. Two types of development occur in *S. benedicti*: lecithotrophic and planktotrophic, providing a classic example of poecilogony. Lecithotrophic larvae with up to 9 to 12 chaetigers (550–650 µm) are retained in brood pouches (Fig. 7.4.1.11 B, C) and then released; they settle within hours or a few days. These larvae lack provisional chaetae, have poorly developed ciliary bands, and are weak swimmers (Fig. 7.4.1.11 D–G). Metamorphosis is relatively rapid, with larvae developing thickened palps and branchiae (Fig. 7.4.1.11 H) and retaining cilia until the first mucous tube is constructed. Thereafter, early juveniles crawl and form tubes (Fig. 7.4.1.11 I). Lecithotrophic populations occur in the Southeastern United States, Gulf of Mexico, and California (Levin 1984b, Blake and Arnofsky 1999). Planktotrophic larvae are released from the brood pouches when they have four to nine chaetigers (200–300 µm long). These larvae have well-developed serrated provisional chaetae, well-developed ciliary bands (Fig. 7.4.1.11 J, K; up to 450 to 550 µm long), and are planktotrophic for up to 45 days. Planktotrophic development occurs along the eastern United States and Gulf of Mexico (Levin 1984b; Blake and Arnofsky 1999; Blake 2006). Planktotrophic populations have also been identified from estuaries on the Atlantic coast of France (Fonseca-Genevois and Cazaux 1987).

Gibson *et al*. (2010) developed a more extensive evaluation of the morphological differences between the planktotrophic and lecithotrophic forms of *S. benedicti*. Superficially, planktotrophic larvae have well-developed provisional larval chaetae, sensory cilia, and anal cirri with bacillary glands. Lecithotrophic larvae lack larval chaetae and have only poorly developed sensory cilia and anal cirri that lack bacillary glands. Other aspects of morphogenesis were found that are not obvious superficially. For example, whereas notopodial chaetal sacs developed early in both larval forms, development proceeded differently. Planktotrophic larvae developed chaetal sacs that produced both larval chaetae and adult capillaries; in contrast, chaetal sacs of lecithotrophic larvae developed early, but did not produce any chaetae until later in development when adult capillaries were formed. Other differences observed were in the development of anal cirri, sensory cilia, prostomial mucous glands, timing of the development of the coelom and septa, and development and functionality of the gut. Gibson *et al*. (2010) also confirmed with the cytochrome oxidase I (COI) gene that the two forms of larval development represented the same species.

Brooding and larval development of *S. gynobranchiata* differ from that of *S. benedicti* in that eggs and larvae are brooded under straplike branchiae that develop on the abdominal segments of females (Rice and Levin 1998). Males produce spermatophores that are incorporated into ventrally located seminal receptacles on the females. There are 100 to 200 larvae produced per female. Larvae are released from the broods after three chaetigers have developed; these are planktotrophic larvae with serrated provisional chaetae and settle after 9 to 12 chaetigers have developed.

Egg capsules containing eggs and embryos are known for genera of the subfamily Spioninae including *Amphipolydora, Boccardia, Boccardiella, Carazziella, Dipolydora, Microspio, Polydora, Pseudopolydora, Pygospio*, and *Spio*. The literature for these genera is extensive and has been reviewed by Blake and Arnofsky (1999) and Blake (2006). Recent accounts of the development of additional spionids having egg capsules with brooding within adult tubes followed by planktic larvae include *Amphipolydora vestalis* by Gibson and Paterson (2003), *Polydora neocaeca* by Williams and Radashevsky (1999), *Boccardia knoxi* by Handley (2000), *Polydora rickettsi* by Radashevsky and Cárdenas (2004), *Polydora ecuadoriana* and *Polydora carinhosa* by Radashevsky *et al*. (2006), *Pseudopolydora rosebelae* by Radashevsky and Migotto (2009), *Polydora* cf. *websteri* by Barros *et al*. (2017), *Pseudopolydora* cf. *kempi* and *Ps*. cf. *reticulata* by Kondoh *et al*. (2017), and *Boccardia berkeleyorum*, *Dipolydora cardalia*, *Polydora pygidialis*, and *Polydora spongicola* by Blake (2017).

One example of this type of development is *B. columbiana*, a common intertidal species in the Eastern Pacific that bores into hermit crab shells, coralline algae, and tests of barnacles (Woodwick 1963a). The larval development was described by Blake and Arnofsky (1999) and Blake (2006). Egg capsules are deposited in a row within

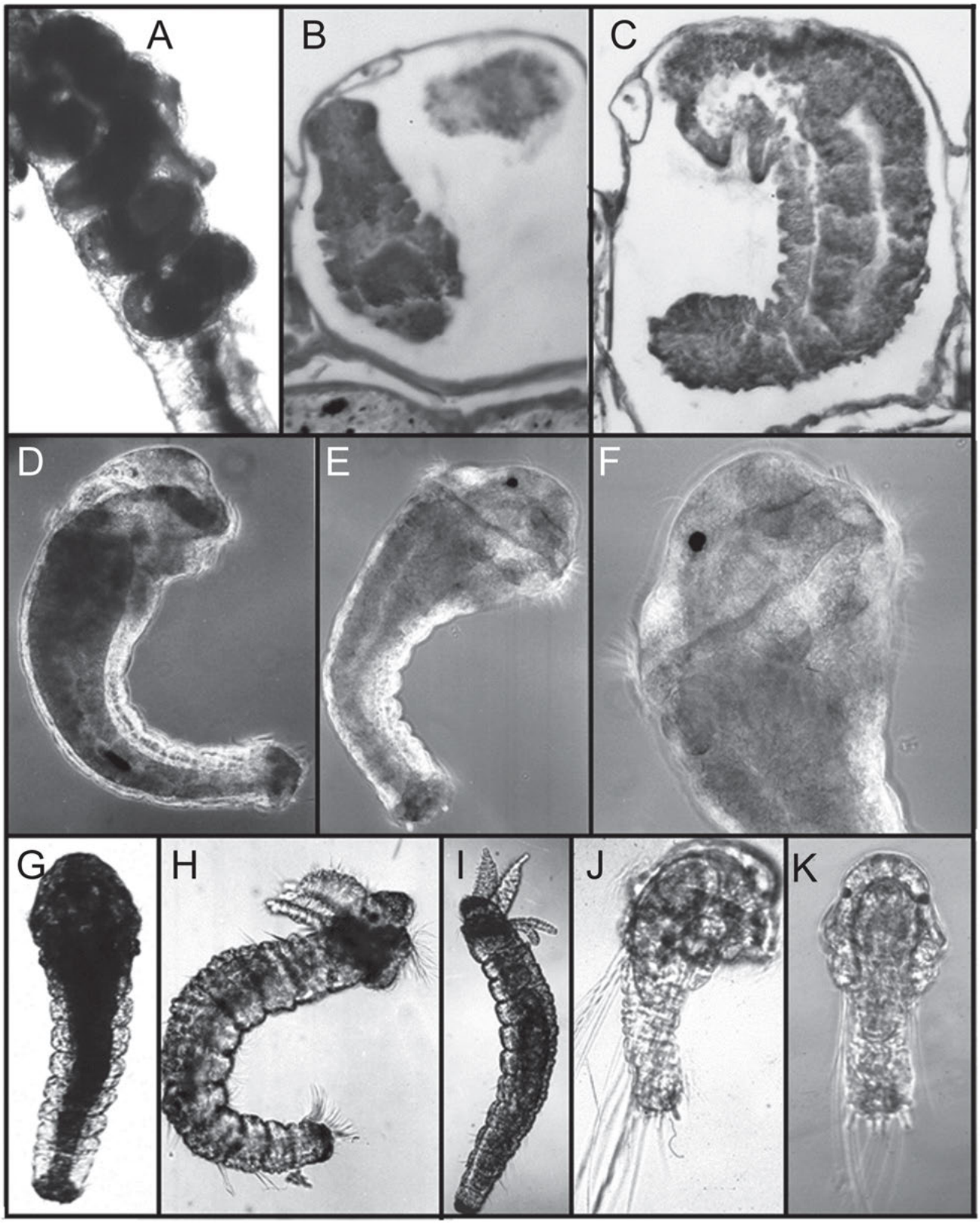


Fig. 7.4.1.11: Development of *Streblospio benedicti*. A–I, lecithotrophic larvae from California: A, five segments of adult female with larvae in brood pouches; B, C, sagittal section of female through brood pouches: B, early encapsulated larva; C, larva ready to hatch; D–F, newly emergent larvae, no provisional chaetae; lateral view; G, planktic larva before metamorphosis; H, juvenile capable of swimming and crawling, prototroch and telotroch still visible; I, crawling juvenile; J, K, planktotrophic larvae (Maine), newly released from brood pouches with long provisional chaetae. A, D, E, H, J, K, after Blake (2006); others original.

burrows excavated by the adult. Each capsule is attached separately to the burrow lining by two thin extensions (Fig. 7.4.1.12 A). Each egg capsule contains 50 to 60 eggs that individually measure 110 to 115 µm in diameter. All eggs are fertilized; this species does not produce nurse eggs.

Early embryos are pretrochophores 120 × 100 µm in size that move slowly in the capsule using a pair of large ciliated patches on their ventral side (Fig. 7.4.1.12 B). An oral opening or vestibule is present; the yolk mass is prominent. The trochophore larvae are present after approximately 24 h and retain the ventral patches, but also have a prototroch and telotroch (Fig. 7.4.1.12 C); a large ciliated vestibule or mouth is prominent. By 48 h, the larvae have developed three chaetigers (Fig. 7.4.1.12 D: 130 µm long) and by 72 h, early four-chaetiger larvae are developed (170 µm long). These early chaetigerous larvae are characterized by having two and then six eyespots, serrated provisional chaetae, a well-developed prototroch and telotroch, but no segmental ciliary bands. The ventral ciliated patches are still present and are retained until the larvae leave the capsules, at which time they are shed.

The four-chaetiger larvae are released into the plankton where they become planktotrophic and continue to develop. A typical four-chaetiger larva on release is 280 µm long, slender in shape, a strong swimmer, and photopositive (Fig. 7.4.1.12 E). The provisional chaetae are long and held close to the body providing the larva with

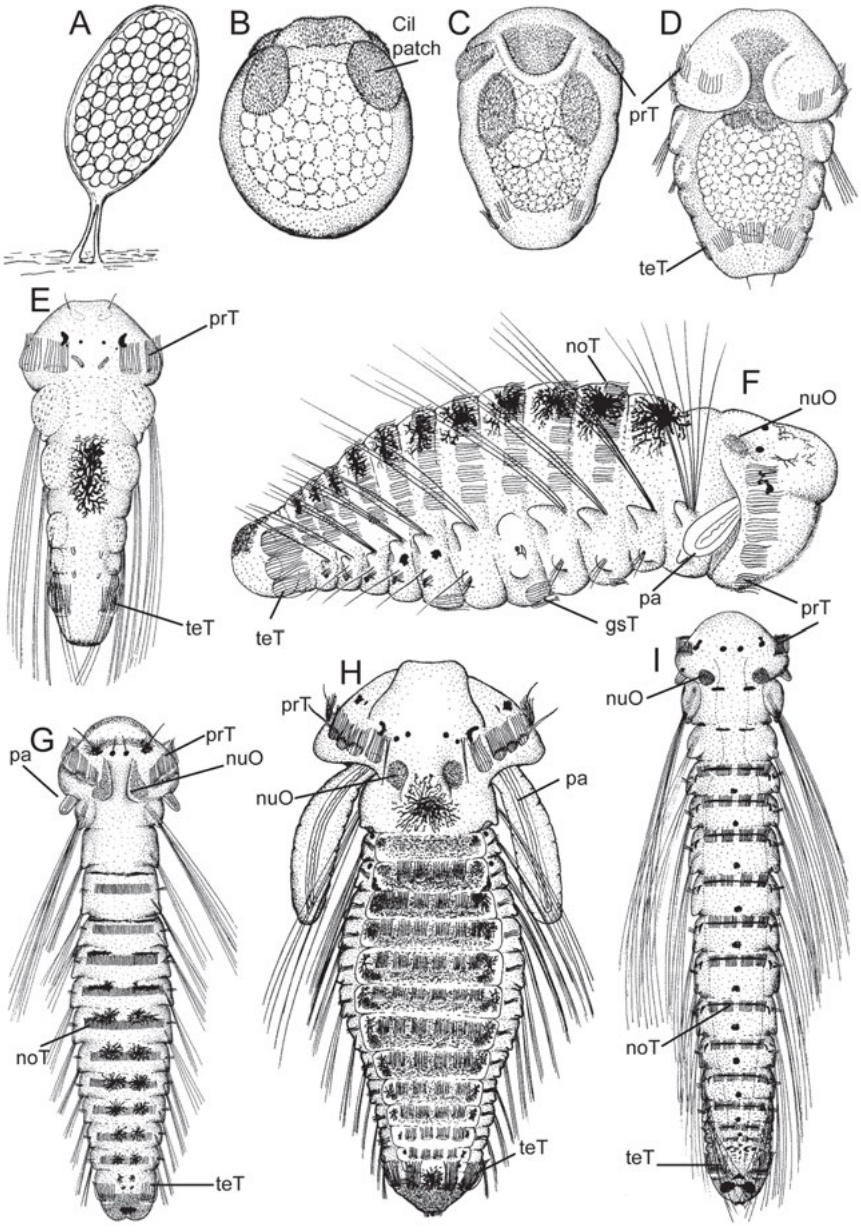


Fig. 7.4.1.12: Larvae of Spioninae. A–F, development of *Boccardia columbiana*: A, egg capsule; B, encapsulated pretrochophore; C, encapsulated trochophore; D, early three-chaetiger larva prior to release from capsule; E, four-chaetiger larva after release from capsule; F, large planktic larva; G, *Polydora websteri*, 12-chaetiger planktic larva; H, *Pseudopolydora paucibranchiata*, 13-chaetiger planktic larva; I, *Dipolydora concharum*, 14-chaetiger larva. A–F, after Blake (2006); G, I, after Blake (1969); H, after Blake and Woodwick (1975). Abbreviations: Cil patch, ciliated patch; gsT, gastrotroch; noT, nototroch; nuO, nuchal organ; pa, palp; prT, prototroch; teT, telotroch.

a streamlined rigid shape. The characteristic pigment pattern eventually consisting of a dorsal medial row of large branching chromatophores is first present from chaetiger 2. These larvae feed on phytoplankton and, in the laboratory, will also feed and grow on cells of algae and diatoms if provided. Eventually, the planktic larvae of *B. columbiana* become large and robust and develop a fusiform shape that characterizes several species of the genus *Boccardia*. The larva shown in the figure has 11 chaetigers and measures 560 µm long (Fig. 7.4.1.12 F). The body has an overall greenish cast; dorsal medial chromatophores begin on chaetiger 2 and continue posteriorly along the dorsum; additional lateral pigment is also present. Segmental cilia include nototrochs from chaetiger 3 and gastrotrochs on chaetigers 3, 5, 7, and another on chaetiger 10 that develops later. The modifications of chaetiger 5 are already evident. Nuchal organs and palps are beginning to develop.

Examples of other species of planktic larvae of polydorids are shown: *Polydora websteri* (Fig. 7.4.1.12 G), *Pseudopolydora paucibranchiata* (Fig. 7.4.1.12 H), and *Dipolydora concharum* (Fig. 7.4.1.12 I). Of note are the different body shapes and pigment patterns that distinguish one species from another. Finer details of the chaetae of chaetiger 5, shape and form of the nuchal organs, eyespot patterns, and segmental ciliary bands also differ between species and genera. Readers are referred to Hannerz (1956), Blake (1969, 2006, 2017), and Blake and Arnofsky (1999) for further information on spionid larvae that produce egg capsules and brood them for variable amounts of time.

Although reports of the development of spionid larvae that have either short or long periods in the plankton are numerous in the literature, direct development has rarely been reported or verified. The viviparous development of nonpelagic juveniles of *S. shrubsolii* by Cazaux (1985) approximates direct development because no free swimming larval stage is produced. Söderström (1920) reported that larvae of *Boccardia natrix* from Patagonia and sub-Antarctic Islands were brooded in epitokous segments and suggested that development was direct. This mode of development has never been subsequently observed or confirmed, however.

The adults of *Polydora curiosa* from the Kurile Islands deposit only one to four eggs into capsules in their tube; these eggs are large, 240 to 330 µm in diameter. The resulting larvae are retained in the capsules until they are approximately 1400 µm long and have approximately 20 chaetigers, subsisting entirely on their intrinsic yolk reserves (Radashevsky 1994). Although most of the typical cilia develop, these larvae settle and undergo metamorphosis almost immediately on release from the capsule, with only a very short planktic period or none at all; they do not feed until after settling (Radashevsky 1994). Although this species undergoes encapsulated lecithotrophic development, it can almost be considered as having direct development. Another species reported to have larvae retained in the capsules and tubes to a very late stage is *P. carinhosa*, as described by Radashevsky *et al.* (2006) from Brazil; these larvae have only a brief period in the plankton prior to settlement. Early development and size of the eggs is, however, unknown.

As part of a cruise to the east Antarctic Peninsula in May 2000, specimens of *Pygospiopsis dubia* were collected from sediments in the Prince Gustav Channel at a depth of approximately 500 m. In addition to adults, small larval and postlarval specimens that seemed to be within tubes of adults were recovered from the same samples. The morphology of these specimens was described by Blake (2006) and Blake and Maciolek (2018). The smallest specimens had 14 chaetigers and measured 780 × 270 µm; they were short, thick, and did not have sufficient morphology to suggest they were planktic larvae. Although noto- and neurochaetae were present, these were not the serrated provisional chaetae typical of spionid larvae. Nototrochs were absent; a partial telotroch and at least one gastrotroch were observed. A pair of short palps was present. These specimens should be capable of slow swimming or crawling movements within a tube. A 16-chaetiger postlarva or juvenile that had no larval morphology at all was also described by Blake (2006) and Blake and Maciolek (2018).

Of particular interest in the study of spionid development is the discovery of variable patterns of larval nutrition among several species belonging to the subfamily Spioninae. The majority of species in this subfamily deposit their eggs into capsules (see previous sections). In some species, all the eggs develop into larvae that initially subsist on yolk reserves derived from their eggs; these larvae are released into the plankton when their yolk reserves are depleted. Once in the plankton, larvae become planktotrophic and subsist on phytoplankton, remaining pelagic for an extended period prior to settlement and metamorphosis.

In other species, both fertilized and nonfertilized eggs are present in the capsules. Here, the developing larvae ingest the nonfertilized eggs and subsist on this extrinsic yolk resource until it is fully consumed. At that time, larvae may leave the capsule and become pelagic for a short time until settlement and metamorphosis. The nonfertilized eggs are called nurse cells or nurse eggs; two distinct types have been reported: (1) eggs that are morphologically identical to the fertilized eggs but do not undergo cleavage and (2) eggs that undergo some or unequal cleavage. The first type is well documented in *Boccardia*

proboscidea, *Dipolydora quadrilobata, Polydora colonia*, *Polydora hoplura*, *Polydora nuchalis*, and other species. The presence of this type of unfertilized egg suggest their origin is due either to a shortage of sperm or to gamete incompatibility; they are engulfed whole by the developing larvae (Wilson 1928; Woodwick 1960, 1977; Blake 1969, 2006; David and Williams 2012a). The second type occurs in *Amphipolydora vestalis*, *Pygospio elegans*, and *Pseudopolydora kempi*; these eggs are fragile and readily break up into small yolk granules (Fig. 7.4.1.8 K) that are devoured by developing larvae (Rasmussen 1973; Blake and Woodwick 1975; Gibson and Paterson 2003; Blake 2006).

The type of development that incorporates nurse eggs in the capsules is termed adelphophagia and probably occurs in at least half the species of Spioninae that have been studied to date (Wilson 1928; Simon 1967; Blake 1969, 2006; Blake and Woodwick 1975; Blake and Kudenov 1981; Gibson and Paterson 2003). Adelphophagia has been considered a form of lecithotrophic development because the adult deposits yolk in nurse eggs that are ingested by the developing larvae instead of initially producing larger eggs (Woodwick 1977; Blake and Kudenov 1981).

To further complicate these two patterns of development, Blake and Kudenov (1981) observed that *Boccardia proboscidea* is capable of producing pelagic larvae that are planktotrophic only after variable periods of producing lecithotrophic larvae that develop entirely in egg capsules and feed on nurse eggs. Many species probably shift seasonally between intrinsic and extrinsic yolk production; this pattern might be related to available organic inputs.

Some species of Spionidae have been found to vary their mode of development throughout their geographic range or from season to season, a phenomenon termed poecilogony. In the species that have been studied, this variability typically includes the length of larval life or presence/absence of nurse eggs in the capsules (Hannerz 1956; Simon 1967, 1968; Blake 1969, 2006; Clark 1977; Blake and Kudenov 1981). Blake and Arnofsky (1999) reviewed the subject of poecilogony in spionids and reported on eight species: *Boccardia proboscidea, Dipolydora quadrilobata, Pygospio elegans, Pseudopolydora kempi, Spio decoratus, Spio martinensis, Spio setosa*, and *Streblospio benedicti*. Recent studies have identified or confirmed additional examples of poecilogony: *Polydora hoplura*, *Boccardia polybranchia,* and *Boccardia wellingtonensis* (Morgan *et al*. 1999; Duchêne 2000; David and Simon 2014; David *et al*. 2014; Oyarzun and Brante 2015). Except for *S. benedicti*, all these species have populations that have been reported with one type of development producing larvae with a long planktotrophic larval development and another type with extended brooding in egg capsules using nurse eggs as an extrinsic yolk source. Not all species exhibiting adelphophagia have been reported to also have planktotrophic development.

There are some examples in which a species thought to have all of the eggs in the capsules developing into larvae sometimes had individual capsules with unfertilized eggs. Blake (1969) first reported this for *Polydora cornuta* (as *P. ligni*). In this example, which was near the end of the breeding season, 2 of 11 capsules in a tube had unfertilized eggs and the developing larvae fed on them. The occurrence of variable modes of development in *P. cornuta* was explained by Rice and Rice (2009) as being the result of females using up their stored sperm during successive spawnings, resulting in the decline in the percentage of fertilized eggs per capsule and the increase of larval size at release. However, MacKay and Gibson (1999) found considerable variability in a Nova Scotia population of *P. cornuta* in which females switched between adelphophagia and planktotrophy with the switch not related to sperm availability. Another similar example of poecilogony was reported by Radashevsky and Cárdenas (2004), who observed that *P. rickettsi* had 10% of the capsules with unfertilized eggs that were consumed by developing larvae.

Polydora cornuta is a polytelic species with females capable of rapidly producing multiple broods in a single summer season. During the reproductive season, a depletion of sperm in the seminal receptacles after production of successive strings of egg capsules would naturally result in some eggs not being fertilized and therefore available as an extrinsic yolk source. According to Rice and Rice (2009), such a pattern could be selected if the larvae that are feeding on nurse eggs required less time in the plankton when the required phytoplankton species were less abundant. The shift to permanent adelphophagia and the eventual evolution of a different type of nonviable nurse egg such as found in *Pygospio elegans* and *Pseudopolydora kempi* would require a modification of oogenesis.

A somewhat different, classic, form of poecilogony occurs in *Boccardia proboscidea*, in which (1) eggs in capsules are all fertilized and develop into larvae that become planktotrophic or (2) egg capsules contain nurse eggs that the developing larvae ingest and use as an extrinsic yolk source. In the second scenario, the larvae are lecithotrophic while in the capsules and become planktotrophic on release. However, in addition, Blake and Kudenov (1981), Gibson (1997), and Gibson and Gibson (2004) observed that two types of larvae were present in the capsules with nurse eggs. Some adelphophagic larvae remained small, apparently unable to feed on the nurse eggs whereas other larvae in the same capsules fed and grew to a large size. Both the large (type A) and small

(type B) larvae were released into the plankton at the same time, but were planktotrophic for different amounts of time. Such capability would allow local populations to be maintained by adelphophagic larval development whereas dispersal of the species over a broad geographic range would be accomplished by planktotrophic larvae (Gibson and Gibson 2004). In contrast to the appearance of unfertilized nurse eggs due to the reduction of stored sperm after successive spawnings as in *Polydora cornuta*, the production of nurse eggs in *Boccardia proboscidea* is an active process (Smith and Gibson 1999). Nurse eggs arise as viable oocytes that produce a fertilization envelope and complete meiosis; however, at this point, the nurse egg's nuclear DNA is lost and the cytoplasm breaks up into small vesicles that contain yolk that is ingested by developing larvae (Smith and Gibson 1999). Oyarzun and Brante (2014) found that both types of larvae in the capsules with nurse eggs were capable of developing normally to metamorphosis. Type B larvae, however, were subject to cannibalism by type A larvae. Smith and Gibson (1999) studied the morphology of planktotrophic larvae that develop without nurse eggs and found that many larval structures were reduced compared with other spionid larvae, suggesting the early development of adult morphology, which facilitated settlement and development into juveniles.

Oyarzun *et al.* (2011) collected *Boccardia proboscidea* from 12 or more locations along the West Coast of North America from Puget Sound to Southern California and, using two genetic markers, discovered a single species that exhibited a geographic break near Point Conception, CA. Simon *et al.* (2009) recorded similar genetic comparability between *B. proboscidea* introduced into South Africa and those from several locations on the West Coasts of North America. *B. proboscidea* probably originated in the Northeastern Pacific but has since spread to Australia, Hawaii, New Zealand, Argentina, and South Africa. It has most recently been reported from Europe, primarily from the Atlantic coast of Spain (Martínez *et al.* 2006), the northern coast of Scotland (Hatton and Pearce 2013), and North Sea locations from France to the Netherlands (Kerckhof and Faasse 2014). As an alien species now in many global locations, it is likely that its variable mode of reproduction and larval development has allowed *B. proboscidea* to successfully colonize new locations.

Oyarzun and Brante (2015) recently reported on poecilogony in *Boccardia wellingtonensis* from Chile. Reproduction in this species is similar to *Boccardia proboscidea*, with both planktotrophic and lecithotrophic development present in the local population. Similar to *B. proboscidea*, *B. wellingtonensis* also has both small nonfeeding larvae and larger feeding larvae in the same capsules. These authors also documented the cannibalism of the large larvae on the smaller ones.

Details on the development of lecithotrophic and planktotrophic larvae of *Streblospio benedicti* were presented earlier (see previous section). Despite considerable differences in both the superficial and internal morphogenesis of these two types of larval development, molecular analysis has demonstrated that specimens producing these larvae belong to a single species (Gibson *et al.* 2010).

Biology and ecology

Behavior

Feeding. An overall review of feeding in spionid polychaetes was recently published by Jumars *et al.* (2015). This represents a significant update of Fauchald and Jumars' (1979) work, necessary due to the large body of research on polychaete feeding over the past three decades that has significantly changed earlier concepts regarding this topic. An intermediate review of some of the spionid research was presented by Blake (1996). A brief overview of some key observations is presented here.

The ability of spionids to remove particles from the water during times of high particle flux is an active sedimentation process in coastal ecosystems (Frithsen and Doering 1986). In a hypothetical situation, water carrying a heavy suspended sediment load could be significantly cleared when it passes over dense populations of spionid polychaetes. The sediment that is collected by the spionids accumulates as part of their tubes or in interstices between the tubes. Flexibility in feeding behavior, coupled with demonstrated plasticity in reproduction and development for many species, undoubtedly contributes to the evolutionary success of spionids and their dominance in coastal ecosystems including the establishment of the dense tube mats that have been reported for some species (Blake 1971).

Taghon *et al.* (1980) discovered that three species, *Boccardia proboscidea*, *Pseudopolydora kempi*, and *Pygospio elegans*, were capable of switching from deposit feeding to suspension feeding when currents at the sediment/water interface carried higher amounts of suspended sediments. Subsequently, Dauer *et al.* (1981) obtained the same result for six species in six different genera. This ability to switch between the water column and sediment surface for a particle source makes it difficult to assign spionids to a single feeding mode category or guild *sensu* Fauchald and Jumars (1979). Dauer *et al.* (1981) proposed the category "interface feeding" for species that are able to switch between the sediment surface and water column for

particle collection. Dauer *et al*. (1981) noted that interface feeders should have broad spatial distributions because of their ability to use a wide variety of food resources.

Food particle collection involves different behaviors relative to the use of the palps if the animal is collecting particles from the water column or sediment surface. Dauer *et al*. (1981) observed differences in palp orientation and palp movement between species. When deposit feeding, both palps are in contact with the sediment, whereas, when suspension feeding, both palps either lash about in regular or irregular patterns, are held rigidly, or a combination of these. Taghon *et al*. (1980) observed another behavior whereby palps are coiled. Individual species may use one or more of these different palp orientations as part of their feeding activity.

Dauer and Ewing (1991), working on the Great Barrier Reef, observed that *Malacoceros indicus* never extended its palps into the water column; instead, this species limited its particle collection activities to surface deposit feeding. *M. indicus* was found to have only one group of functional cilia on the palps, thus differing from other spionids with three or more different groups of cilia. This species inhabits coarse sediments that are not easily resuspended.

Detailed accounts of palp morphology, particle collection, and waste removal were presented for *Scolelepis squamata, Streblospio benedicti*, and *Paraprionospio pinnata* by Dauer (1983, 1984, 1985). *Scolelepis* differs from other spionids in lacking a ventral ciliated groove on the palps; particles are transported to the mouth by palp contractions or coiling. When currents are present, individuals come to the sediment surface, extend their palps into a coiled orientation, and feed nonselectively on suspended and resuspended particles. The guts of *S. squamata* were found to contain sand particles, remains of small invertebrates, and fecal pellets (Dauer 1983). *S. benedicti* has complex food-collection and particle-sorting mechanisms, suggesting that a high degree of food resource partitioning is possible (Dauer 1984). A high degree of particle selection on the palps and at the pharynx was also demonstrated for *P. pinnata* by Dauer (1985). Particle selection is also known for four species of *Polydora*, including *P. cornuta, P. websteri, P. ciliata,* and *P. commensalis* (Dorsett 1961a; Dauer *et al*. 1981; Dauer 1991).

The feeding biology of spionids that bore into calcareous substrates is not well known. The palps of spionids extended above various mollusk shells when placed in aquaria are easy to observe, but studies of their individual feeding habits are harder to detect. It is likely, however, that similar to their sediment-dwelling congeners, they take advantage of suspended particles in the water column and possibly the inhalant and exhalant currents generated by their hosts. *P. ecuadoriana* bore into a wide variety of calcareous substrates in South America and have been observed to both suspension and deposit feed (Radashevsky *et al*. 2006). *P. bioccipitalis* is known from California, Peru, and Chile from shells of intertidal bivalves. In Peru and Chile, the species was observed to concentrate in parts of the shell surrounding the siphons of local surf clams (Riascos *et al*. 2008). Williams (2002) observed *Polydora umangivora* and *Polydora robi* in the Philippines that fed on the eggs and embryos of their hermit crab hosts.

The biology of *Dipolydora commensalis* is especially interesting because it lives in a shallow burrow that is excavated along the columella of a gastropod shell occupied by a hermit crab. This specialized species has short palps with an unusually narrow food groove that seems to be adapted to capturing particles that are stirred up or suspended by the activities of the hermit crab (Dauer 1991). Dualan and Williams (2011) determined that the short palp length, characteristic for this species, was influenced by the hermit crab host, which cuts or damages them. Worms taken out of the shells developed palps of a length typical for other species of *Polydora*.

Levin (1981) studied the feeding biology of two spionids, *Streblospio benedicti* and *Pseudopolydora paucibranchiata* (Okuda) from the standpoint of interspecific and intraspecific competition for resources. Dried particles of *Enteromorpha* sp. were made available to several individuals of *P. paucibranchiata*, and this resulted in food fights in 98% of these tests. When the same experiments were tried for *S. benedicti*, food fights occurred in only 24% of these tests. *P. paucibranchiata* was thus more aggressive than *S. benedicti*. For *P. paucibranchiata*, Levin (1981) observed considerable interaction between the long palps of adjacent individuals and it was common for up to five worms to fight over a single food particle including algae, invertebrate larvae, or other polychaetes. She also observed individuals of *P. paucibranchiata* biting off a palp of another worm. The palps of *S. benedicti* were rarely used in such aggressive behavior. These results suggest that intense competition for food and space play a major role in regulating which species of spionids dominate at any one time.

Tube building. Particles collected by spionids are used both as food and as building materials for their tubes. Few species have been studied in detail, but particle selection apparently plays an important role in both processes. For *Polydora ciliata* (Johnston), Dorsett (1961a) found that smaller particles are carried to the gut as food, whereas larger particles are used in tube construction. When

adding particles to the tube, *P. ciliata* uses the lateral lips surrounding the mouth to place them in a precise pattern. The tube is strengthened by mucous secretions from segmental glands or, as for example in *Spiophanes*, by β-chitin produced by parapodial glandular organs (see previous section, External details of the integument). It is likely that the majority of particles collected by spionids, when they are in the suspension feeding mode, are used in tube building because it is in such situations that the dense tube mats are formed.

Within the *Polydora* complex are many species that are able to bore into calcareous substrates (Blake and Evans 1973; see related comments on the morphology of epidermal glands). Polydorids have been reported from virtually every type of calcareous structure including mollusc shells, living corals, coral rubble, and coralline algae. Many of the associations include commercially important bivalves such as oysters, other bivalves, and abalone (e.g., Moreno *et al*. 2006; Simon *et al*. 2006; Sato-Okoshi *et al*. 2008; Simon 2011; Walker 2011). Other species, such as *Polydora armata*, bore into different kinds of coral (Radashevsky and Nogueira 2003). Most species are not limited to a single host species or type of calcareous structure (Simon 2011). The burrows have various forms depending on which species is involved (Blake and Evans, 1973). Burrows may be either U-shaped (*P. ciliata, P. giardi*), pear-shaped (*P. websteri*), Y-shaped with a single branch (*P. websteri*), or with multiple branches (*Dipolydora concharum*). *P. websteri* burrows will differ depending on which bivalve host is involved. Although the structure and form of the burrows has been well documented, the actual mechanism by which the worms initially penetrate the substrate, enlarge, and continue to bore is poorly understood. There have been two conflicting hypotheses, involving either (1) a mechanical process that involves the major spines of chaetiger 5 or (2) a chemical process that includes secretion of an acid to dissolve the calcareous matrix. A third idea is that boring is accomplished by a combination of these two processes. The historical background of this controversy was reviewed by Blake and Evans (1973). These authors favored a chemical mechanism because experiments by Haigler (1969) demonstrated that *P. websteri* could still bore after the major spines of chaetiger 5 were removed. In addition, Evans (1969) demonstrated that large species with complex burrows, such as *P. concharum*, are able to enlarge their burrows at various points simultaneously, precluding a dependence on the spines of chaetiger 5.

Zottoli and Carriker (1974) assessed burrow morphology, formation of the detrital tube within the burrow, and the ultrastructure of the bored surface in shells of *Crassostrea virginica* and *Mytilus edulis* formed by *P. websteri*. During initial larval settlement, *P. websteri* was found to prefer crevices in the shell surface that presumably provide the juvenile with a place to form a simple tube, anchor itself, and then initiate shell dissolution and subsequent burrow enlargement. Juveniles slowly penetrate the shell and form a U- or flask-shaped cavity. Detritus collected by the palps is carried into the burrow forming an internal detrital tube. Evans (1969) had earlier observed that detrital material is absent in those areas where burrows are being enlarged. Zottoli and Carriker (1974) found that *P. websteri* secretes a viscous fluid that dissolves the interprismatic organic matrix and then etches the exposed mineral prisms. The ends of the prisms were often noted to be broken off, presumably by chaetal abrasion as the worm moved back and forth. These dissolved and abraded substances were sometimes reincorporated into the detrital tube. Evans (1969) considered this substance to be redeposited. Sato-Okoshi and Okoshi (1993) studied shells of scallops and oysters that were infested with four different species of *Polydora*. Using SEM, these authors discovered numerous concentric-like holes along the inner surfaces of the burrows. Scratches, presumably from chaetae, were also observed. The nature of the holes suggested that some chemical substance that probably dissolves the shell was being secreted by the worms along the length of its body. Sato-Okoshi and Okoshi (1993) support a chemical/physical mechanism to boring and suggest that the scratches they observed in the burrows were due to noto- and neurochaetae that may participate in the formation of the concentric holes. Liu and Hsieh (2000), working in Taiwan, studied the burrows of *Polydora villosa*, which bores into live coral. The worms initially form U-shaped burrows similar to those of species that bore into mollusc shells, but as the coral grows, the worms elongate their burrows, forming multiple straight passages that are lined with mucous and sediments. A mud-lined tube extended from the burrows into the water column where the worms extend their palps and feed. Despite the long history of research on the mechanism of boring by *Polydora* and its relatives, the source and chemical composition of the acidic secretions have not been identified.

Distribution

Habitat. A review of the large literature pertaining to benthic ecology and the role of spionids in benthic communities is beyond the scope of this review. The few examples given subsequently serve to demonstrate that spionids are often the most abundant and diverse components of benthic communities.

Spionids are found in a wide variety of habitats and range from the intertidal to the deep sea. In bays,

estuaries, and nearshore environments, they build tubes in a full range of sediments from sand to silt. Populations frequently are so large that dense tube-mats form, serving to stabilize sediments and bury or otherwise smother the substrates or other organisms on which they settle (Blake 1971, 1996). Rapid build-up of dense sediment mats of *P. cornuta*, for example, has been reported to cause extensive mortalities in oysters (Galtsoff 1964).

Pygospio elegans and *P. californica* occupy positions high in the intertidal zone of sand flats in estuaries and are subject to exposure at low tides (Armitage 1979; Blake 1996). In central California embayments, *Boccardia proboscidea* and *Pseudopolydora kempi* are found most abundantly at the high and middle regions of the intertidal zone, whereas *P. paucibranchiata* is most abundant at the low intertidal zone (Blake 1996). On more exposed and cleaner sandy beaches, species of the genus *Scolelepis* are sometimes abundant. In subtidal sediments, species of *Prionospio, Spio,* and *Spiophanes* often dominate.

Spionid population density has been found to be seasonal and to exhibit patterns of spring/summer abundance in temperate environments (e.g., Holland 1985). A typical season starts with overwintering adults responding to increasing spring temperatures and increased food supply by initiating gametogenesis and producing egg capsules. As polytelic species, individual females are capable of producing several clutches of eggs and strings of egg capsules during a single year. Larvae produced by these adults settle, build their own tubes, mature rapidly, and in turn produce more egg capsules and larvae. Zajac (1991) monitored intertidal populations of *P. cornuta* for two years in Connecticut, where densities peaked between June and August, and then decreased to low levels by October.

Because of the great densities that have sometimes been recorded for species of Spionidae, research has focused on how such populations become established and are maintained. Interest has centered on the ability of spionids to switch between deposit and suspension feeding (see previous section). Taghon (1992) found that deposit-feeding individuals of *Boccardia pugettensis* and *Pseudopolydora kempi* maintained a constant distance to their nearest neighbor regardless of density. When suspension feeding, however, distances between neighbors decreased at high densities. These results, when taken with those of Levin (1981) on competition between nearest neighbors (see previous section), suggests that densities are more tightly controlled when worms are in deposit-feeding mode than in a suspension-feeding mode. Blake (1969, 1971) collected *Dipolydora quadrilobata* from a low intertidal beach at Cobscook Bay in northern Maine. The site was subject to a great tidal range and the *D. quadrilobata* zone was narrow, no more than 2 m wide, when exposed at low tide. The tubes of *D. quadrilobata* were positioned equidistant from one another, approximately 2.5 cm apart, and the entire array of tubes resembled a cribbage board (Blake 1996). Although few quantitative samples were taken at the time, nearest-neighbor distances would suggest that no more than 250 individuals of *D. quadrilobata* could occupy one square meter of the bottom. The distance between these worms was obviously maintained by the length of the palps, suggesting that this population was mostly deposit feeding. In contrast, the same species was collected in Massachusetts Bay in dense tube mats that were dominated by *Spio limicola*. Densities of *S. limicola* and *D. quadrilobata* at one station were calculated at 72,373 and 8,442 individuals per square meter, respectively (Blake 1996). These dense populations of *D. quadrilobata* would only be possible in a high-flux environment in which food is brought to the worms via the water column.

In deep-water environments, spionids are among the most dominant of benthic communities both in terms of the number of species and the individuals comprising these assemblages. Blake and Grassle (1994) recorded 64 species of Spionidae in continental slope samples from off North and South Carolina. Among these, 53 were believed to be new to science. Similarly, from slope sediments off Northern California, 17 of 26 species were believed to be new to science (Blake *et al*. 2009). In these locations, species of *Aurospio, Laonice*, *Prionospio*, and *Spiophanes* are the most common spionid genera. In the Northern California location, *Prionospio delta,* a widespread deep-water species, was dominant in lower slope communities and seemed to be an early colonizer of disturbed sediments (Blake *et al*. 2009).

In the original description of *Aurospio dibranchiata*, Maciolek (1981a) reported that the species comprised 5.1% of the fauna in core samples taken by Grassle (1977) at 1760 m off Woods Hole, MA; this species was also found in recolonization experiments conducted at the same site, suggesting an opportunistic lifestyle. In later studies along the US Atlantic coast, *A. dibranchiata* was consistently found to be among the top five numerical dominants in areas deeper than 2000 m (e.g., Blake and Grassle 1994). The systematics and biology of deep-water spionids is poorly known. A recent article by Paterson *et al*. (2016) reported on seven new species of abyssal spionids, indicative of the effort needed to document the diversity of deep-sea spionids.

Because of opportunistic life histories and variable modes of development, several spionids and other polychaetes have been distributed over great distances by vectors such as ballast water used in transoceanic

shipping or export of commercially important oysters or other molluscs intended to support local fisheries or aquaculture ventures. Several of these species are now so widespread that their point of origin is in question.

The following species of Spionidae are believed to have been transported to new geographic locations in ballast water, by hull fouling, or via transport of shellfish intended for commercial aquaculture. For several of these species, such as *Boccardia proboscidea*, *Polydora hoplura*, *P. paucibranchiata*, and *Marenzelleria viridis*, introductions into new geographic areas seem to be recent. For others, the timing of movements or introductions are not known and the species are likely cryptogenic, with introductions having occurred within the last 400 years commensurate with the expansion of global commerce and shipping. For some species, such as *P. hoplura*, there is the potential for damage to local shellfisheries due to the borings produced by the worm. For *Marenzelleria* spp. in northern Europe, at least two cryptic species have been identified as having been introduced from North America; these species have become dominant and have altered the composition of local benthic communities. For species such as *P. cornuta* there is the potential that cryptic species occur among some populations. The 11 species discussed subsequently are certainly not the only spionids that have colonized sites beyond their place of origin, but are those for which introductions have been noticed and documented in various manners.

Boccardia proboscidea was originally described by Hartman (1940) from intertidal zones along the California coast from Mendocino to San Diego. The species was reported as abundant in shale and limestone reefs where it bored into and formed tubes in softer rocks. Hartman (1940) was also the first to observe that *B. proboscidea* produced egg capsules with both lecithotrophic and planktotrophic larvae (see larval biology, discussed previously). Subsequent to Hartman's article, the species was reported farther north from Oregon to British Columbia by Hartman and Reish (1950), Berkeley and Berkeley (1950), and later by Sato-Okoshi and Okoshi (1997). Woodwick (1963a) reported the species from additional habitats in California including soft sandy sediments and as a borer in shells occupied by hermit crabs. Fauchald (1977) recorded the species from Panama. The species therefore occupies a wide array of habitats in the intertidal zone over most of the Northeast Pacific from Canada to Panama.

The first report of *Boccardia proboscidea* outside of the Northeast Pacific was from Japan by Imajima and Hartman (1964); Sato-Okoshi (1999b) subsequently provided additional data on the distribution and habitats from Japan. Blake and Kudenov (1978) found the species to be the numerically dominant polychaete near a sewage outfall in Port Phillip Bay, Victoria, Australia. The species was subsequently identified from Hawaii (Bailey-Brock 2000), New Zealand (Read 2004), South Africa (Simon *et al*. 2010), Argentina (Jaubet *et al*. 2011, 2018), Spain (Martínez *et al*. 2006), Scotland (Hatton and Pierce 2013), along the Belgian and Dutch coasts (Kerckhof and Faasse 2014), and from the Atlantic coast of Morocco (Goumri *et al*. 2017 as *Boccardia polybranchia*).

The opportunistic nature of *Boccardia proboscidea* includes tolerance for a wide range of habitats, including variable salinities and temperatures and a larval biology that includes both lecithotrophic and planktotrophic larvae in the same populations. The species has obviously been transported, presumably from the Northeast Pacific to distant locations and now has a distribution that is nearly cosmopolitan.

Boccardia chilensis was originally described by Blake and Woodwick (1971) from specimens collected along the Chilean coast as part of the Lund University Chile Expedition of 1948 to 1949. It was subsequently reported from New South Wales and Victoria, Australia by Blake and Kudenov (1978) and from New Zealand by Read (1975). This species seems to be a trans-Pacific species limited to the Southern Hemisphere, where it inhabits soft sediments.

Boccardia wellingtonensis was originally described by Read (1975) from New Zealand and subsequently reported from Chile by Blake (1983 as *B. polybranchia fide* Sato-& Takatsuka 2001) and Oyarzun and Brante (2015) and from South Africa by Simon *et al*. (2010). This species has a variable mode of reproduction and larval development similar to that of *B. proboscidea*. The presence of both lecithotrophic and planktotrophic larvae suggests that the species is capable of being widely distributed. Although first described from New Zealand, the actual place of origin is unknown.

Polydora hamata was originally described from Virginia on the US Atlantic coast by Webster (1879a), who also reported it from New Jersey (Webster 1879b); Hartman (1951) reported the species from the Gulf of Mexico (Louisiana). On the Pacific coast, Berkeley (1927) described *Boccardia uncata* from British Columbia; this species was subsequently reported as far south as Southern California and Western Mexico (Berkeley and Berkeley 1952; Hartman 1961; Reish 1963). Okuda (1937), Imajima and Hartman (1964), and Radashevsky (1993) reported the species from Japan. Blake (1966) examined specimens from both the US Atlantic and Pacific coasts and concluded that they were the same species and referred all records to *Boccardia hamata*. D. Dean and J.A. Blake combined their separate

life history studies into a single article describing larvae of *B. hamata* from both the East and West Coasts of North America (Dean and Blake 1966). The East Coast studies were conducted in Connecticut, representing the first reports of the species from New England. Additional collections in New England suggest that the northern limit of the species is Cape Cod Bay, MA (Blake unpublished). Blake and Kudenov (1978) established the genus *Boccardiella* and assigned *B. hamata* as the type species. The habitats for *B. hamata* are primarily as a shell borer on the US Atlantic and Gulf coasts and in sediments and shells on the Pacific Coast.

Until recently, *Boccardiella hamata* was limited to all three coasts of North America and Japan. However, Kerckhof and Faasse (2014) provided the first report of the species from Europe, where it was found among Pacific oysters being cultured on the southwestern delta in the Netherlands. This discovery suggests that *B. hamata* and possibly *Boccardia proboscidea*, which was found in the same habitat, may have been introduced into Europe with the oyster cultures. However, Kerckhof and Faasse (2014) do not rule out shipping and ballast water as the vector.

Boccardiella ligerica was originally described from the Estuary of Loire, France by Ferronniére (1898); it is the senior synonym of *Polydora redeki* described by Horst (1920) from Holland (*fide* Blake and Woodwick 1971). The species has been reported several times from estuarine locations along the English Channel in France (Rullier 1960; Dauvin *et al*. 2003) and northern Germany (Augener 1939; Hempel 1957a,b). The systematics and morphology of the species was addressed by Blake and Woodwick (1971), with additional records clarified by Blake (1983). Based on these two latter accounts, the species inhabits sediments in estuarine locations with very low salinities.

Globally, *Boccardiella ligerica* has been identified from California (Blake and Ruff 2007) with records from San Francisco Bay and the San Joaquin River Delta (Light 1977, 1978) and Newport Bay river outlets in Southern California (Kudenov 1983). US Atlantic records of the species extend from Florida to Virginia and Delaware Bay; dense populations of the species have been seen in the Cooper River near Charleston, SC (Blake unpublished). *Boccardiella ligerica* has been identified from various Caribbean islands and was identified from samples in Uruguay and Argentina in brackish water (Blake 1983). Global records of *B. ligerica* and other invasive species are summarized in a variety of online databases, some summarized in the World Register of Marine Species and World Polychaeta Database (Read and Fauchald 2017; Molnar *et al*. 2008). As with many widespread spionids, the actual point of origin of *B. ligerica* is not known.

Polydora cornuta is a widely distributed species, reported from all three coasts of North America, the Caribbean Sea south to Brazil and Argentina, Europe, Australia–New Zealand, Asia from Russia, Japan, and Korea to China, and India. The origin of the species is unknown, but is likely the Pacific Ocean due to the presence of numerous congeners and closely related species. Radashevsky (2005) compared adult and larval morphology of the species from widely separated populations but was unable to detect consistent differences and concluded that all reports were of single species.

There is, however, evidence that *Polydora cornuta* is potentially composed of several genetically distinct incipient or sibling species (Rice *et al*. 2008; Rice and Rice 2009). These authors attempted to crossbreed North American populations from Florida with West Coast (California) and East Coast (Maine) populations. The compatibility was low in all combinations (0%–7%) except for crosses with Florida females and California males in which compatibility was 42%. Interestingly, a comparison of the COI gene among these same three populations and from specimens from New Zealand demonstrated that three clearly defined and well-supported groups were present: (1) Florida, (2) California and New Zealand, and (3) Maine. The Maine haplotypes and California–New Zealand haplotypes were closer to one another than to Florida. The results of the cross-breeding experiments and low reproductive compatibility for the separate populations together with the genetic differences with the COI gene, suggest that morphologically similar yet genetically distinct populations of *P. cornuta* likely represent sibling or incipient species. More extensive genetic studies of these and other populations are needed to further understand the distribution of this species globally and whether one or several species are present.

Polydora hoplura is a large spionid that bores tunnels into the shells of commercially important bivalve molluscs and other calcareous habitats and has likely been transported globally with shellfish being introduced to enhance local aquaculture. The species was originally described from Naples, Italy by Claparède (1869) and has subsequently been reported from the Mediterranean and northern Europe including the UK (Carazzi 1893; Lo Bianco 1893; Marion and Bobretzky 1875; McIntosh 1909; 1915; Wilson 1928; Soulier 1903; Mikac 2015). At the same time, *P. hoplura* has been reported from South Africa (Day 1955, 1967; Simon *et al*. 2006, 2010), New Zealand (Read 1975), and Australia (Blake and Kudenov 1978). Radashevsky *et al*. (2017) redescribed specimens from the type-locality in the Gulf of Naples and established a neotype. These authors also reported on new materials from South Korea.

A closely related species, *Polydora uncinata* was described by Sato-Okoshi (1998) from Japan and later identified from southwest Australia (Sato-Okoshi *et al.* 2008; Sato-Okoshi and Abe 2012) and Brazil (Sato-Okoshi and Takatsuka 2001; Radashevsky and Olivares 2005). Two recent articles, appearing at effectively the same time, using morphology and molecular data have determined that *P. uncinata* is in fact a junior synonym of *P. hoplura* (Radashevsky and Migotto 2017; Sato-Okoshi *et al.* 2016). Radashevsky and Migotto (2017) also reported *P. hoplura* from California, the first records from North America.

Polydora hoplura thus occurs widely in Europe, Japan, South Korea, Australia–New Zealand, South America, and South Africa and is a significant pest of oysters and abalone as a borer into their shells. The molecular data from Sato-Okoshi *et al.* (2016) show no difference between populations in Japan, Australia, and South Africa. The recent identification of *P. hoplura* from several habitats in California by Radashevsky and Migotto (2017) seems to be a new arrival that might cause problems with local shellfisheries. The species has not been recorded in regional California faunal guides (Blake and Ruff 2009).

Polydora colonia is a small spionid that builds tubes in soft sponges on which it feeds. Moore (1907) originally described the species from sponges collected from pilings near Woods Hole, MA, USA. The species has since been reported from Massachusetts to North Carolina and Florida along the US Atlantic coast, Jamaica (as *P. ancistrata* Jones), South Africa, Brazil, and Argentina in the western North and South Atlantic (Blake 1971, 1983; Dauer 1974; Neves and Rocha 2008; Cangussu *et al.* 2010), and from Europe (Aguirre *et al.* 1986; Tena *et al.* 2000; Zenetos *et al.* 2010; Occhipinti-Ambrogi *et al.* 2010). David and Williams (2012) described the larval development and architomic asexual reproduction of the species from off Long Island, NY. The wide distribution of *P. colonia* in the Atlantic Ocean suggests its distribution has been the result of movement with the host sponge, *Microcion prolifera* on the hulls of ships and subsequent colonization of the sponge and polychaete assemblages on docks and pilings in major harbors. However, the point of origin of the species is not known and careful comparison of molecular and morphological data is required to ascertain the origin and status of the polychaete as a cryptogenic or more recently introduced alien species in certain locations. The worm does not seem to cause any harm, but the role of the host sponge in local ecologies where it has been introduced needs to be investigated.

Polydora websteri, often called the mud-blister worm, was originally described by Hartman (1943) from oyster shells in Long Island Sound, CT, USA, but the actual geographic origin of this species is not known. Blake (1971) redescribed and documented the species from Newfoundland and Quebec in eastern Canada and from Maine to South Carolina along the US Atlantic coast. The species has been recorded widely from all three coasts of North America; it has also been recorded and studied in Hawaii (Bailey-Brock and Ringwood 1982), western South America (Blake 1983), Japan (Sato-Okoshi 1999a), Australia (Blake and Kudenov 1978), and New Zealand (Read 2010), where it is considered invasive. *P. websteri* is known to produce mud-blisters in commercial oyster shells throughout its range, thus lowering the market value of the oysters. It has therefore been the subject of several biological studies related to shell boring and effects on commercial molluscs (Hartman 1945, 1951, 1954, 1961, 1969; Medcof 1946; Owen 1957; Hopkins 1958; Foster 1971; Haigler 1969; Evans 1969; Blake and Evans 1973; Zottoli and Carriker 1974; Bergman *et al.* 1982).

Sato-Okoshi and Abe (2012) provided the first molecular analysis using 18S rRNA comparing *Polydora websteri* (Japan and Australia) with two closely related species: *P. calcarea* (Japan and Australia) and *P. haswelli* (Japan). Their results demonstrated that although closely related, the three species were distinct. The results also demonstrated that there was no genetic difference between specimens of *P. websteri* from Japan and Australia. Although the origin of *P. websteri* has not yet been confirmed, the species has most certainly been transported to distant locations with oysters and other molluscs intended for commercial aquaculture. Further molecular analysis will help understand the movement of this species globally.

Pseudopolydora paucibranchiata is a relatively small tube-building spionid polychaete that forms dense assemblages in low intertidal to shallow subtidal sediments. The species was first described from Japan by Okuda (1937) and in Asia it ranges from the Kuril Islands and Japan south to the Yellow Sea and Taiwan (Imajima and Hartman 1964; Radashevsky 1993; Sato-Okoshi 1999b, Radashevsky and Hsieu 2000b). *P. paucibranchiata* also occurs in the Eastern Pacific from Washington to Baja California (Blake 1975; Blake and Woodwick 1975; Light 1977, 1978; Blake and Ruff 2007). The species has been introduced to Australia–New Zealand (Read 1975; Blake and Kudenov 1978; Hutchings and Turvey 1984) and more recently into Europe where it has been recorded from Norway (Ramberg and Schram 1982), Portugal (Rodrigues *et al.* 2011), Spain (Cacabelos *et al.* 2008), and the eastern Mediterranean Sea including the south coast of Turkey, the Aegean Sea, and the Sea of Marmara (Dagli and Çinar 2008; Çinar *et al.* 2011, 2012;

Dagli *et al*. 2011). The larvae of *P. paucibranchiata* are illustrated in Larink and Westheide (2011), a guide to European coastal plankton. There are no published accounts of *P. paucibranchiata* from either the US Atlantic or Gulf coasts; however, several specimens were identified by one of us (JAB) from the east coast of Florida as part of the U.S. EPA National Coastal Condition Assessment program in 2010. Larval development has been described for populations in the Sea of Japan (Myohara 1980) and California (Blake and Woodwick 1975). The species is assumed to have originated in the northwest Pacific and spread from there perhaps to California and Australia. Further expansion of the range could have continued from new locations; however, molecular data is required to confirm the point of origin of the species. Possible vectors for dispersal include ballast water, hull fouling, and sediments associated with transplants of the Pacific oyster (*Crassostrea gigas*) to new locations as an effort to develop commercial populations.

Marenzelleria viridis was originally described by Verrill (1973) as *Scolecolepis viridis* from offshore New England. Hartman (1942), as part of a review of Verrill's collections, transferred the species to *Scolecolepides* without explanation. Maciolek (1984b) redescribed *S. viridis* and transferred it to *Marenzelleria* based on the close similarity of the species to *Marenzelleria wireni*, the type species of the genus. She also redescribed *M. wireni* based on syntypes and new materials from the Arctic. Maciolek (1984b) also reviewed the then known records of the species, which ranged from Nova Scotia to Virginia along the eastern coast of North America. George (1966) had earlier described the reproduction and larval development of the species from Nova Scotia (as *S. viridis*).

Marenzelleria spp. was introduced, probably several times into northern Europe in the 1970s with abundant populations first observed in the North Sea (ca. 1979) and subsequently in the Baltic Sea in 1985 (Bick and Burckhardt 1989; Bastrop *et al*. 1997). The vector for the original introductions in Europe was likely through ballast water. Initially, the northern European species was identified as *M*. cf. *viridis* but with at least three types (I, II, and III) were identified based on allozyme polymorphisms (Röhner *et al*. 1996) and the mitochondrial gene marker, 16S rRNA (Bastrop *et al*. 1997). Types I and II were present in several North American and European populations. Type III was also present in *Marenzelleria* collected in North Carolina (Bastrop *et al*. 1997).

Given the invasive nature of the introductions of *Marenzelleria* spp. into European waters, numerous articles on the biology, ecology, and systematics have been published (see Zettler 1997 for bibliography). Sikorski and Bick (2004) reviewed the taxonomic history of *Marenzelleria* and revised the genus, describing four species with synonyms including the assignment of types I and II identified in the genetic studies. A fifth species from North Carolina was indicated as provisional, but not named until described by Bick (2005b). Bick (2005b) provided a key to all five species; the species and their known distributions are listed in the following:

1. *Marenzelleria wireni* Augener, 1913. Restricted to but widely distributed in Arctic regions.
2. *Marenzelleria arctia* (Chamberlin, 1920). Including some *M. wireni* records; restricted to Arctic estuaries.
3. *Marenzelleria viridis* (Verrill, 1873). Including genetic type I, distributed on the North American Atlantic coast from Nova Scotia to Virginia and in Europe including Scotland and the North Sea.
4. *Marenzelleria neglecta* Sikorski and Bick, 2004. Including some previous *M. viridis* records and genetic type II; distributed on the US Atlantic coast from North Carolina to Georgia and in Europe in the North Sea and Baltic Sea; also introduced into California in the San Joaquin River delta, part of the San Francisco Bay system.
5. *Marenzelleria bastropi* Bick, 2005b. At present, this species, which is genetic type III, seems to be rare, having been collected only from Currituck Sound, NC, USA.

A phylogenetic analysis using 16S rDNA, cytochrome *b*, and COI was developed by Blank and Bastrop (2009), which indicated that the basal species were *M. wireni* and *M. arctia*, thus suggesting an Arctic origin for the genus. Based on the morphological and genetic studies, it was evident that two North American species, *M. viridis* (genetic type I) and *M. neglecta* (genetic type II) were introduced into Europe independently as hypothesized by Bastrop *et al*. (1998). Studies on larval development of *M. viridis* by George (1966) and Bochert and Bick (1995) suggest that the species has a sufficiently long larval life to survive for up to 8 weeks, which is more than enough time to survive a trip across the Atlantic in ballast water and discharge into European waters. Bastrop *et al*. (1998) postulated that *Marenzelleria* in the North Sea (type I = *M. viridis fide* Sikorski and Bick 2004) was derived from populations introduced from North American sites north of Chesapeake Bay to New England and Nova Scotia, whereas *Marenzelleria* in the Baltic Sea (type II = *M. neglecta fide* Sikorski and Bick 2004) was derived from populations south of Chesapeake Bay in the southeast United States.

Recently, *Marenzelleria neglecta* has invaded the mouth of the Don River, Taganrog Bay, and other sites in the mouth of Sea of Azov, which borders both Ukraine and Russia; the species is now dominant in several locations (Syomin *et al*. 2017). These authors also report *M. neglecta* in the Strait of Kertch and some sites in the Black Sea.

Phylogeny and taxonomy

Spionidae comprise approximately 590 species in 38 genera. Although more than 70% of species belong to the eight largest genera, 19 genera are monotypic.

Taxonomic history

The systematic literature of the Spionidae is one of the most extensive among all of the Polychaeta. Currently, the Spionidae includes approximately 590 species and 38 valid genera (Read and Fauchald 2017; and additional references). The family Spionidae was established by Grube (1850) to include the genera *Spio* Fabricius, 1785, *Polydora* Bosc, 1802, *Scolelepis* Blainville, 1828, and *Malacoceros* Quatrefages, 1843. The first efforts to synthesize spionid systematics were by Carazzi (1893) and Mesnil (1896). Carazzi (1893) reviewed species of *Polydora* and established the genus *Boccardia*, which has branchiae anterior to chaetiger 5 and two types of modified spines. Mesnil (1896) divided the family into two groups based on external morphology: (1) species with a narrow prostomium, including *Polydora, Boccardia, Laonice, Spio, Microspio, Nerinides, Aonides, Nerine, Spionides* (= *Laonice*), and *Pygospio*; and (2) species with lateral processes or horns on the prostomium, including *Scolelepis* (= *Malacoceros*) and *Marenzelleria*. Mesnil (1896) also considered the distribution of branchiae, form of anal cirri, occurrence of dorsal hooded hooks, and presence of capillaries in segments with hooded hooks as significant generic characters. He removed the genus *Disoma* to a separate family (currently the genus *Trochochaeta*, family Trochochaetidae Pettibone).

Söderström (1920) emphasized internal morphology, including reproductive characters. He observed that certain genera, including *Spio, Microspio, Pygospio,* and *Polydora* formed a well-defined group having similar nephridia, thin-membraned eggs, long-headed sperm, and produced egg capsules that were incubated by females within their tubes. For these genera, he established the subfamily Spioninae. Other spionids having thick-membraned eggs, a different nephridial structure, and short-headed sperm included the genera *Nerine* (= *Malacoceros*), *Colobranchus* (= *Malacoceros*), *Scolecolepis* (= *Scolelepis*), and *Aonides* were referred to the subfamily Nerininae. Söderström (1920) also considered the nephridia and genital structures of *Laonice* to be sufficiently different to establish yet another subfamily, the Laonicinae. These categories were supported by studies of larval development by Hannerz (1956), sperm morphology by Franzén (1956), and adult morphology by Orrhage (1964).

In the years since Söderström's 1920 monograph, spionids have increasingly been reported globally, mostly from shallow-water habitats but also from the deep sea. Important works treating multiple species include:

1. *European waters*: Fauvel (1927); Sigvaldadóttir (1992, 2002); Sigvaldadóttir and Mackie (1993); Hartmann-Schroder (1996); Bick *et al*. (2010); Meißner *et al*. (2011).
2. *South Africa*: Day (1961, 1967); Simon (2009, 2011).
3. *US Atlantic coast*: Pettibone (1962; 1963); Blake (1971); Day (1973); Maciolek (1984a,b, 1985, 1987, 1990, 2000).
4. *Gulf of Mexico and Caribbean Sea*: Hartman (1951); Foster (1971); Delgado-Blas (2006, 2008).
5. *Northeastern Pacific*: Berkeley and Berkeley (1952); Hartman (1936, 1941, 1969); Banse and Hobson (1968); Hobson and Banse (1981); Light (1978); Woodwick (1963a,b); Blake and Woodwick (1971, 1972); Blake (1996).
6. *Northwestern Pacific*: Imajima (1959, 1989, 1990a–e, 1991, 1992); Radashevsky (1993; 1994a,b); Sato-Okoshi (1998, 1999a,b).
7. *Taiwan*: Radashevsky and Hsieh (2000a,b).
8. *Central and Southern Pacific*: Woodwick (1964); Ward (1981).
9. *Australia–New Zealand*: Blake and Kudenov (1978); Hutchings and Rainer (1979); Hutchings and Turvey (1984); Rainer (1973); Read (1975); Blake (1984);. Wilson (1990), Meißner and Götting (2015); Radashevsky (2015); Walker (2011).
10. *South America and Antarctica*: Hartman (1967); Blake (1983); Radashevsky and Lana (2009); Radashevsky *et al*. (2006).

Deep-water taxa are now being treated more regularly. For example, most of Maciolek's articles cited previously include species from the deep-water collections made in the Atlantic Ocean by Dr. Howard Sanders of the Woods Hole Oceanographic Institution; Paterson *et al*. (2016) described new species from worldwide deep-sea locations. Meißner *et al*. (2014) described spionids from Northeast Atlantic seamounts. However, large numbers of deep-sea spionids from the US Atlantic and Pacific slopes and elsewhere remain undescribed (Blake and Maciolek unpublished).