



1979

Observations on the reproductive morphology of some California spionid polychaetes : a thesis ...

F. Scott McEuen
University of the Pacific

Follow this and additional works at: https://scholarlycommons.pacific.edu/uop_etds



Part of the [Life Sciences Commons](#)

Recommended Citation

McEuen, F. Scott. (1979). *Observations on the reproductive morphology of some California spionid polychaetes : a thesis* University of the Pacific, Thesis. https://scholarlycommons.pacific.edu/uop_etds/2013

This Thesis is brought to you for free and open access by the Graduate School at Scholarly Commons. It has been accepted for inclusion in University of the Pacific Theses and Dissertations by an authorized administrator of Scholarly Commons. For more information, please contact mgibney@pacific.edu.

OBSERVATIONS ON THE REPRODUCTIVE MORPHOLOGY OF
SOME CALIFORNIA SPIONID POLYCHAETES

A Thesis

Presented to the Graduate Faculty
of the University of the Pacific

In Partial Fulfillment
of the Requirements for the
Degree of Master of Science

by

F. Scott McEuen

August 17, 1979

This thesis, written and submitted by

F. Scott McEuen

is approved for recommendation to the
Committee on Graduate Studies, University
of the Pacific.

Department Chairman or Dean:

Thesis Committee:

James A. Blake Chairman
Edward W. Smith
Steven Chelowski

Dated June 15, 1979

ACKNOWLEDGMENTS

A number of people have been instrumental in seeing this thesis to its completion. Appreciation is expressed to Dr. James Blake for help in all phases of the research, especially for the use of his literature, equipment, and for his patience and knowledgeable suggestions. I am grateful to Dr. Edmund Smith for introducing me to the fundamentals of histological and histochemical laboratory methods and techniques. Thanks are also due to Dr. Steven Obrebski for reviewing the manuscript. My studies at Dillon Beach were greatly facilitated by the moral and financial support of my parents, to whom I am greatly indebted.

TABLE OF CONTENTS

	PAGE
Acknowledgmentsiii
Table of Contents	iv
List of Figures and Table	v
Abstract.	1
Introduction.	3
Materials and Methods	4
Observations.	6
Discussion.	13
Literature Cited.	20
Explanation of Text-Figures	25
Figures	26
Table	41

LIST OF FIGURES AND TABLE

FIGURE	PAGE
1 <u>Boccardia proboscidea</u> : secondary spermatocytes26
2 <u>Boccardia proboscidea</u> : rosette26
3 <u>Boccardia proboscidea</u> : early spermatid26
4 <u>Boccardia proboscidea</u> : tetrad26
5 <u>Boccardia proboscidea</u> : tetrad ready to separate.26
6 <u>Boccardia proboscidea</u> : spermatid26
7 <u>Boccardia proboscidea</u> : late spermatid.26
8 <u>Boccardia proboscidea</u> : mature spermatozoon27
9 <u>Polydora convexa</u> : late spermatid27
10 <u>Polydora convexa</u> : late spermatid27
11 <u>Polydora convexa</u> : mature sperm27
12 <u>Polydora websteri</u> : tetrad.27
13 <u>Polydora websteri</u> : late spermatid.27
14 <u>Polydora websteri</u> : late spermatid.27
15 <u>Polydora websteri</u> : mature sperm.27
16 <u>Pseudopolydora kemp</u> : platelet in transition to a rosette.28
17 <u>Pseudopolydora kemp</u> : rosette.28
18 <u>Pseudopolydora kemp</u> : tetrad ready to separate.28
19 <u>Pseudopolydora kemp</u> : late spermatid28

(con.)

LIST OF FIGURES AND TABLE

20	<u>Pseudopolydora kemp</u> : mature sperm.28
21	<u>Pseudopolydora kemp</u> : mature sperm.29
22	<u>Pseudopolydora paucibranchiata</u> : secondary spermatocytes.29
23	<u>Pseudopolydora paucibranchiata</u> : late spermatid.29
24	<u>Pseudopolydora paucibranchiata</u> : late spermatid.29
25	<u>Pseudopolydora paucibranchiata</u> : late spermatid.29
26	<u>Pseudopolydora paucibranchiata</u> : mature sperm. .	.29
27	<u>Pygospio californica</u> : secondary spermatocyte. .	.30
28	<u>Pygospio californica</u> : formation of platelet from secondary spermatocyte.30
29	<u>Pygospio californica</u> : early spermatid30
30	<u>Pygospio californica</u> : mature spermatozoon30
31	<u>Pygospio californica</u> : mature spermatozoon30
32	<u>Pygospio elegans</u> : rosette30
33	<u>Scoelelepis tridentata</u> : early spermatid.31
34	<u>Scoelelepis tridentata</u> : tetrad31
35	<u>Scoelelepis tridentata</u> : late spermatid31
36	<u>Scoelelepis tridentata</u> : mature sperm31
37	<u>Spiophanes bombyx</u> : tetrad31
38	<u>Spiophanes bombyx</u> : spermatid.31
39	<u>Spiophanes bombyx</u> : mature sperm31

(con.) LIST OF FIGURES AND TABLE

40	<u>Streblospio benedicti</u> : tetrad32
41	<u>Streblospio benedicti</u> : early spermatid32
42	<u>Streblospio benedicti</u> : late spermatid32
43	<u>Streblospio benedicti</u> : late spermatid32
44	<u>Streblospio benedicti</u> : late spermatid32
45	<u>Streblospio benedicti</u> : late spermatid32
46	<u>Streblospio benedicti</u> : mature sperm32
47	<u>Boccardia proboscidea</u> : epitokal nephridium, female33
48	<u>Pseudopolydora kemp</u> : epitokal nephridium, female33
49	<u>Pseudopolydora paucibranchiata</u> : epitokal nephridium, female33
50	<u>Pygospio californica</u> : epitokal nephridium, female33
51	<u>Pygospio californica</u> : male with sperm aligned in the coelomostome33
52	<u>Pseudopolydora paucibranchiata</u> : epitokal nephridium, male34
53	<u>Scoelelepis tridentata</u> : epitokal nephridium, female34
54	<u>Scoelelepis tridentata</u> : unmodified nephridium, gravid male35
55	<u>Streblospio benedicti</u> : female seminal receptacle36
56	<u>Pseudopolydora paucibranchiata</u> : female seminal receptacle36

(con.) LIST OF FIGURES AND TABLE

57	<u>Pseudopolydora paucibranchiata</u> : female seminal receptacle36
58	<u>Pygospio californica</u> : female seminal receptacle36
59	<u>Pseudopolydora paucibranchiata</u> : single nephridiopore.37
60	<u>Boccardia proboscidea</u> : double nephridiopores. .	.37
61	<u>Pygospio californica</u> : aligned sperm in coelomostome of male38
62	<u>Scoelelepis tridentata</u> : bulky nephridia, female38
63	<u>Streblospio benedicti</u> : seminal receptacle, female39
64	<u>Pygospio californica</u> : seminal receptacle, female39
65	<u>Boccardia proboscidea</u> : ovary and vitellogenesis, female40
	Table of spionid sperm measurements.	41-42

ABSTRACT

Several aspects of the reproductive morphology of the polychaete family Spionidae were investigated. Spermiogenesis follows a common pattern among species of the subfamily Spioninae, with the mature aberrant spermatozoon of each species having its own characteristic morphology and dimension. With other spionids, interesting variations occur in the primitive sperms of Scoelepis tridentata and Spiophanes bombyx and with the aberrant sperm of Streblospio benedicti. The modified nephridia of epitokal segments in mature females of species of the Spioninae possess columnar cells filled with basophilic granules, which are thought to produce the mucous material for egg capsules. Males of Pygospio californica have a swollen zone of granular cells just posterior to the coelomostome in epitokal nephridia which suggests that mucous is produced here to aid in the formation of spermatophores. Mature sperm of this species align themselves side by side along the interior of the dorsal lip of the coelomostome with heads pointed in the same direction. Epitokal nephridia of male Scoelepis tridentata are unmodified, while those of the female are large and bulky and are probably responsible for the cocoon spawned by this species.

Intra-epidermal seminal receptacles are present in Pseudopolydora kemp, P. paucibranchiata, Pygospio californica, and Streblospio benedicti. The unusually large size of the seminal receptacle in S. benedicti may be correlated with the long sperm head of this species. Histological sections show the ovaries and testes of all species to be attached directly to, or an outgrowth of, the ventral coelomic epithelium and situated just posterior to the intersegmental septum. An exception is Scoelelepis tridentata, in which the female oocytes are not bound in a structurally distinct gonad, but remain connected to the germinal epithelium until reaching a large size.

INTRODUCTION

Sexual reproduction in polychaetes is highly diverse ranging from the free spawning of gametes into seawater to highly specialized modes of copulation with subsequent brooding of embryos. Polychaetes of the Family Spionidae also possess a variety of unique modifications in reproduction. Our knowledge of spionid reproduction comes largely from the works of Söderström (1920), Hannerz (1956), Franzén (1956), Dorsett (1961), Simon (1967), Blake (1969), Rice and Reish (1976), and Rice (1978). From this information a general picture of spionid reproduction has emerged, but numerous details concerning gametogenesis and fertilization are still incompletely known.

The Spionidae have been divided into several subfamilies based upon reproductive characteristics (Söderström, 1920; Hannerz, 1956; Orrhage, 1964). Franzén (1956) in his studies of polychaete spermiogenesis connects an elongated, modified middle piece of the mature sperm to a specialized "biology of fertilization" and also asserts that in some cases, the sperm morphology can be used as a complementary characteristic in studies of phylogeny and taxonomy.

This study considers the morphology of the sperm, nephridia, seminal receptacles, and gonads among a number

of California spionid species. The data collected provide support for the general observations of other workers.

MATERIALS AND METHODS

Sexually mature adults of 11 species from seven spionid genera were collected from a variety of habitats in Tomales Bay and Bodega Harbor, California. Species living in sand and muddy sand (Boccardia proboscidea Hartman, Polydora ligni Webster, Pseudopolydora kemp (Southern), P. paucibranchiata (Okuda), Pygospio californica Hartman, P. elegans Claparede, Scoelelepis tridentata (Southern), Spiophanes bombyx (Claparède), and Streblospio benedicti Webster) were collected by hand and separated from the sediment with a 0.701mm sieve; shell-boring species (Polydora convexa Blake and Woodwick, P. websteri Hartman) were picked from galleries in the shells of Pododesmus cepio (Gray) and Crassostrea virginica (Gmelin). Individuals were kept in Stender dishes with fresh seawater and a small amount of sand.

For histology and histochemistry with light microscopy, gravid adults were anesthetized in magnesium chloride for 15 minutes and fixed for one hour in 5% glutaraldehyde, followed by 15 minutes in a 0.5M sodium

phosphate buffer at a pH of 7.4 (Galigher and Kozloff, 1971). Specimens were then dehydrated up through absolute isopropanol, infiltrated and embedded in butoxyethanol-glycol methacrylate (Bennett et al., 1976), and sectioned on an American Optical 820 microtome in a warm humid room. Serial sections of 3 μ m thickness were obtained by applying Softseal Tackiwax (Cenco Scientific Products) to the top side of the plastic block and paraffin (melting point 54-58°C) to the bottom side. Best results were obtained with a 4mm-square block. Sections were immersed in Lee's methylene blue-basic fuchsin stain for five seconds (Bennett et al., 1976).

Live material was used for the study of spermiogenesis. Testicular tissue was stained with 0.05% concentrations of Janus green B and neutral red seawater solutions and placed on a slide in a moist chamber for 15 minutes (Franzén, 1956).

Microscopes used for all observations and measurements included a Wild M-5 stereomicroscope, a Leitz Wetzlar SM with camera lucida, and a Zeiss RA having bright field and phase contrast illumination and equipped with a Honeywell Pentax 35mm camera.

OBSERVATIONS

Spermiogenesis

The stages of spermiogenesis for 11 species were examined. Eight species (Boccardia proboscidea, Polydora convexa, P. ligni, P. websteri, Pseudopolydora kempi, P. paucibranchiata, Pygospio californica, and P. elegans) belong to the subfamily Spioninae and possess a similar morphology in the development of the primary spermatocyte to the mature spermatozoon.

Secondary spermatocytes of B. proboscidea (Fig. 1) have a dictyosome and two pairs of mitochondrial spheres. Subsequent meiotic divisions produce a rosette of eight spermatids that later split and form the tetrad arrangement. The spermatid tetrad then breaks up and the individual spermatids complete their development into mature sperms (Figs. 2-8). This whole process of maturation includes formation of the acrosome and middle piece and elongation of the nucleus. The mitochondrial spheres and grains present in early stages disperse to form a homogeneous distribution of mitochondrial material in the middle piece.

The late spermatids of Polydora convexa (Figs. 9-10) illustrate the backward shift of plasm that is concurrent

with the lengthening of the nucleus. Here, as in B. proboscidea, the acrosome is composed of two parts. Polydora websteri was noted to have a ring of mitochondria (Fig. 12) where the tail filament emerges from the young spermatid. Figure 14 shows the neutral red vacuole to be the last, large, dark staining cytoplasmic component of any size prior to final completion of the middle piece. A long, pointed, conical acrosome and axial filament are characteristic of this species.

Head dimensions of the morphologically mature sperms of Pseudopolydora kemp and P. paucibranchiata are very similar. The anterior half of the nucleus tapers towards the pointed acrosome (Figs. 20-21). An axial filament extends through the middle piece and nucleus in P. kemp, but not in P. paucibranchiata. A platelet making the transition to a rosette is shown in Figure 16. The acrosome of the sperm of Pygospio californica ends in a refractive knob and actively pivots at its junction with the nucleus (Figs. 30-31).

Three species not of the subfamily Spioninae provide interesting deviations in sperm morphology. The nuclei of mature spermatozoa of Scolecopsis tridentata (subfamily Nerininae) are triangular with an extended apex (Fig. 36). A refractive zone is present at the tip of the nucleus,

but no specific acrosomal structure could be discerned. The middle piece is composed of four circular bodies that do not stain with Janus green B. Each circular body contains a small mitochondrial sphere. The sperms of Spiophanes bombyx (subfamily Laonicinae) are characterized by having a square-shaped nucleus, a broad-based acrosome narrowing sharply to a point, and four large mitochondrial spheres (Figs. 38-39).

The latter two species (Scolelepis tridentata and Spiophanes bombyx) possess the primitive type sperm whereas those of the subfamily Spioninae are of the aberrant type. A unique aberrant form was found in Streblospio benedicti (subfamily Laonicinae). The head of the early spermatid undergoes a tremendous elongation to form a very long, thin, filiform, mature sperm (Fig. 46). It is not possible to resolve the nucleus from the acrosome or middle piece with light microscopy.

Comparative measurements of the mature sperm of 22 species of Spionidae are listed in Table 1.

Epitokal Nephridia

Sections were made of mature adults of Boccardia proboscidea, Pseudopolydora kempfi, P. paucibranchiata,

Pygospio californica, Scoelepis tridentata and Streblospio benedicti. Males and females having ripe gametes also had epitokal nephridia.

Females of B. proboscidea, Pseudopolydora kempi, P. paucibranchiata, and Pygospio californica have a similar epitokal nephridial structure (Figs. 47-50). The columnar cells of the modified nephridia are densely packed with dark staining basophilic granules. These cells occur along the entire organ, except for the enlarged ciliated funnel. The dorsal and ventral lips of the ciliated funnel may be fused to the septum, wrapped around the nephridial blood vessel, or hang free in the coelom. The two nephridia in each segment meet dorsally to form a common nephridiopore in Pseudopolydora kempi and P. paucibranchiata or two separate paired openings on either side of the mid-line in B. proboscidea (Figs. 59-60).

In the ciliated funnel of Pygospio californica males, the mature sperms are arranged in an orderly compact column along the interior of the dorsal lip (Figs. 51, 61). The dimensions of these sperms are the same as those taken from the coelom during the studies of spermiogenesis. A spermatophore, similar to that described by Söderström (1920) for P. elegans, was also observed in a male nephridium of P. californica. This spermatophore contained

mucous but the mature sperms aligned along the lip of the coelomostome did not. Posterior to the ciliated funnel is a swollen area of granular columnar cells that continue to the septum. From the septum to the nephridiopore, the nephridium is heavily ciliated with agranular thin-celled walls. Occasional granular cells occur in the otherwise unmodified male epitokal nephridium of Pseudopolydora paucibranchiata (Fig. 52).

The nephridia of male and female Scoelelepis tridentata contrast greatly with each other and with other spionids (Figs. 52-52, 62). The female nephridium is large and bulky with granular columnar cells. This cell type ends shortly before the ciliated funnel, where it is replaced by a short section of cuboidal cells. The male has little if any modification to its epitokal nephridium. Cuboidal cells in the ascending upper half of the nephridium narrow to where individual cells of the nephridial wall are not discernible. In both sexes, the two nephridiopores of each segment are laterally located. In all spionids examined, the entire canal of every epitokal nephridia is ciliated from the nephridiopore through the ciliated funnel. No epitokal nephridia were encountered in Streblospio benedicti.

Seminal Receptacles

Seminal receptacles or gamete storage sacs occur in the epitokous region of some spionid species. Those mature females of Pseudopolydora kemp, P. paucibranchiata, Pygospio californica, and Streblospio benedicti having the coelom filled with eggs also possessed seminal receptacles full of sperm. No spermatophores were observed in any of the receptacles.

Streblospio benedicti has only three seminal receptacles per female, but they are the largest receptacles encountered. Each receptacle occupies the entire length of a segment (192 μ m) and extends 82 μ m into the epidermis (Figs. 55, 63). The sac, lined with a layer of long, thin cells, opens anteriorly by way of a ventrally-directed duct. A combination of non-ciliated cuboidal and columnar cells comprise the duct. The three receptacles are located consecutively at about segments 14-16. There is no opening from the seminal receptacle to the coelom.

The paired receptacles of Pseudopolydora kemp and P. paucibranchiata are also intra-epidermal, but positioned dorsally (Figs. 56-57). They lie anteriorly in a position close to the upper nephridial canal of the neighboring segment and are present in all epitokal segments. The oval-shaped sac of P. kemp is 62 μ m deep and is connected

to the exterior via a vertically-directed duct. The U-shaped duct of P. paucibranchiata is lined with cuboidal cells; the sac has a depth of 29 μ m.

Three of the seven pairs of seminal receptacles encountered in Pygospio californica are in the three atokal segments preceding the epitokous region; the other four being situated in the subsequent epitokal segments. Cuboidal cells constitute the duct wall that leads to a 67 μ m-deep receptacle made of flattened cells. Lying ventral to the nototroch, the circular and longitudinal muscles border the seminal receptacle on the top and bottom, respectively (Figs. 58, 64).

Gametogenesis

Structurally distinct gonads of male and female spionids are found immediately posterior to the intersegmental septum and attached to the ventral coelomic epithelium. It is assumed that the germ cells have their origin in the germinal epithelium and migrate up into the gonad. The developing oocytes of Scolecopsis tridentata remain attached to the coelomic epithelium until they are nearly full size, but are not contained in a gonadal structure during any phase of their development. Vitellogenesis in Boccardia proboscidea takes place while the oocytes are

still part of the gonad (Fig. 65).

DISCUSSION

The wide scope of variation in polychaete reproduction has been reviewed by Schroeder and Hermans (1975) and Olive and Clark (1978). Semi-continuous reproduction is common to small interstitial polychaetes and is usually associated with sperm storage vesicles, spermatophores, direct copulation, and cocoon deposition (Olive and Clark, 1978). Many spionid polychaetes are known for their specialized modes of reproduction, but many details remain to be understood.

Söderström (1920) divided the Spionidae into three subfamilies using reproductive characteristics for some of the distinguishing traits. The subfamily Spioninae (Boccardia, Microspio, Polydora, Pseudopolydora, Pygospio, Spio) possesses greatly modified epitokal nephridia, seminal receptacles in the female, thin-membraned eggs, long-headed sperm, and internal fertilization involving spermatophores and copulation. The other two subfamilies Laonicinae (Laonice, Prionospio, Spiophanes) and Neriniinae (now including Scoelelepis sensu Pettibone, 1963 and Aonides) lack great modification to the nephridia or seminal receptacles, but do have thick-membraned eggs,

highly vesicular eggs, short-headed sperm, and pelagic development. Hannerz (1956), as part of his larval monograph, further characterized the Spioninae as having brood protection in that all of the species pass part of their development in formed structures.

The observation by Söderström and Hannerz that long-headed sperm were connected with a specialized biology of fertilization was clarified by Franzén (1956) who showed that this connection lay principally in the composition of the middle piece of the sperm and not in the structure of the head. Those species having a specialized mode of reproduction usually possess an elongated head with a modified middle piece whereas other spionid species normally have primitive type sperm with the middle piece consisting of 4-5 mitochondrial spheres. Each species of the subfamily Spioninae examined in the present study (Boccardia proboscidea, Polydora convexa, P. ligni, P. websteri, Pseudopolydora kempi, P. paucibranchiata, Pygospio californica, and P. elegans) were all very much alike in the morphology of their sequential stages of spermiogenesis. The following is a listing of these consecutive stages as they occur in the development of a primary spermatocyte to a mature sperm, similar to those proposed by Franzén (1956) and Gibbs (1971).

1. A primary spermatocyte is produced from spermatogonial cells in the testis and through meiosis is split into two secondary spermatocytes.
2. Two secondary spermatocytes divide into four spermatids, with each forming a platelet of eight cells.
3. The platelet of eight cells becomes a rosette upon formation of the tail pieces. This rosette then separates into two groups of tetrads.
4. Nuclei of the tetrads elongate and the mitochondrial spheres and grains begin to diffuse. The tetrads detach from one another to become eight individual spermatids.
5. Lengthening of the nucleus, receding of the cytoplasmic sheath and diffusion of the mitochondrial material, and formation of a pointed, conical acrosome complete the maturation of the sperm.

Comparisons of the measurements contained in Table 1 for species of the subfamily Spioninae reveal that for the most part they fall into a common size range.

Scolecopsis tridentata and Spiophanes bombyx which belong to the subfamilies Nerininae and Laonicinae respectively, and have a primitive type sperm, and are in agreement with Franzén's hypothesis concerning the biology of

fertilization. The middle piece of mature sperm of Scoelelepis squamata as described by Richards (1970) and S. tridentata (this study) fail to stain with Janus green B, but S. tridentata does have a small mitochondrial sphere in each of the circular bodies constituting its middle piece. The sperm of these two related species are alike with respect to their both being of the primitive type, but they differ greatly in the shape of the nucleus and middle piece. Richards also found female S. squamata to have leaf-like, irregularly-shaped spermatophores bound in a matrix attached to the body surface; no comparable structures were discovered for S. tridentata. In keeping with its unusual mode of reproduction of rearing its young in dorsal brood chambers, Streblospio benedicti (Campbell, 1957; Dean, 1965) has sperm of the aberrant type. More studies are needed to determine what there is in the biology of fertilization of this species to require such a highly modified sperm that is unlike any other known sperm type in spionids. According to current nomenclature, Streblospio is related to the Prionospio-complex (Blake and Kudenov, 1978). Söderström (1920) placed this group in the subfamily Laonicinae. Streblospio thus differs from the generalization that species not of the Spioninae spawn freely into seawater and possess the primitive type sperm.

The Spionidae belong to a group of sedentary polychaete families possessing mixonephridia. These are U-shaped nephridia having a dorsal nephridiopore at one end and large coelomostome at the other that may undergo various specializations according to whether they are more excretory or genital in function (Goodrich, 1945). Söderström (1920) has proposed that the epitokal nephridia participate in the formation of spermatophores and gelatinous egg capsules. The histological sections of male Pygospio californica suggest that when mature sperm align themselves along the dorsal lip of the coelomostome they then somehow combine with mucous from the nearby mucous cells of the nephridium to form the spermatophore. Söderstrom also describes the spermatophore of P. elegans similarly in saying that the sperm heads are clearly arranged in regular rows entirely in the vicinity of the nephrostome. The lack of similar structures (viz., aligned sperms) in other spionids may be due to a different mechanism of spermatophore production. The complete absence of granular cells in nephridia of mature male Scolelepis tridentata indicates that there is probably no distinct spermatophore structure for this species, the sperm probably being emitted either through the nephridia or by a rupture of the body wall. The large, bulky epi-

tokal nephridia of female S. tridentata are thought to produce the mucous material for the cocoon containing soft-membraned eggs it spawns in winter and spring months (Blake, unpublished data). Epitokal nephridia are also present in S. squamata (Richards, 1970). The modified nephridia, along with the cocoon and soft-membraned eggs of S. tridentata, are an exception to Söderström's and Franzén's classification criteria in reproductive morphology for the subfamily Nerininae. Other nephridia in epitokal segments of the other species studied are in the usual hypertrophied condition common to most of the Spionidae (see Cunningham, 1888; Dorsett, 1961; Goodrich, 1945; Mortensen, 1945; Simon, 1967). The number of dorsal nephridiopores in Pseudopolydora kempi are in agreement with the number of egg capsule stalks described by Blake and Woodwick (1975). The two nephridiopores found in sections of B. proboscidea also verify the double stalks of the egg cases mentioned by Hartman (1941).

The only previous detailed description of a spionid seminal receptacle is for Spio setosa (Simon, 1967). Brief mention is made of those in Streblospio benedicti by Collier and Jones (1967), in Polydora by Blake (1969), and in Microspio, Polydora, Pygospio, and Spio by Söderström (1920). The cuboidal and flattened cell types of

the duct and receptacle, respectively, are seen also in the receptacles described in this paper. The unusually large receptacle in S. benedicti and the smaller sizes of those in Pseudopolydora kempi, P. paucibranchiata, and Pygospio californica might in part be attributed to the length of the head of the sperm; the sperm head of S. benedicti being more than three times the length of any other sperm head of other species (see Table 1).

It is not known how sperm from these receptacles fertilize the eggs, whether by penetrating the wall of the receptacle and entering the coelom or by being forced out of the receptacle by muscular contractions in coordination with spawning of the eggs.

LITERATURE CITED

- Bennett, H.S., Wyrick, A.D., Lee, S.W., McNeil, Jr., J.H.:
Science and art in preparing tissues embedded in
plastic for light microscopy, with special reference
to glycol methacrylate, glass knives and simple
stains. *Stain Tech.* 51(2), 71-97 (1976)
- Blake, J.A.: Systematics, reproduction and larval devel-
opment of Polydora from eastern North America (Poly-
chaeta: Spionidae). Ph.D. Diss., 259 pp., Universi-
ty of Maine (1969)
- Blake, J.A.: Reproduction and larval development of Poly-
dora from northern New England (Polychaeta: Spionidae).
Ophelia 7, 1-63 (1969)
- Blake, J.A., Kudenov, J.D.: The Spionidae (polychaeta)
from southeastern Australia and adjacent areas with
a revision of the genera. *Mem. Nat. Mus. Vic.* 39,
17-280 (1978)
- Blake, J.A., Woodwick, K.H.: Reproduction and larval devel-
opment of Pseudopolydora paucibranchiata (Okuda) and
Pseudopolydora kempi (Southern) (Polychaeta: Spioni-
dae). *Biol. Bull.* 148(4), 109-127 (1975)
- Campbell, M.A.: Larval development of Streblospio benedicti
Webster. *Biol. Bull.* 113, 336-337 (1957)

- Clark, R.B.: Reproduction, speciation, and polychaete taxonomy. In: Essays on polychaetous annelids in memory of Dr. Olga Hartman (D.J. Reish, K. Fauchald, eds.), pp. 477-501. Los Angeles: Allan Hancock Foundation 1977
- Collier, M., Jones, M.L.: Observations on the reproductive and general morphology of Streblospio benedicti Webster. Biol. Bull. 133, 462 (1967)
- Cunningham, J.T.: On some points in the anatomy of polychaeta. Quart. J. Microsc. Soc. 281, 239-279 (1888)
- Day, R.L., Blake, J.A.: Reproduction and larval development of Polydora giardi Mesnil (Polychaeta: Spionidae). Biol Bull. 156(1), 20-30 (1979)
- Dean, D.: On the reproduction and larval development of Streblospio benedicti (Webster). Biol Bull. 128, 67-76 (1965)
- Dorsett, D.A.: The reproduction and maintenance of Polydora ciliata (Johnst.) at Whitstable. J. Mar. Biol. Ass. U.K. 41, 383-396 (1961)
- Franzén, Å.: On spermiogenesis, morphology of the spermatozoon and biology of fertilization among invertebrates. Zool. Bidr. Uppsala 31, 355-482 (1956)
- Galigher, A.E., Kozloff, E.N.: Essentials of Practical Microtechnique. Philadelphia: Lea and Febiger 1971

- George, J.D.: Reproduction and early development of the spionid polychaete Scolecopides viridis (Verrill). Biol. Bull. 130, 76-93 (1966)
- Gibbs, P.E.: A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. J. Mar. Biol. Ass. U.K. 48, 225-254 (1971)
- Goodrich, E.S.: The study of nephridia and genital ducts since 1895. Quart. J. Microsc. Sci. 86, 113-392 (1945)
- Hannerz, L.: Larval development of the polychaete families Spionidae Sars, Disomidae Mesnil, and Poecilochaetidae n. fam. in the Gullmar Fjord (Sweden). Zool. Bidr. Uppsala 31, 1-204 (1956)
- Hartman, O.: Some contributions to the biology and life history of Spionidae from California: with keys to species and genera and descriptions of two new forms. Allan Hancock Pac. Exped. 7, 287-324 (1941)
- Lo Bianco, S.: Notizie Biologiche riguardanti specialment il periodo di maturita sessuale degli animali del golfo di Napoli. Mitt Zool. Stat. Neapel 13, 448-573 (1899)
- Mortensen, E.E.: The morphology, behavior, and habits of Polydora ligni. Dissertation, George Washington

Univ. 1945

Olive, P.J.W., Clark, R.B.: Physiology of Reproduction.

In: Physiology of Annelids, ed. Mill, P.J., pp. 271-368. New York-London-San Francisco: Academic Press 1978

Orrhage, L.: Anatomische und morphologische Studien über die Polychaeten familien Spionidae, Disomidae und Poecilochaetidae. Zool. Bidr. Uppsala 36, 335-405 (1964)

Pettibone, M.H.: Revision of some genera of polychaete worms of the family Spionidae, including the description of a new species of Scolelepis. Proc. biol. Soc. Wash. 76, 89-104 (1963)

Rice, S.A.: Spermatophores and sperm transfer in spionid polychaetes. Trans. Amer. Microsc. Soc. 97(2), 160-170 (1978)

Rice, S.A., Reish, D.J.: Egg capsule formation in the polychaete Polydora ligni: confirmation of an hypothesis. Bull. So. Cal. Acad. Sci. 75(3), 285-286 (1976)

Richards, S.L.: Spawning and reproductive morphology of Scolelepis squamata (Spionidae: Polychaete). Can. J. Zool. 48, 1369-1379 (1970)

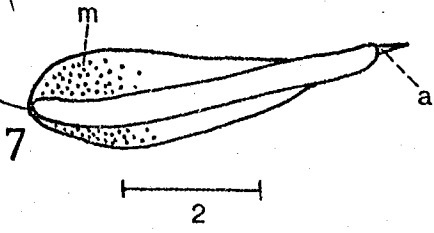
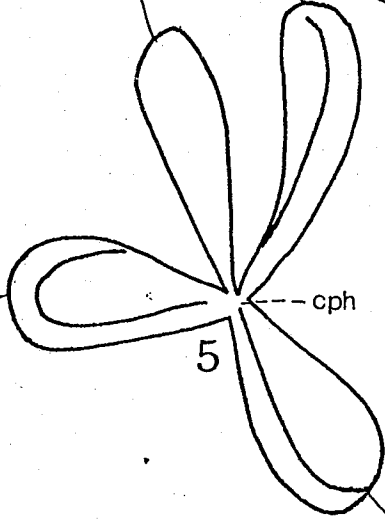
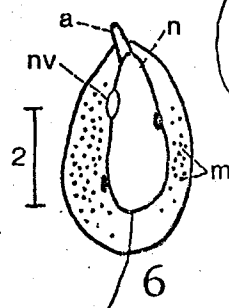
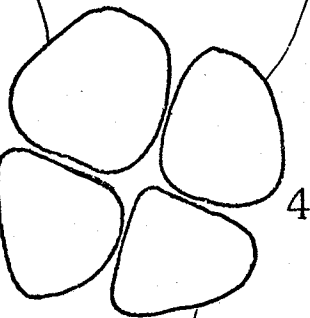
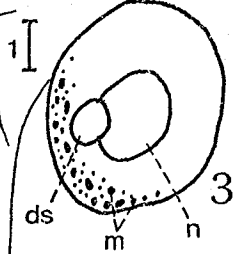
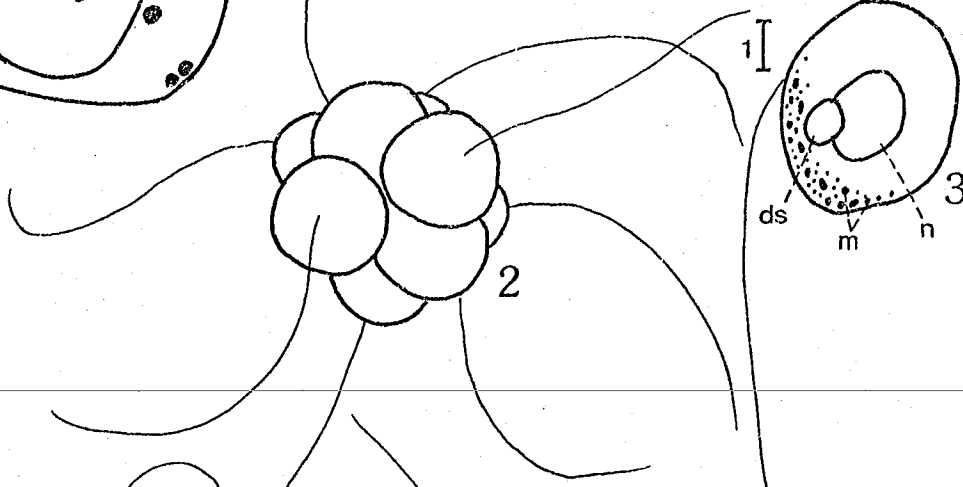
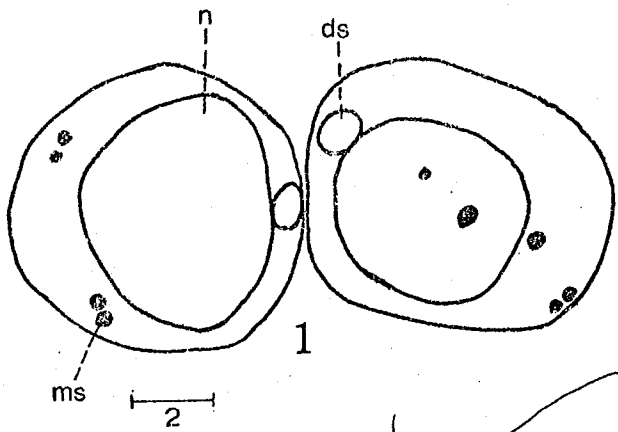
- Rullier, F.: Morphologie et development du Spionidae
(Annelide polychaete) Polydora (Boccardia) redeki
Horst. Cah. Biol. Mar., I, 231-244 (1960)
- Schroeder, P.C., Hermans, C.O.: Annelida: Polychaeta.
In: Reproduction of Marine Invertebrates, eds.
Giese, A.C., Pearse, J.S. Vol. 3, Annelids and
Echiurans, pp. 1-213. New York: Academic Press
1975
- Simon, J.L.: Reproduction and Larval development of
Spio setosa (Spionidae: Polychaete). Bull. Mar.
Sci. 17(2), 398-431 (1967)
- Söderström, A.: Studien über die Polychaetenfamilie
Spionidae. Dissertation, Uppsala: Almqvist and
Wicksells (1920)
- Woodwick, K.H.: Life history and ecology of Polydora
nuchalis Woodwick, a spionid polychaete. Ph.D.
Diss., University of Southern California (1955)

EXPLANATION OF TEXT-FIGURES

a	acrosome	m	mitochondria
af	axial filament	mp	middle piece
bg	cells with basophilic granules	ms	mitochondrial sphere
c	cuticle	n	nucleus
cb	circular body	nbv	nephridial blood vessel
cm	circular muscle	nc	nephridial canal
cph	cytophore	nm	nephridium
cst	coelomostome	np	nephridiopore
d	duct	nt	nototroch
d1m	dorsal longitudinal muscle	nv	neutral red vacuole
ds	dictyosome	pp	parasitic protozoa
e	egg	rc	residual cytoplasm
ge	golgi element	s	sperm
gw	gut wall	t	tail
h	head piece	v	vacuolated cells
is	intersegmental septum	v1m	ventral longitudinal muscle
k	refractive knob		

All indicated measurement scales are in microns, unless indicated otherwise.

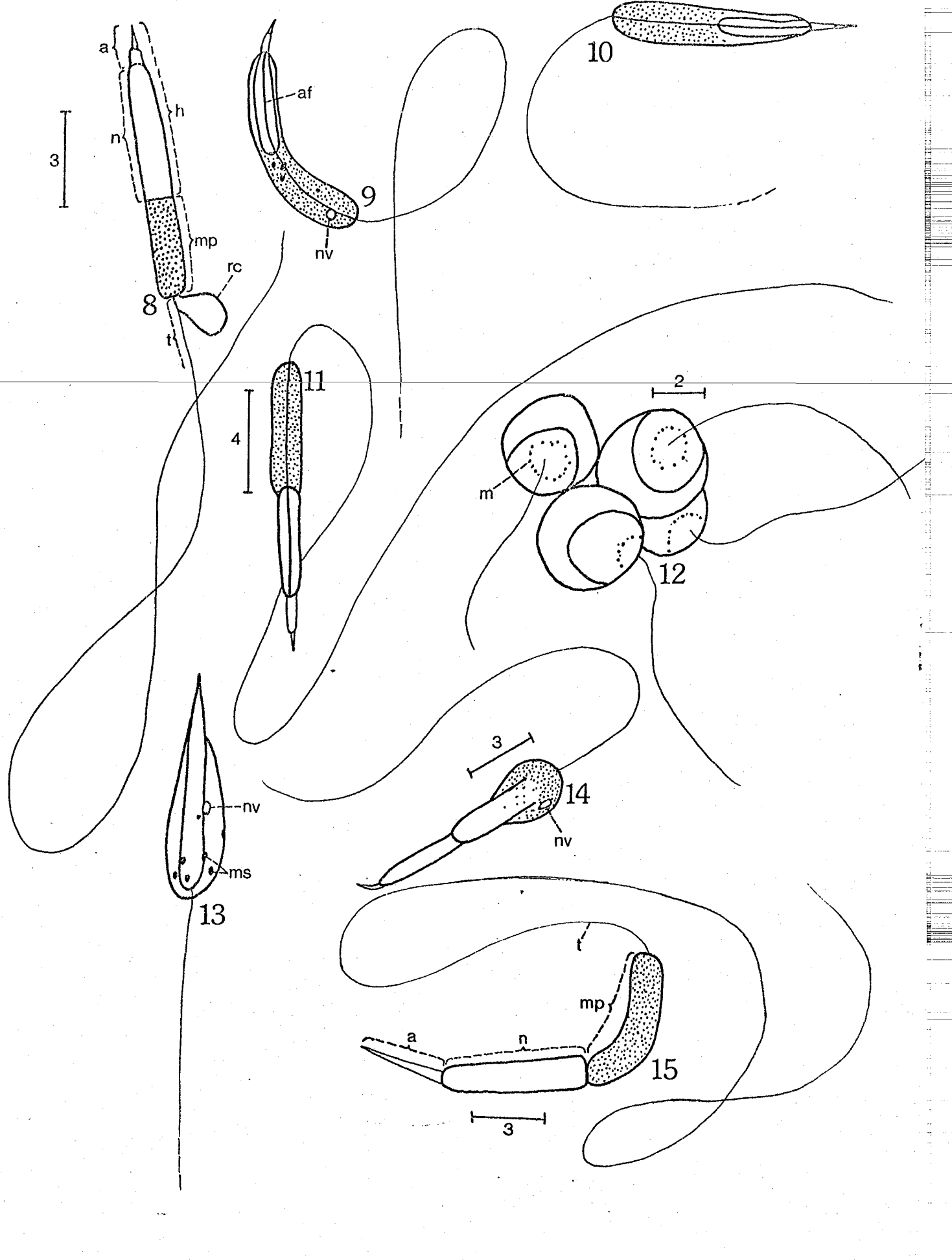
Figures 1-7: Boccardia proboscidea: 1) secondary spermatocytes; 2) rosette; 3) early spermatid; 4) tetrad; 5) tetrad ready to separate; 6) spermatid; 7) late spermatid.



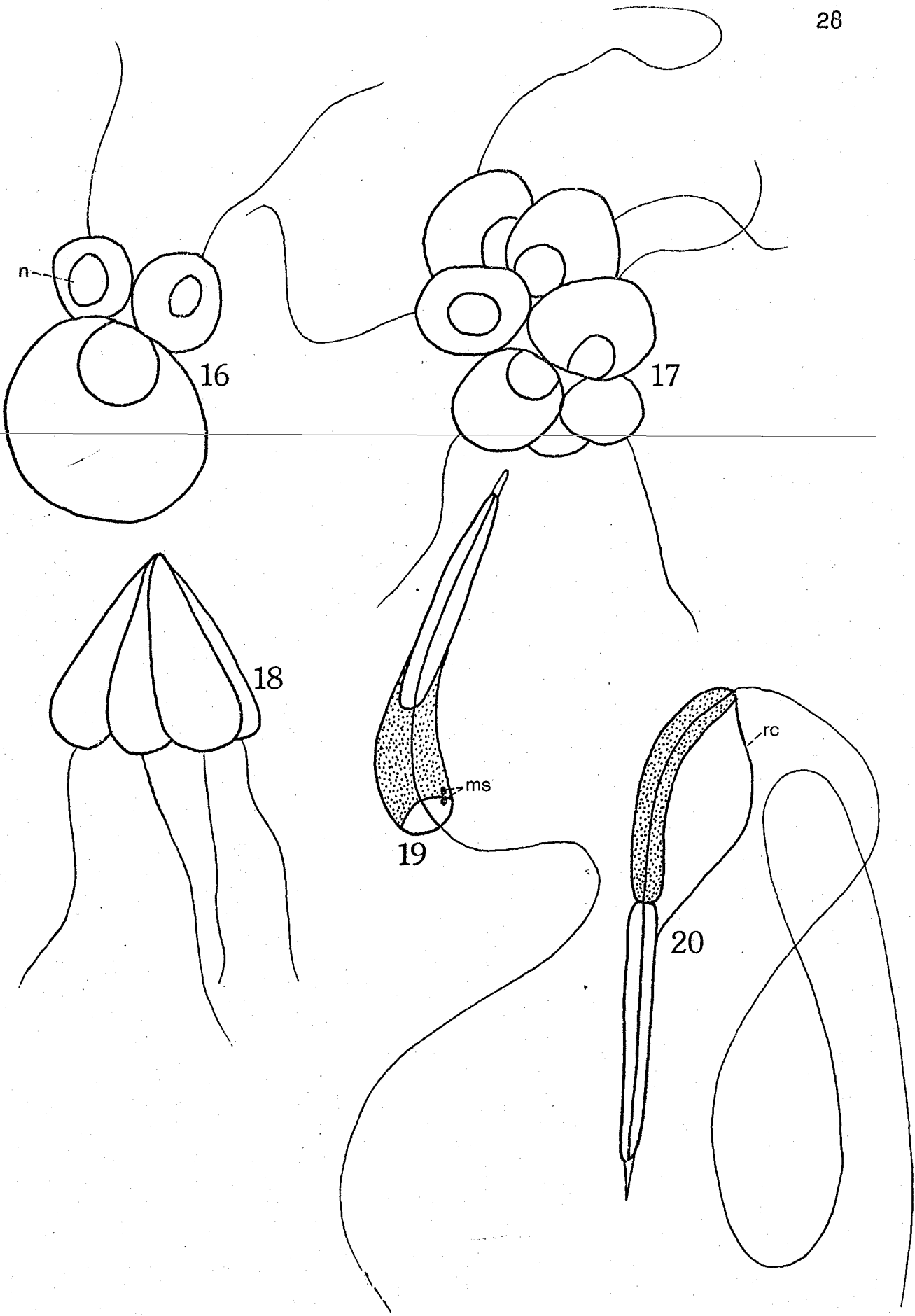
Figures 8-15: Boccardia proboscidea: 8) mature
spermatozoon.

Polydora convexa: 9-10) late spermatids;
11) mature sperm.

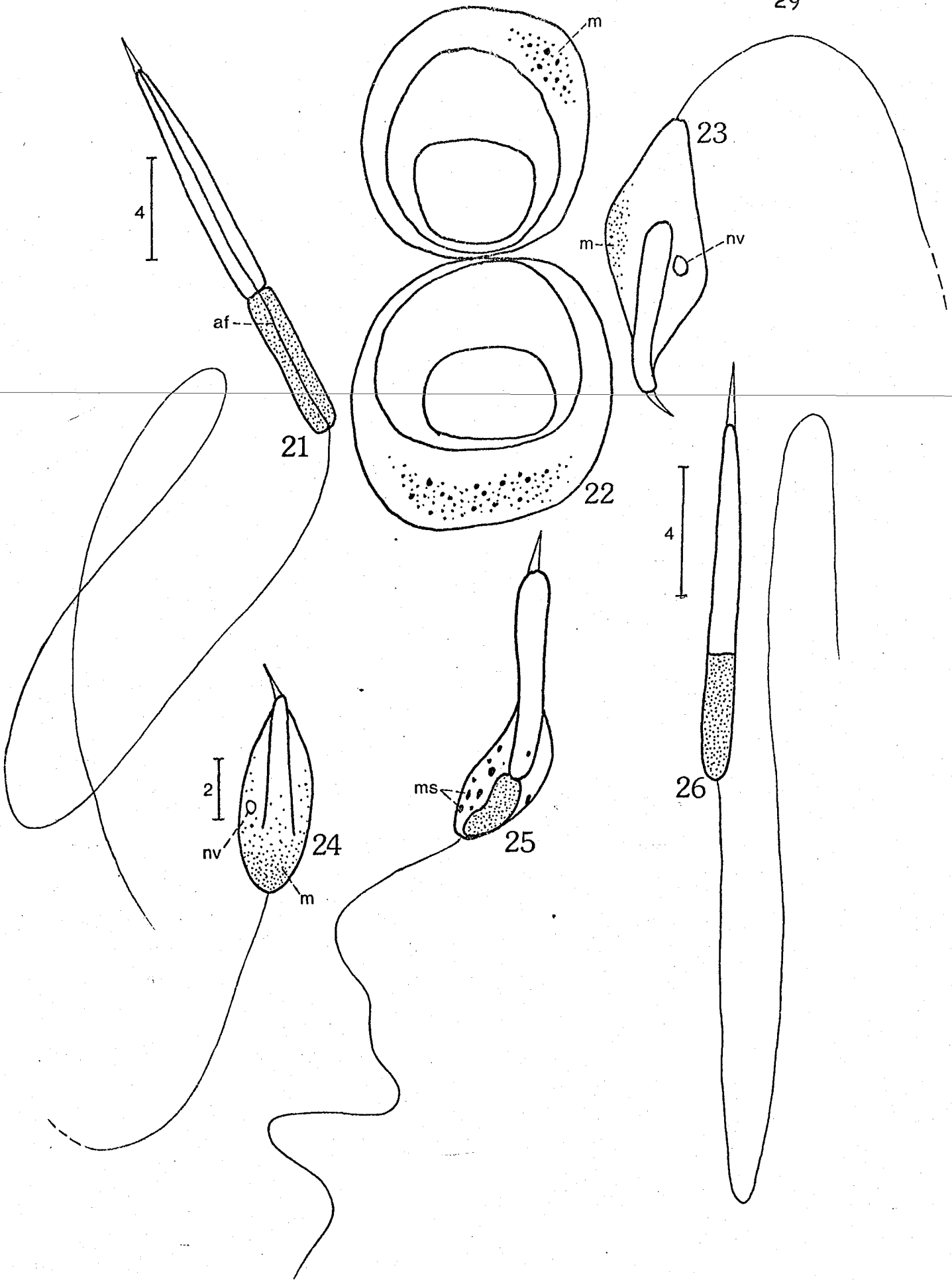
Polydora websteri: 12) tetrad; 13-14)
late spermatids; 15) mature sperm.



Figures 16-20: Pseudopolydora kempi: 16) platelet in transition to a rosette; 17) rosette; 18) tetrad ready to separate; 19) late spermatid; 20) mature sperm.

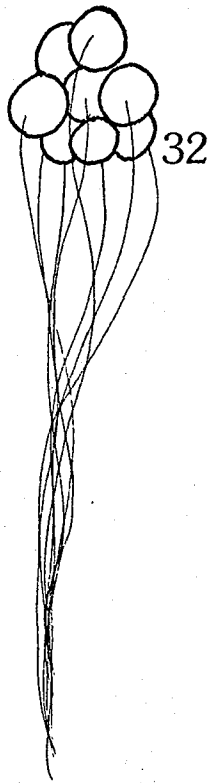
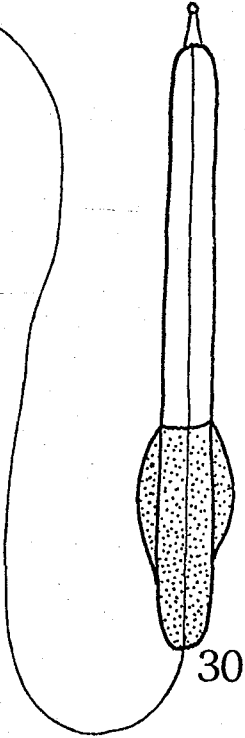
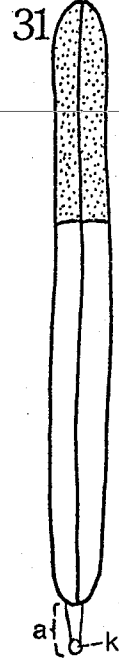
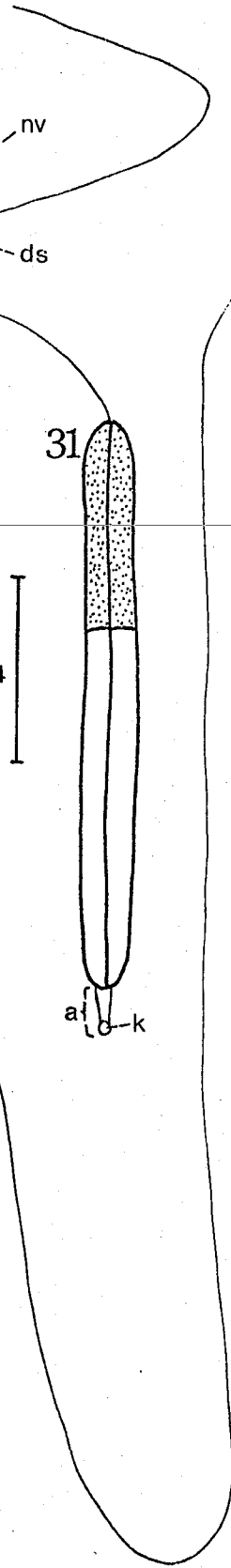
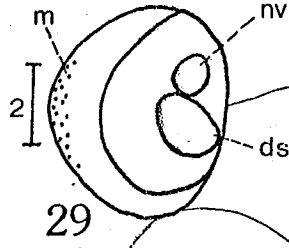
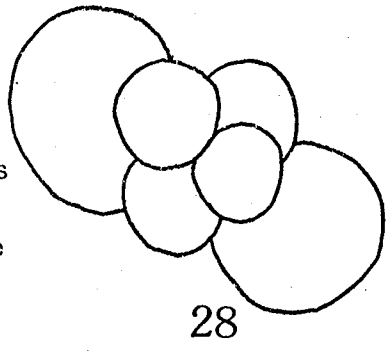
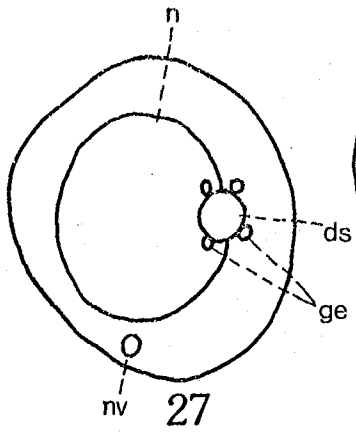


Figures 21-26: Pseudopolydora kemp: 21) mature sperm.
Pseudopolydora paucibranchiata: 22)
secondary spermatocytes; 23-25) late
spermatids; 26) mature sperm.

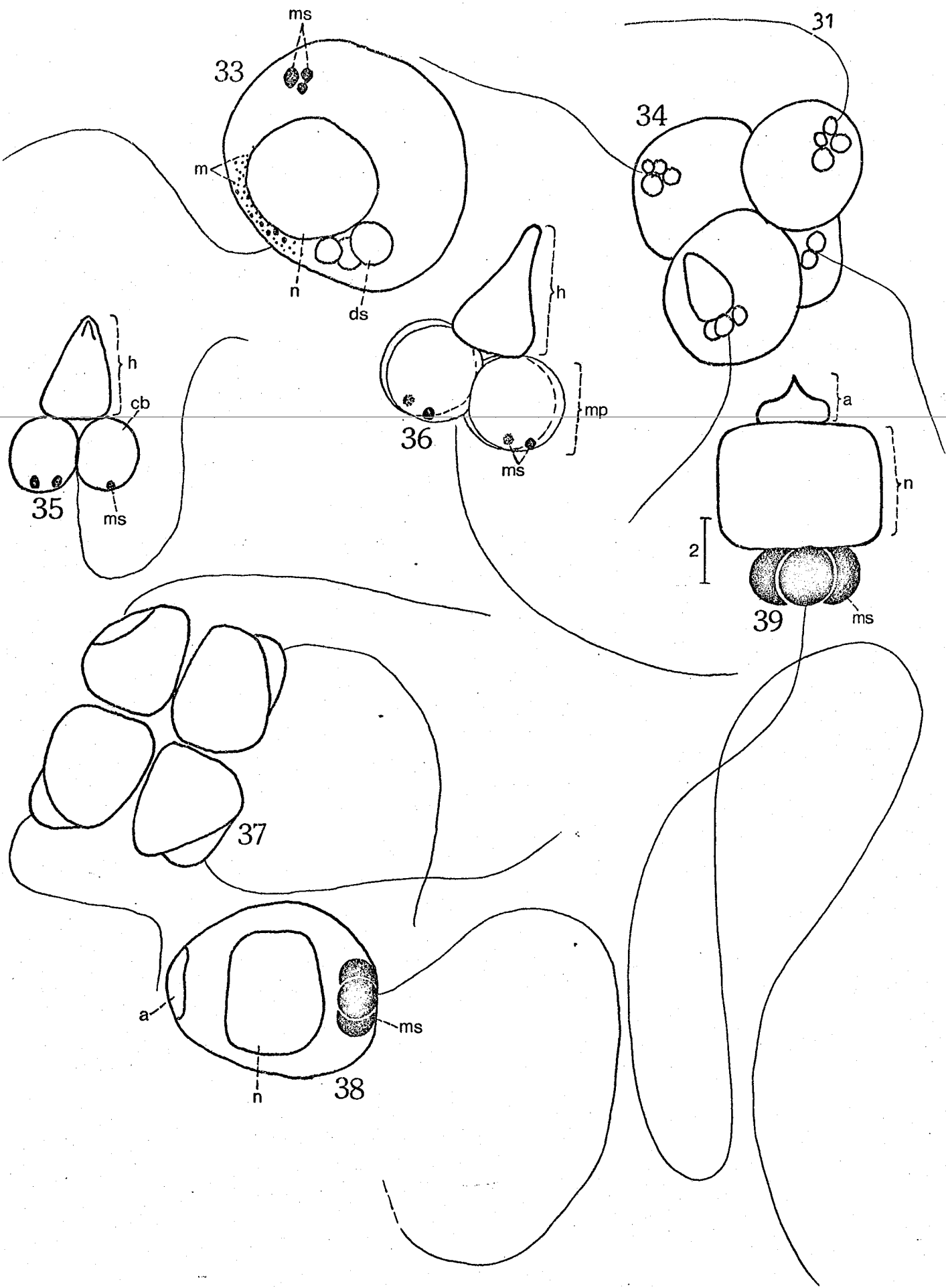


Figures 27-32: Pygospio californica: 27) secondary spermatocyte; 28) formation of platelet from secondary spermatocytes; 29) early spermatid; 30-31) mature spermatozoa.

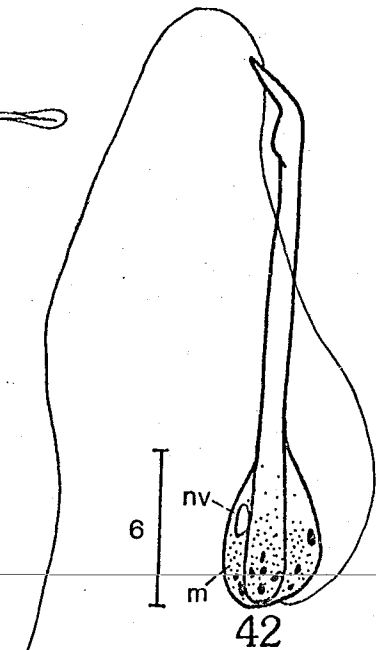
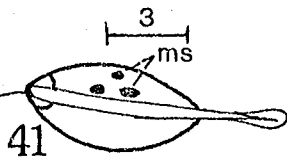
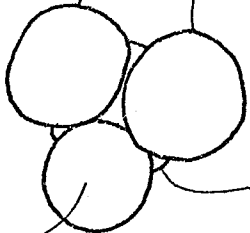
Pygospio elegans: 32) rosette.



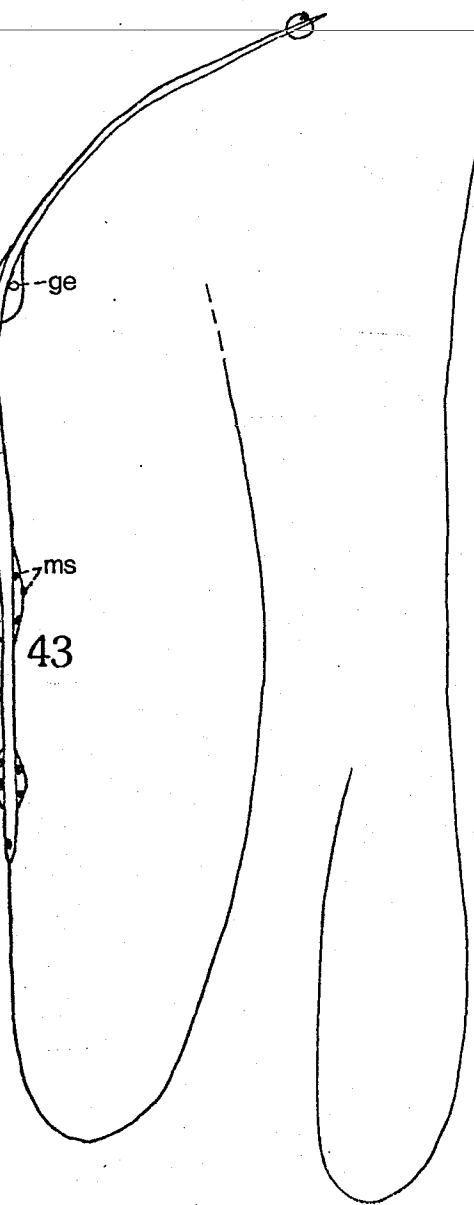
Figures 33-39: Scolecopsis tridentata: 33) early
spermatid; 34) tetrad; 35) late sperma-
tid; 36) mature sperm.
Spiophanes bombyx: 37) tetrad; 38)
spermatid; 39) mature sperm.



Figures 40-46: Streblospio benedicti: 40) tetrad;
early spermatid; 42-45) late spermatids;
46) mature sperm.



nv
m



ge

ms

10



nv

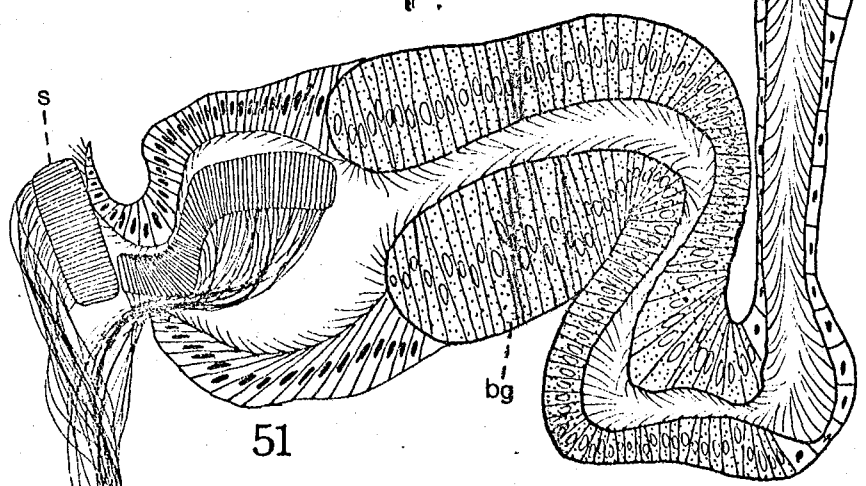
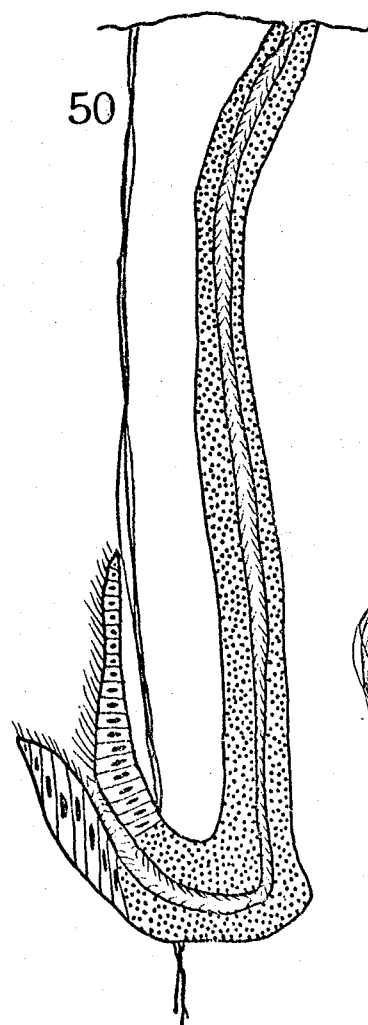
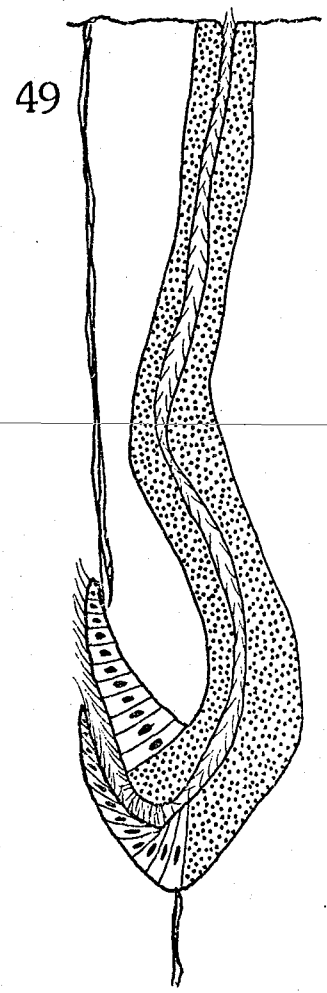
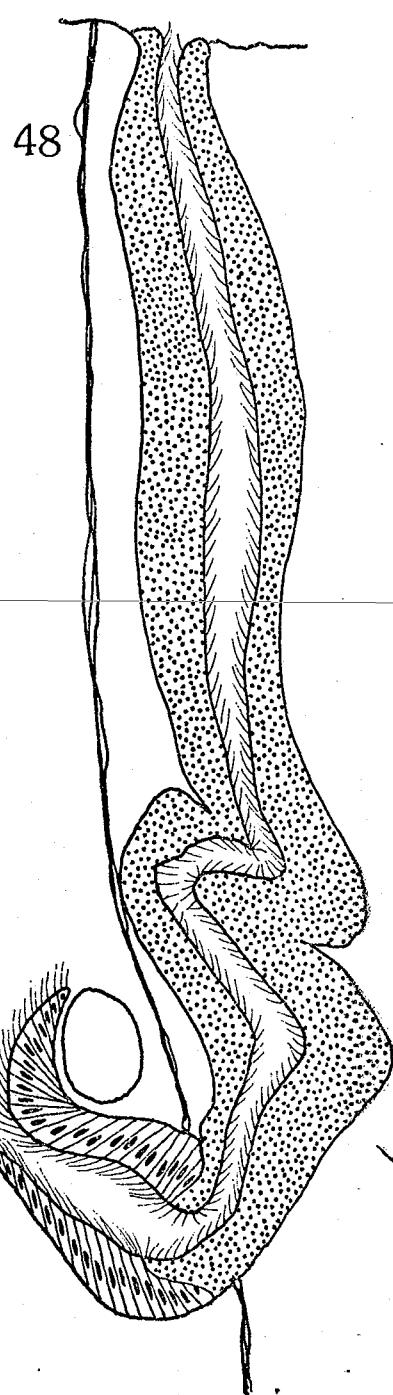
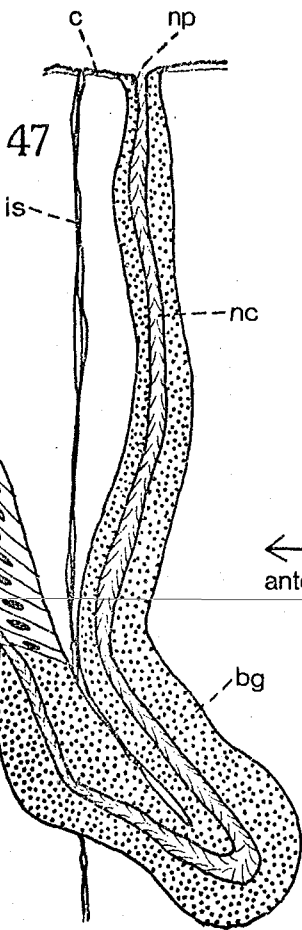


rc

46

32

Figures 47-51: Epitokal nephridia, sagittal sections:
47) female, Boccardia proboscidea;
48) female, Pseudopolydora kempi; 49)
female, Pseudopolydora paucibranchiata;
50) female, Pygospio californica; 51)
male with sperm aligned in the coelomo-
stome, Pygospio californica.



Figures 52-53: Epitokal nephridium, sagittal section:

52) male, Pseudopolydora paucibranchiata.

Epitokal nephridium, transverse section:

53) female, Scoelelepis tridentata.

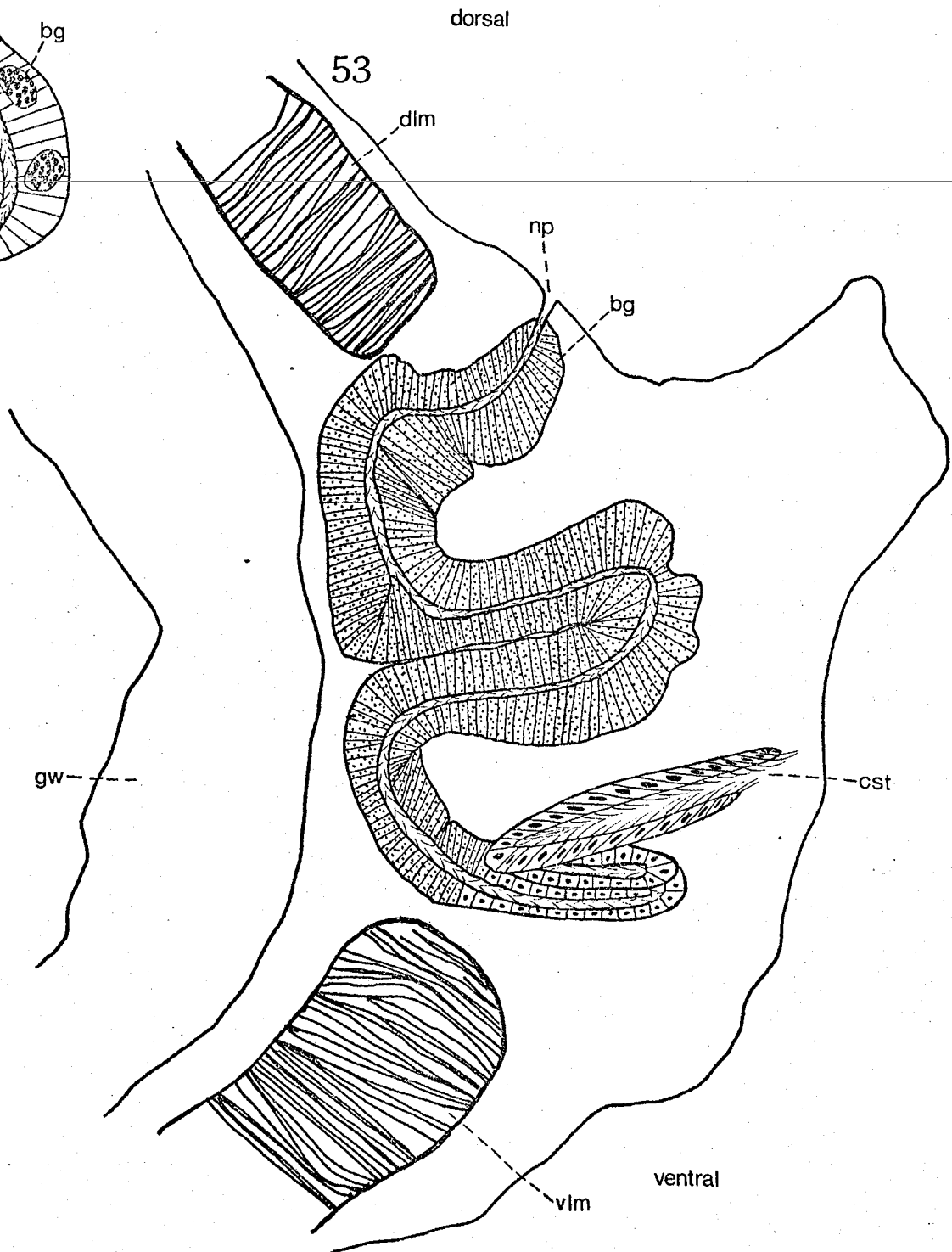
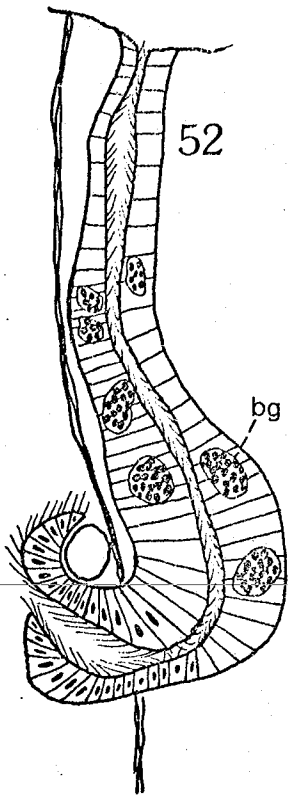


Figure 54: Unmodified nephridium, transverse section:
54) gravid male, Scolelepis tridentata.

dorsal

54

np

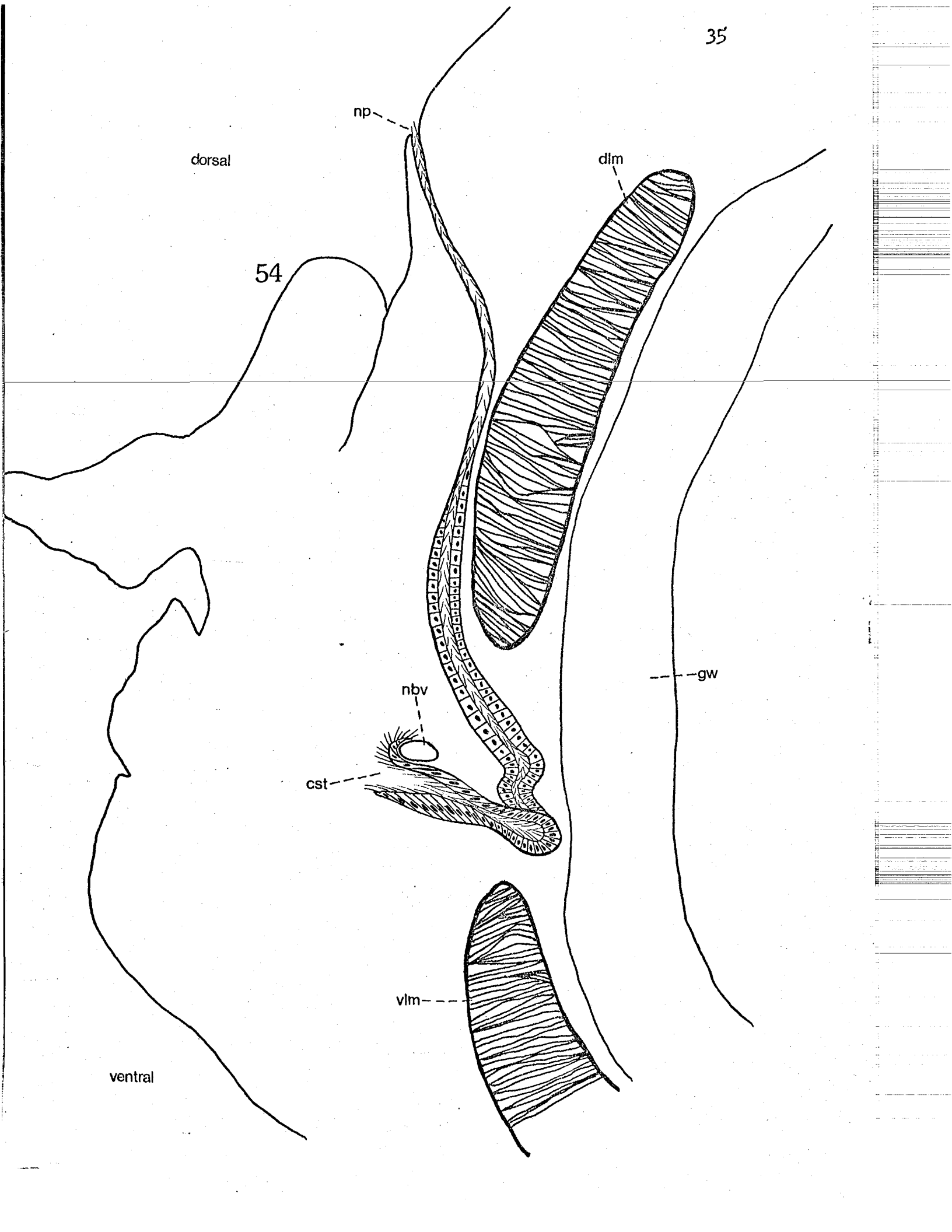
d1m

nbv
cst

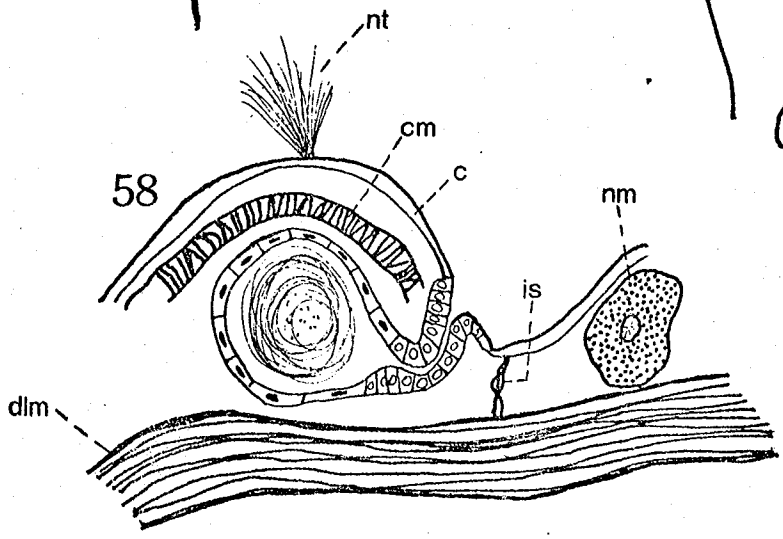
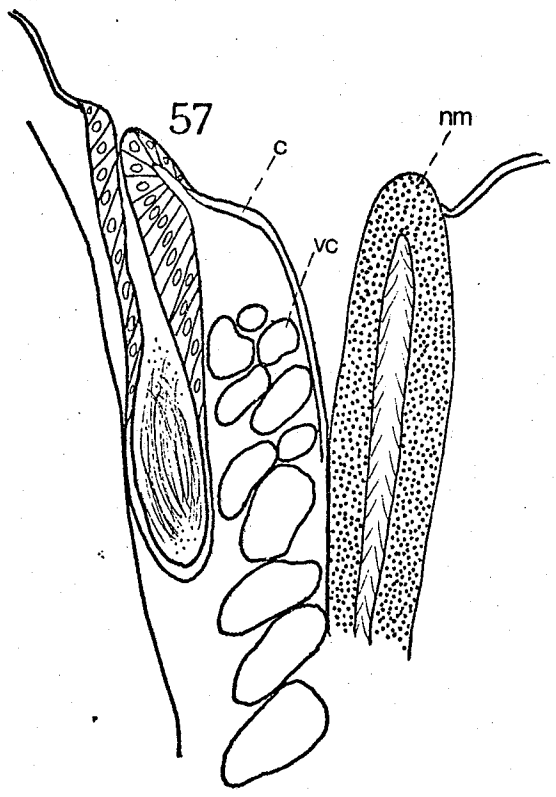
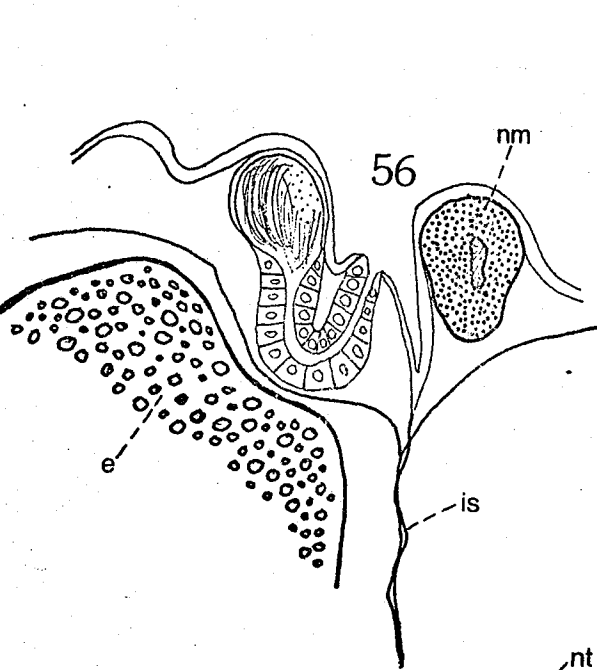
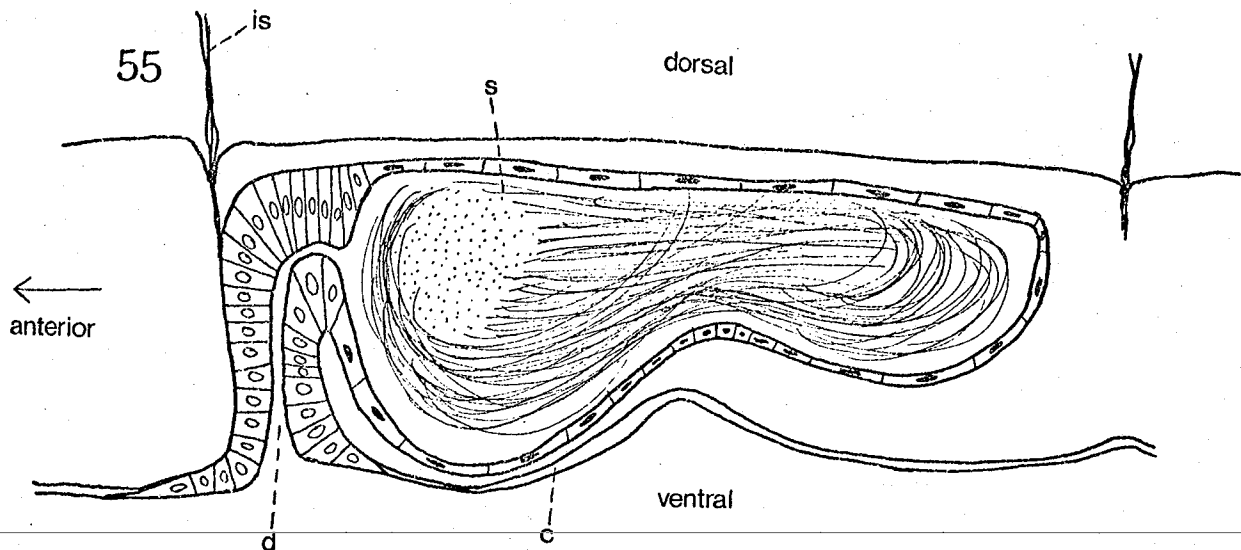
gw

v1m

ventral



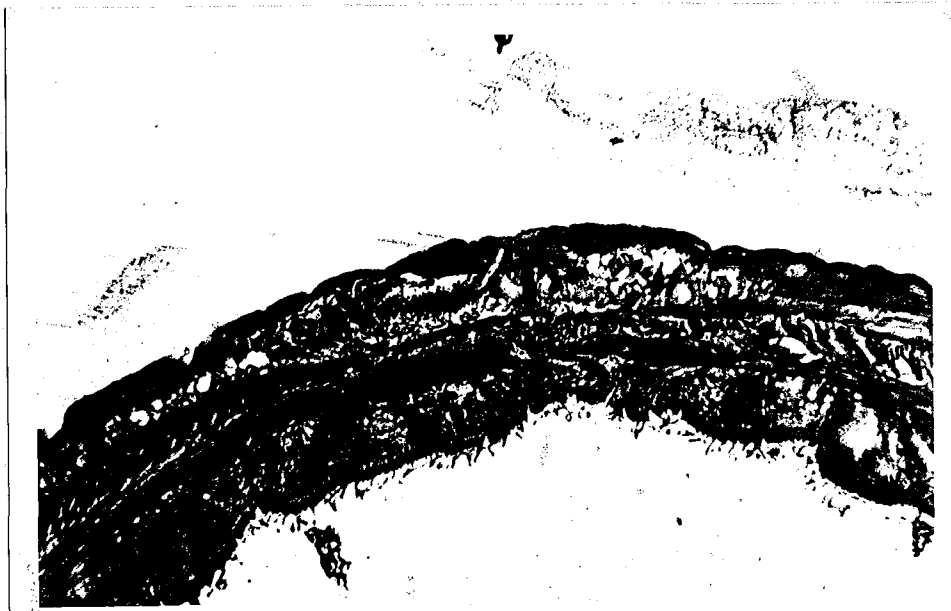
Figures 55-58: Sagittal sections of female seminal
receptacles: 55) Streblospio benedicti;
56) Pseudopolydora paucibranchiata; 57)
Pseudopolydora kemp; 58) Pygospio cali-
fornica.



Figures 59-60: Nephridiopores, transverse sections:
59) single dorsal nephridiopore of
Pseudopolydora paucibranchiata; 60)
double dorsal nephridiopores of Boccar-
dia proboscidea.

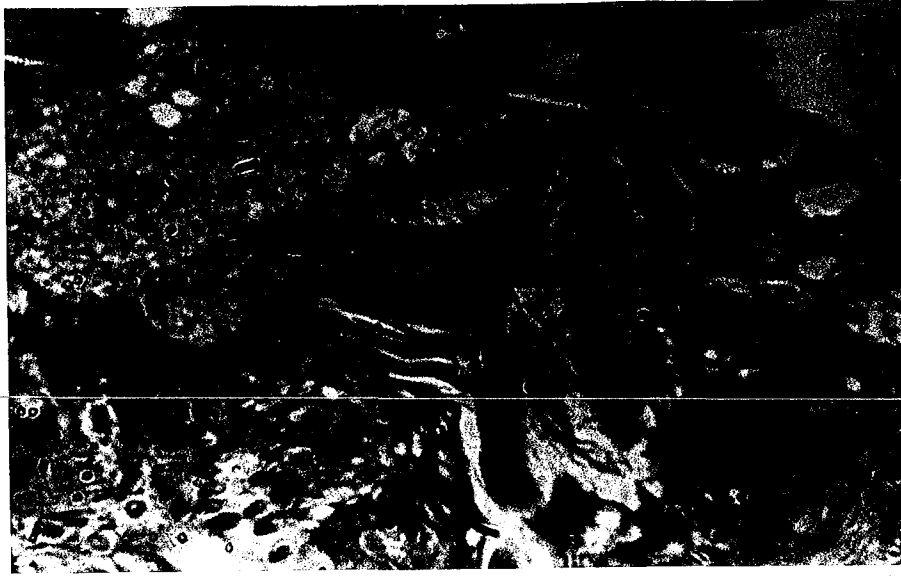


59



60

Figures 61-62: Epitokal nephridium, sagittal sections:
61) aligned sperm in coelomostome of
male Pygospio californica; 62) large,
bulky nephridia of female Scolelepis
tridentata.

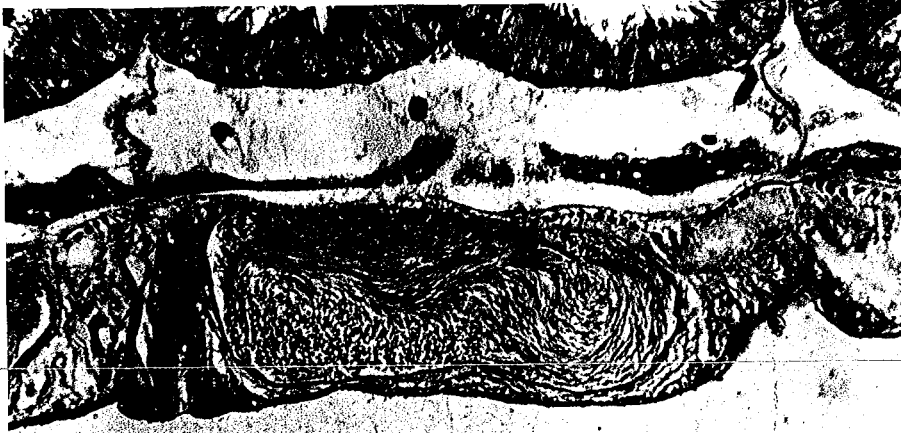


61

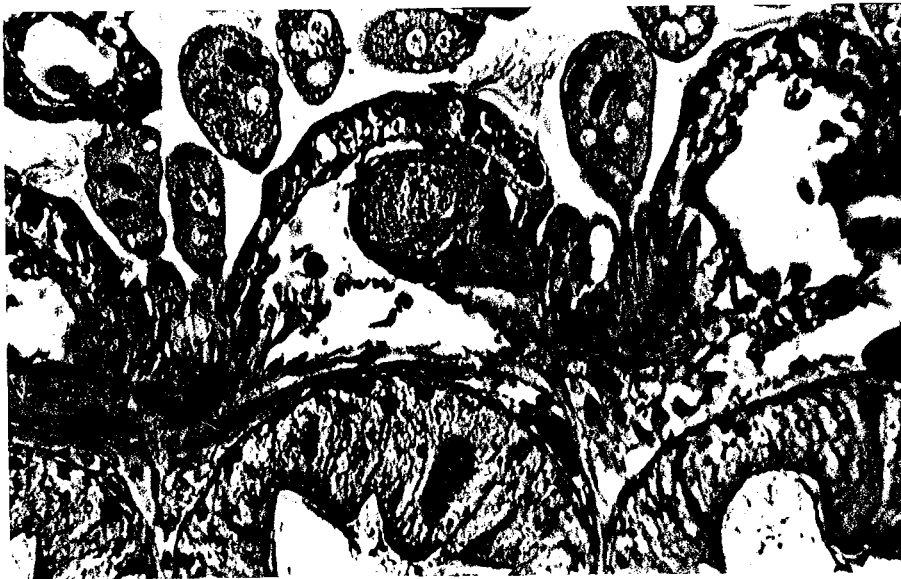


62

Figures 63-64: Sagittal sections of female seminal
receptacles: 63) Streblospio benedicti;
64) Pygospio californica, with attached
parasitic protozoa.



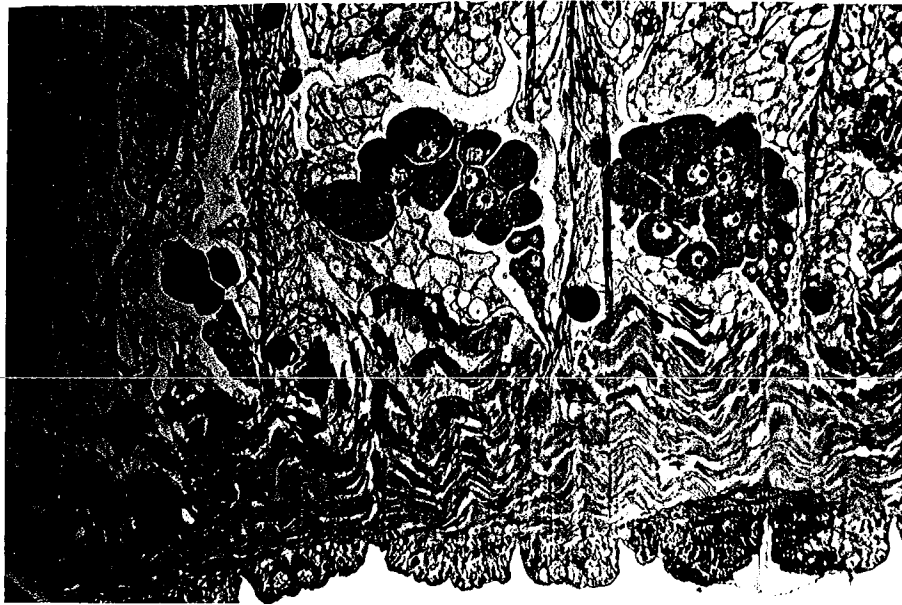
63



64

Figure 65:

65) female ovary of Boccardia proboscidea
attached to ventral coelomic epithelium
at posterior base of intersegmental
septum. Vitellogenesis takes place in
gonad.



65

Table 1*

Species	Acrosome	Nucleus	Middle piece	Tail	Total	Author
<u>Boccardia</u> <u>proboscidea</u>	1.5	4.5	3	38	47	this paper
	--	--	--	--	60	Woodwick, 1979
<u>Microsprio</u> <u>mecznikowianus</u>	-----6.5-----			42	49	Lo Bianco, 1899
<u>Polydora</u> <u>aggregata</u>	3	5	5	50	63	Blake, 1969
<u>P.</u> <u>ciliata</u>	--	--	--	--	65	Dorsett, 1961
	-----5-----		4	46	55	Franzén, 1956
<u>P.</u> <u>concharum</u>	3	5	5	46	59	Blake, 1969
<u>P.</u> <u>convexa</u>	2	5	5	54	68	this paper
<u>P.</u> <u>giardi</u>	1.85	5.7	1.8	33.3	42.7	Day and Blake, 1979
<u>P.</u> <u>ligni</u>	2.5	5.5	4.5	65	77.5	this paper
	2	7.5	5	60	74.5	Blake, 1969
	-----0.03(mm)-----			--	--	Rice, 1978
<u>P.</u> <u>nuchalis</u>	--	--	--	--	120	Woodwick, 1955
<u>P.</u> <u>quadrilobata</u>	2	11	3	40	56	Blake, 1969
<u>P.**</u> <u>redeki</u>	25(?)	7-8(?)	3(?)	50	86	Rullier, 1960
<u>P.</u> <u>socialis</u>	3	5	5	50	63	Blake, 1969

Table 1 (con.)

<u>P.</u> <u>websteri</u>	3	6	5	70	84	this paper
	2	5.5	4.5	56	68	Blake, 1969
<u>Prionospio</u> <u>malmgreni</u>	-----4-----			--	0.10 (mm)	Hannerz, 1956
<u>Pseudopolydora</u> <u>kempi</u>	1.5	8	6	53	68.5	this paper
	0.8	7.5	4.6	44.6	57.5	Blake and Wood- wick, 1975
<u>P.</u> <u>paucibranchiata</u>	2	7	4	43	56	this paper
	2.1	10.8	3.2	40	56.1	Blake and Wood- wick, 1975
<u>Pygospio</u> <u>californica</u>	1	7.5	4.5	77	90	this paper
<u>Scoelelenis</u> <u>squamata</u>	1	3	2	--	--	Richards, 1970
<u>S.</u> <u>tridentata</u>	--	4	3	15	22	this paper
<u>Spio</u> <u>setosa</u>	-----7.2-----			--	--	Simon, 1967
<u>Spionhanes</u> <u>bombyx</u>	1.5	4	1.5	55	62	this paper
<u>Streblospio</u> <u>benedicti</u>	-----49-----			73	122	this paper
	--	--	60	--	100- 130	Dean, 1965

*--all measurements in microns, unless indicated otherwise.

**--Boccaniella ligERICA (Blake and Kudenov, 1978).