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The Reproductive System of Gastrotrichs. III.

Genital organs of Thaumastodermatinae subfam. n. and Diplodasyinae subfam. n. with discussion of reproduction in Macrodasysida¹

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A comparative structural and ultrastructural investigation is made of genital organs of selected genera of Thaumastodermatidae and their constructions are defined. Two new subfamilies are designated within the family based on reproductive features and other characteristics. The occurrence of bounding epithelia about the gonads, ova and central body region is noted. Paramyosin type muscles are noted for *Platydasys*. General and specific features of spermatogenesis, oogenesis and fertilization are defined and discussed. The evolution of accessory reproductive organs in Macrodasysida is discussed.

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1. Introduction

The Gastrotricha is one of several small phyla of invertebrates generally considered to be early offshoots of the major evolutionary lines in Metazoa. Although they are neither obvious nor of major economic importance, the "low grade" organization of Gastrotricha is valuable as a source of basic cell types, behavioral patterns, developmental patterns and perhaps physiological mechanisms. The gastrotrichs share this feature with several other groups, e.g. Turbellaria, some aschelminth phyla, Pogonophora and Lophophorata, to name a few. It is exciting to anticipate a revised general understanding of invertebrate evolution derived from the application of new methods to these taxa.

Remane (1963) considered a knowledge of gastrotrich structure an important prerequisite to any understanding of relationships among pseudocoelomates. The gastrotrichs were studied in detail in a recent definition of the basic metazoan cell type (Rieger 1976). The gastrotrichs provide a ground plan for the analysis of cuticle structure in Aschelminthes (Rieger & Rieger 1977). They offer a model for zoogeography and speciation in interstitial marine fauna (Ruppert 1977). Finally, the gastrotrichs have the most primitive mode of sperm transfer in pseudocoelomates (Ruppert 1978a) that, in its details, is unique in Metazoa.

The marine Gastrotricha are, for the most part, simultaneous hermaphrodites with internal fertilization. Their spermatozoa are elongate, uniflagellated cells with mitochondrial derivatives forming a helically wound keel about the nucleus. The acrosome may also assume a helical form (Teuchert 1976; Ruppert 1978a). In both their simultaneous hermaphroditism with internal fertilization, and, their special sperm structure, the gastrotrichs show interesting parallels to the Gnathostomulida and to the opisthobranch molluscs (Sterrer 1968; Thompson 1973). The Gastrotricha, however, lack a penis in the large majority of cases. The absence of this feature in the primitive plan of the genital system immediately distinguishes the gastrotrichs from the Turbellaria as well as

the Gnathostomulida and higher gastropod molluscs. This fact, in turn, defines the special condition underlying the evolution of reproductive organs in this phylum.

The overall aim of the papers in this series is to identify the general structural and functional patterns of a reproduction in Gastrotricha. The first paper in the series documented the structure of genital organs in *Dolichodasys* and outlined the general issues associated with reproduction in gastrotrichs (Ruppert & Shaw 1977). The second paper described the structure and ultrastructure of genital organs in *Macrodasys* and described the functional morphology of sperm transfer in the genus. This paper attempts to refine further the definition of the gastrotrich genital system by examining a homogeneous family, the Thaumastodermatidae, a group that has evolved an internal connection between the testis and one of the accessory reproductive organs.

2. Material and methods

Thaumastoderma heideri Remane was collected at a wave-sheltered flood delta at the North Inlet of Debidue Beach, S.C. (1975) in coarse shelly sand in the shallow subtidal.

Tetranchyroderma bunti Thane-Fenchel was collected intertidally in medium sand on Bogue Inlet Beach, N.C. (1971-76); in medium sand in the shallow subtidal on a sheltered beach at Lake Worth, Florida (1977), and, in the intertidal in medium sand on a wave sheltered spoil island near Jack Island in the Indian River, Ft. Pierce, Florida (1977).

Tetranchyroderma sp. 2 was collected in the shallow subtidal, 20 m from MLWM, in medium sand on Bogue Banks, N.C. (1976).

Tetranchyroderma sp. 1 (Rieger & Rieger 1977, =*T.* sp. B, Ruppert 1977) was collected in the lower part of the intertidal zone on Bogue Inlet Beach, Bogue Banks, N.C. (R.M. Rieger).

Acanthodasys sp. 4 (see Rieger 1976; Rieger & Rieger 1977) was collected on a fine sand flat along the White Oak River in Swansboro, N.C. (1975, R. M. Rieger).

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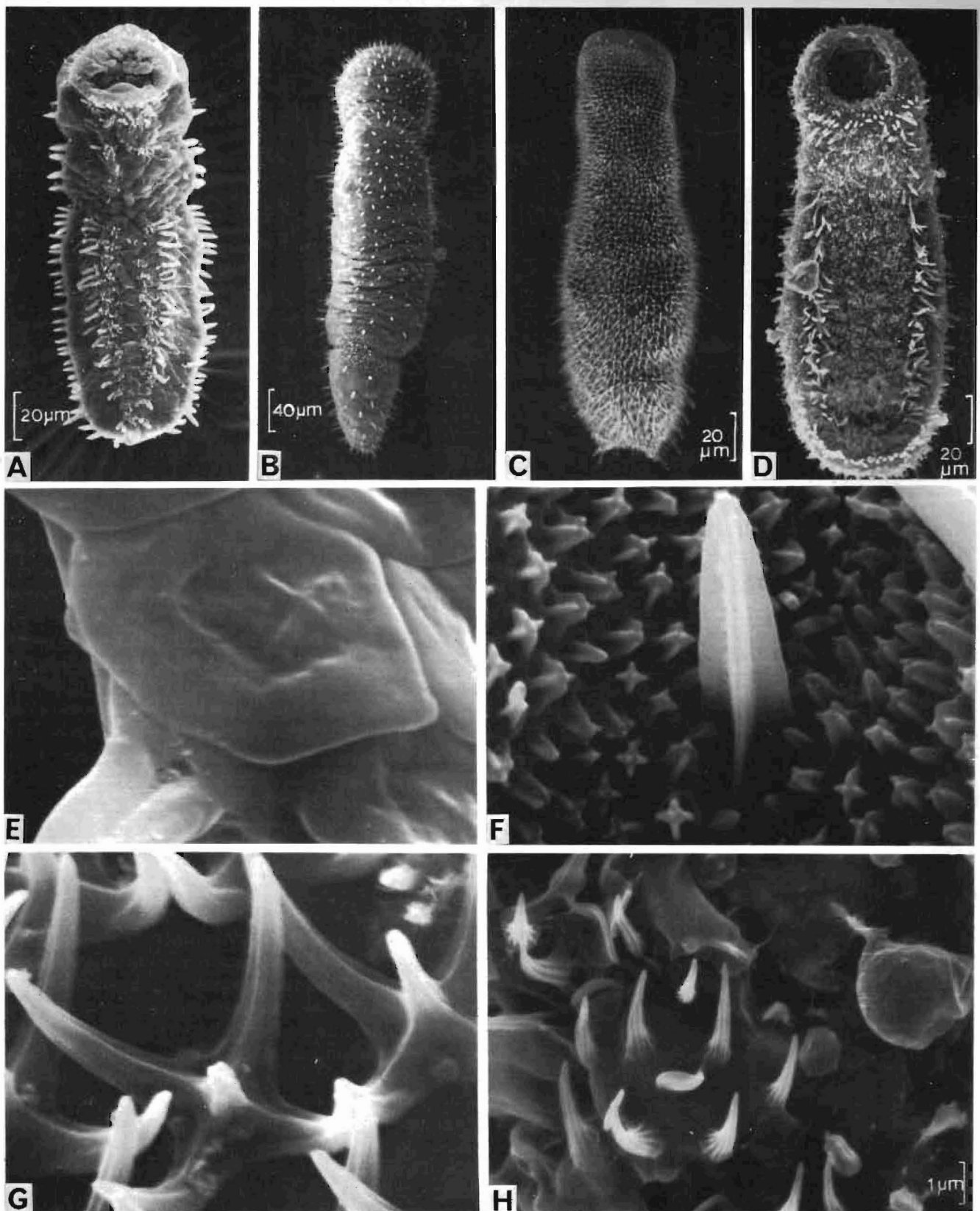


Fig. 1. — A, *Diplodasys ankeli*, ventral view. — B, *Acanthodasys tetranchyodermatoides*, dorsal view. — C, *Tetranchyoderma* cf. *hirtum*, dorsal view. — D, *Platydasys* cf. *ocellatus*, ventral view. — E, *D. ankeli*, ventrolateral scaleplate and lateral spine. — F, *A.*

tetranchyodermatoides, principal dorsal spine and pentancere-like spines. — G, *T. cf. hirtum*, dorsal pentanceres. — H, *P. cf. ocellatus*, ventrolateral spines. (All scanning electron micrographs.)

Acanthodasys thrinx Ruppert was collected on a sheltered flood delta at the North Inlet of Debidue Beach, S.C. in medium-fine sand (1975) and on a spoil island near Jack Island in the Indian River, Ft. Pierce, Florida (1976).

Acanthodasys tetranchyodermatoides Ruppert, *Tetranchyoder-*

ma cf. *hirtum* Luporini et al. and *Platydasys* cf. *ocellatus* Clausen were found subtidally off Ft. Pierce, Florida, during R. V. Gosnold cruise no 279, 27°31'0" N 80°08'3" W, 15 m water depth, in coarse, shelly sand (Nov. 1976, courtesy D. Putnam).

Acanthodasys vermiformis Ruppert was collected subtidally in

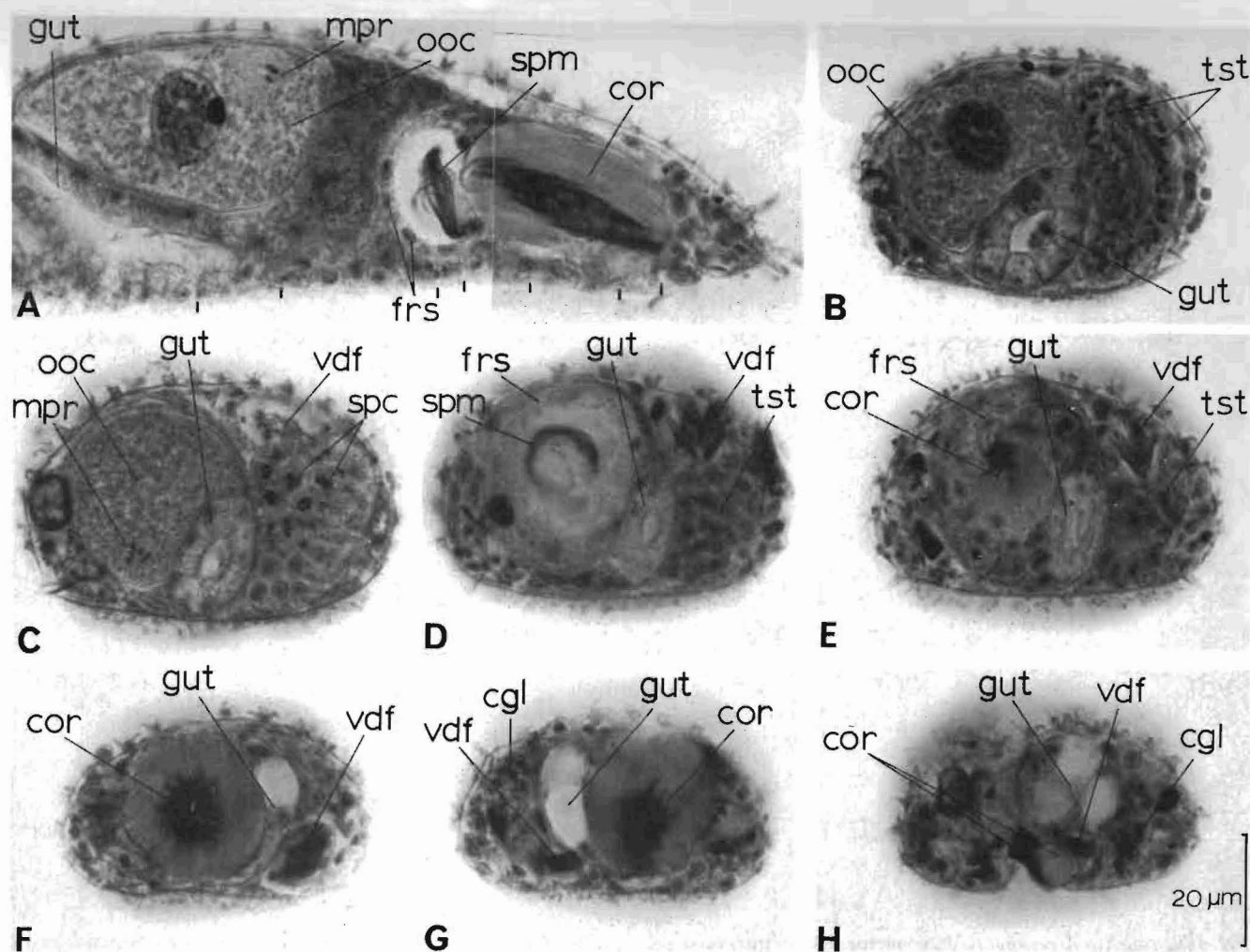


Fig. 2. *Thaumastoderma heideri*, photomicrographs of histological sections. — A, parasagittal section of caudal half of specimen. —

B–H, transverse sections, anterior to posterior; approximate levels are indicated in A.

fine sand off Ft. Pierce, Florida on R. V. Gosnold cruise no. 284, 27°30'2" N 80°01'7" W, 36 m water depth (Jan. 1977, courtesy R. Virnstein).

Extraction, handling, and histological techniques are given in Ruppert & Shaw (1977).

3. Structural data

The terms caudal organ, frontal organ and frontal sac are defined in Ruppert & Shaw (1977); also see chapter 5.

3.1. *Thaumastoderma heideri* Remane, 1926

(Figs. 2; 4C, D; 11A, B)

The genital system of *Thaumastoderma* consists of a right testis, a left ovary located dorsolateral to the gut, a glandulo-muscular caudal organ communicating with a frontal sac and a pair of gland cells associated with the common ventral opening of the caudal organ and vas deferens (Fig. 2A; 4C, D).

The right testis is located posterior to the pharyngo-intestinal junction and extends to the caudal organ. There are "cap" cells anteriorly and these, presumably, are continuous with the vas deferens. The posterior portion of the vas deferens is ensheathed in a layer of circular muscles. The vas deferens terminates (Fig. 2H) in gut tissue immediately behind the ventral opening of the caudal organ. The anterior and most obvious portion of the vas deferens consists of the germinal cells of the testis. All stages of spermatogenesis were

observed in the testis. Spermatocytes mature from posterior to anterior. Spermatozoa are located along the length of the vas deferens in mature individuals (Fig. 2).

The oocytes develop from the ventral portion of a mass of germinal cells located immediately to the right of the gut and caudal organ. This mass also represents the posteriormost portion of the testis. The oocytes migrate anteriorly and toward the left side of the body as they grow and undergo vitellogenesis. The larger oocytes are located dorsolateral to the gut and anterior to the frontal sac. The largest oocyte was observed to contain a male pronucleus ($n=8$) in three individuals. In all three cases, the germinal vesicle was intact. The oocytes are bounded by a flattened oviduct epithelium that may be continuous with the frontal sac epithelium and a mass of cells in front of the anteriormost oocyte. This mass of cells ends blindly between the gut and epidermis. (Fig. 4C, D).

A spindle-shaped caudal organ is located in front of the anus on the left side of the gut. A narrow lumen extends from a midventral opening to a proximal pore communicating with the frontal sac. This lumen stains intensely with iron haematoxylin obscuring other details. The entire organ is thickly invested in a sheath of circular or spiral muscles (Fig. 2A, G, H). Sphincter muscles are developed at both the distal and proximal ends of the organ.

The frontal sac extends around the proximal opening of the caudal organ and consists of a flattened epithelium frequently

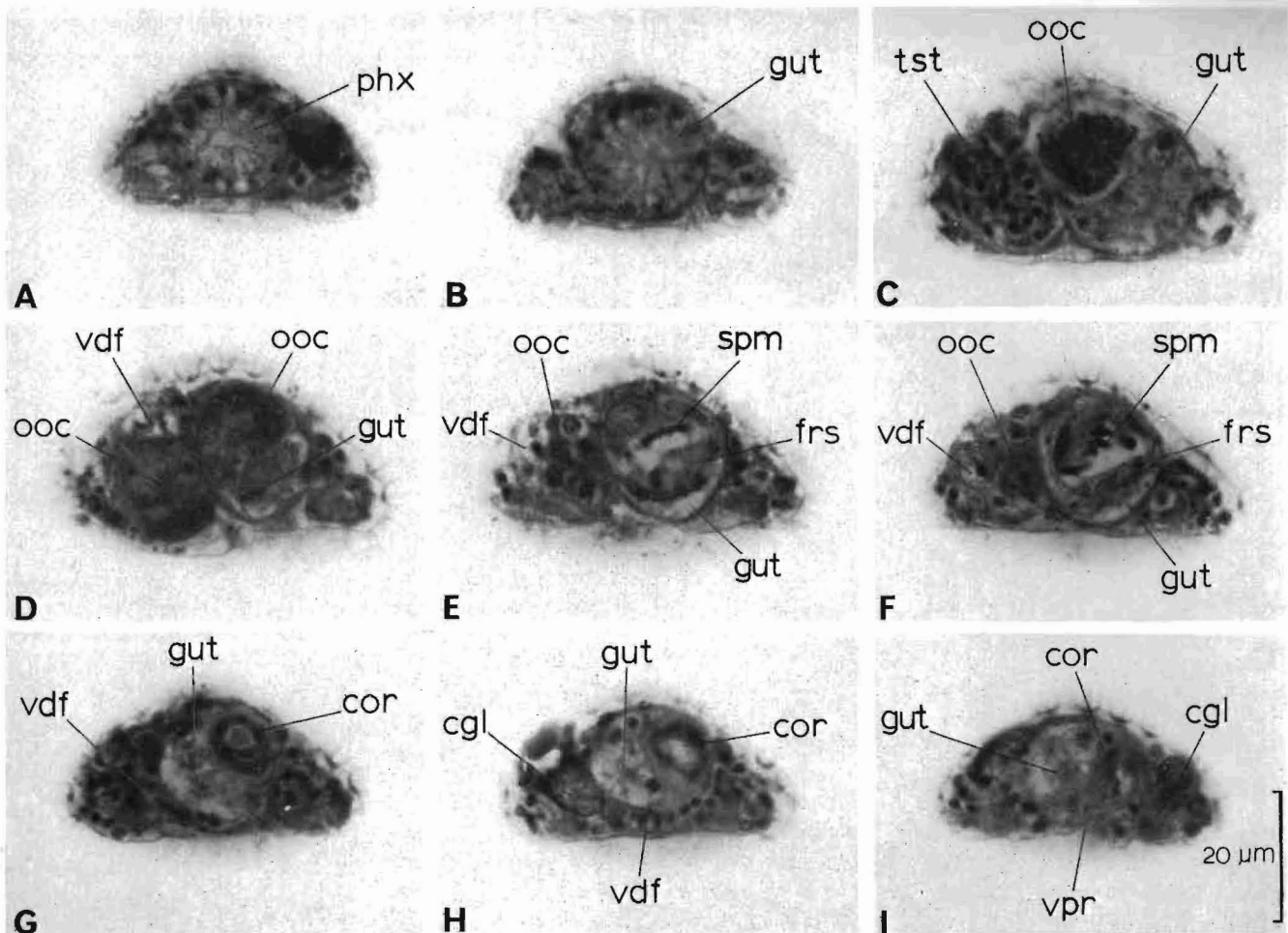


Fig. 3. *Tetranchyroderma bunti*, photomicrographs of transverse sections (A-I) anterior to posterior. — A, posterior pharyngeal region. — B, anterior gut region. — C, level of largest oocyte. — D, level

of ovary. — E, anterior part of frontal sac. — F, posterior part of frontal sac. — G, proximal "neck" of caudal organ. — H, "body" of the caudal organ. — I, ventral opening of caudal organ.

surrounding a cluster of active spermatozoa. This sac opens to the oocytes (Fig. 2A).

A pair of large gland cells is located lateral to the caudal organ and vas deferens. The necks of these cells reach to a pore on each side of the ventral opening of the caudal organ and vas deferens (Fig. 2G; 4C, D).

3.2. *Tetranchyroderma bunti* (Thane-Fenchel, 1970) (Figs. 3; 4A, B; 11C, D)

The organization of the genital system of *Tetranchyroderma* closely parallels that of *Thaumastoderma*. The principal difference is the smaller size of the caudal organ of *Tetranchyroderma* (Fig. 4A, B).

The testis is located on the right side of the body and extends from the anterior portion of the gut to the level of the proximal end of the caudal organ. The terminal part of the vas deferens is ensheathed in a layer of circular muscles. The vas deferens opens in common with the caudal organ midventrally in front of the anus. *T. bunti* has only a single, large sperm in the posterior portion of the vas deferens. Progressive stages of spermatogenesis can be observed, from posterior to anterior, in the walls of the vas deferens.

The caudal organ is a small, glandulomuscular organ with outer circular or spiral muscles and an inner secretory epithelium bounding a central lumen. Proximally, it communicates with the frontal sac via a pore controlled by a sphincter muscle. Distally, it opens midventrally with the vas deferens (Fig. 11C, D).

The frontal sac is a flattened epithelium enclosing usually 2 or 3 active spermatozoa (Fig. 3E, F). The sac opens anteriorly to the largest oocytes located dorsal to the gut. An anterior continuation of this sac as an oviduct was not observed but a compact band of cells anterior to the frontal oocyte is present (Fig. 4A, B). This band may represent the anteriormost extension of an extremely thin epithelium about the largest oocytes.

Oocytes grow out of a common germinal mass with spermatocytes (Fig. 3C, D). This cellular mass is located on the right side of the caudal organ and gut. The oocytes grow anteriorly for a short distance and then migrate dorsally, coming to lie in the oviduct anterior to the frontal sac.

There is a pair of eosinophilic gland cells opening near the ventral pore of the caudal organ (Fig. 3H, I, 4A, B).

3.3. *Platydasys cf. ocellatus* Clausen, 1965 (Figs. 1D; 5; 6; 15A-C)

The genital system of *Platydasys* consists of a single right testis that extends posteriorly to the caudal organ, a bipartite caudal organ that opens ventrally near the anus, a frontal sac that communicates with the caudal organ and the largest oocytes, and paired ovaries located lateral to the gut (Fig 6).

The right testis is located lateral to the gut from the pharyngo-intestinal junction to a position just anterior to the caudal organ. The germinal cells of the testis define the bulk of the vas deferens but a very thin bounding epithelium may also be present since small nuclei, peripheral to the germinal cells,

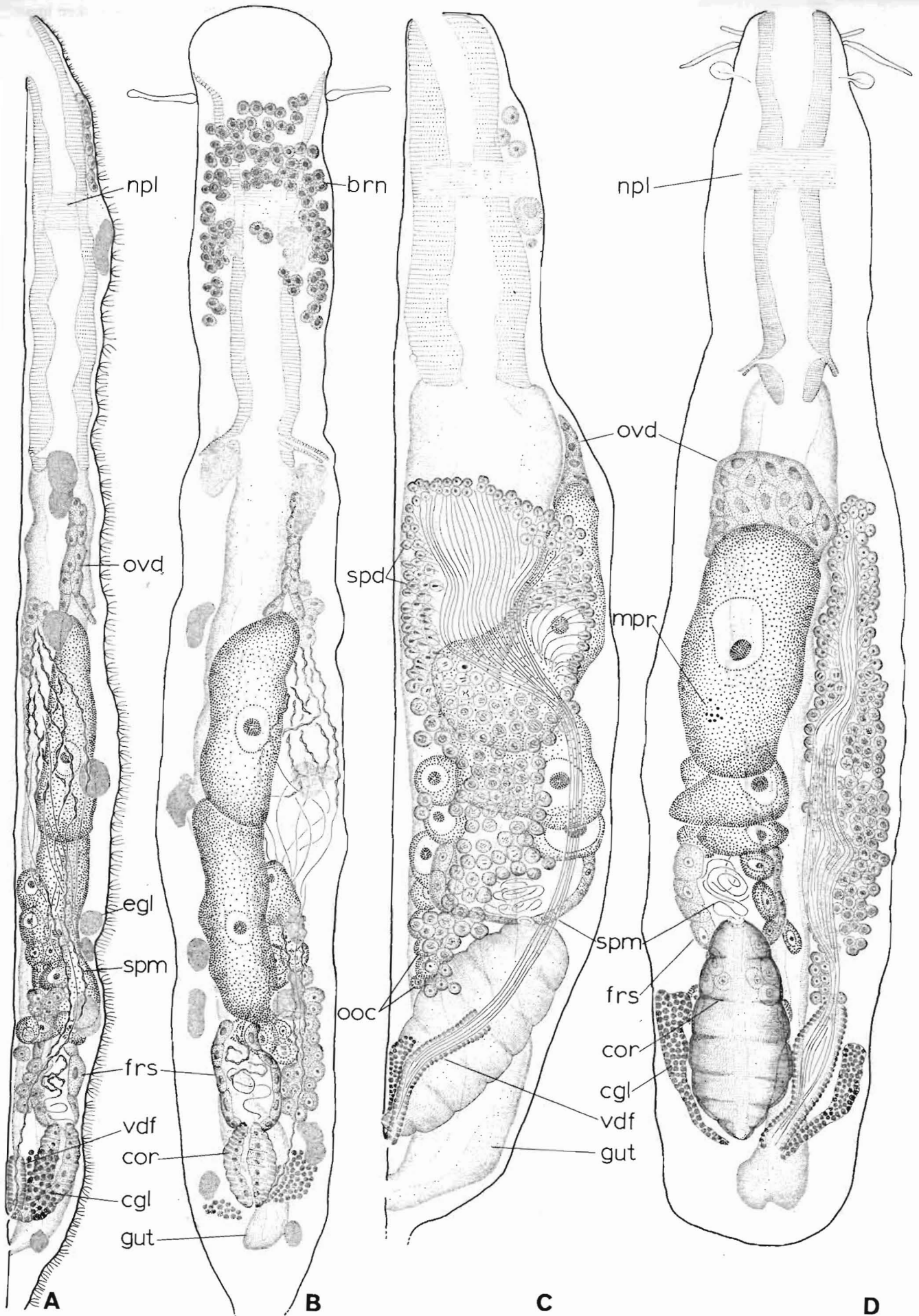


Fig. 4. Reconstructions of the genital system of *Tetranchyroderma buntii* and *Thaumastoderma heideri* after serial transverse sections.

— A, B, *T. buntii*, lateral and dorsal views. — C, D, *Th. heideri*, lateral and dorsal views.

were observed in some sections. The germinal cells in the caudalmost portion of the testis apparently give rise to the oocytes on the right side of the body (see below). In the posterior fourth of the body, the vas deferens bends medially to join the right side of the caudal organ (Fig. 5D). The spermatozoa pass through a canal surrounded by circular muscles and enter the caudal organ (Fig. 5E). In one specimen, the spermatozoa were observed to enter the right canal of the caudal organ for a short distance and then loop anteriorly in the direction of the frontal sac.

The ovaries are paired in *Platydasys cf. ocellatus*. The ovary on the right side of the body is dorsal in position along its length. The smallest oocytes are located in the dorsal angle between the gut and testis at approximately the point where the vas deferens curves to join the caudal organ (Fig. 5D). The left ovary is on the ventral side of the body in the angle between the gut and frontal sac (Fig. 5C). The oocytes migrate anteriorly and dorsally coming to lie anterior to the frontal sac and dorsal to the gut (Fig. 5B). The oocytes on the right side migrate anteriorly and come to occupy a similar position. Both these bands of oocytes are derived from oogonia located in the lateral body regions. On the right side of the body, the oogonia are found continuous with the posterior end of the testis; on the left side, they are found in a mirror image position but no testicular cells are present.

There is a distinct but extremely flattened bounding epithelium about each of the bands of growing oocytes. This cellular epithelium separates the oocytes from the gut and muscle layer posteriorly, and from each other, the gut and the muscle layer anteriorly. The "cap" cells depicted in Fig. 6 represent the anteriormost continuation of these oviductal cells.

The frontal sac, functioning as a storage organ prior to fertilization of the oocytes, is dorsolateral to the left side of the gut (Fig. 5C). This organ is constructed of at least one layer of flattened cells that joins the oviducts anteriorly and the left half of the caudal organ posteriorly. A spherical cluster of spermatozoa was observed in this organ in all of the mature specimens, and, in most of the subadult specimens that lacked a fully developed caudal organ.

The caudal organ, located in the posterior quarter of the body, contains two morphologically distinct canals. The canal of the right side of the organ receives spermatozoa from the individual's vas deferens and is packed with numerous basophilic secretory granules. The left canal is an epithelial tube that stains weakly with iron haematoxylin and may contain long filaments. Both canals are surrounded by a common sheath that is very thin and intensely basophilic. Caudally, this presumed muscular sheath gives way to a peripheral layer of glandular sheath cells. The two canals have a common, midventral opening just in front of the anus (Fig. 5D-G; 6C, D).

The development of the caudal organ can be described partially from the subadult specimens. The left half of the caudal organ first appears as a cluster of cuboidal cells between the flattened cells of the frontal sac and the left ovary. Posteriorly, it forms a gut-like tube of 10-12 cells with centrally located nuclei. These nuclei are not apparent in the mature canal. The right half of the caudal organ begins as an irregular mass of cells located ventral to the testis and gut. This mass of cells forms a slightly less regular tube, lacking any clear lumen, beside the first tube. Each canal is surrounded by a thin sheath of underdetermined character. In addition, both tubes are enclosed in a common layer of flattened cells. Pos-

teriorly, the two canals become smaller in size and their lumina become difficult to observe. Near the caudal opening, the canals appear to become confluent forming a single canal with a distinct lumen. This canal, consisting of 10-12, small cuboidal epithelial cells, opens midventrally just in front of the anus.

Late prophase mitotic figures were commonly observed in the posterior 3 or 4 oocytes in each ovary. A metaphase figure was observed in one specimen. There are apparently no reductional divisions until after sperm penetration, since the germinal vesicle was intact in all cases where a sperm pronucleus was present. The sperm pronucleus typically forms an amphiaster with its chromosomes located equatorially, and it is eccentrically located in the cytoplasm of the oocyte (Fig. 5A, 6A). Those oocytes with a male pronucleus also show a thin, weakly staining egg envelope, which may be elaborated after sperm penetration. It is assumed that breakdown of the germinal vesicle, meiosis and fertilization occur well after sperm penetration.

The oocytes observed along the female tract are undergoing mitotic divisions, growth and vitellogenesis. From posterior to anterior, the oocytes show a general increase in size and increasing basophilia of the nucleoplasm and nucleolus. At least two types of yolk granules are laid down, one strongly basophilic, the other staining weakly with iron haematoxylin (Fig. 6A). No corresponding activity was noted in any of the cells peripheral to the oocytes so it is assumed that yolk is synthesized within the egg.

Most stages of spermatogenesis can be observed in a single individual (Fig. 6B). In mature specimens the first reductional division occurs at about the level of the frontal sac. Secondary spermatocytes are located in the region of the testis ventral to the two largest oocytes. The second meiotic division occurs in a narrow region anterior to the secondary spermatocytes, and spermatids are located anteriormost in the testis. Spermatogonia are present in the posterior portion of the testis and can be distinguished from the spermatocytes by a larger nucleus and more granular chromatin. Mitotic figures are visible anterior to the spermatogonia.

The haploid chromosome number of 7 was determined both from observations of the male pronucleus and of metaphase figures in the testis.

3.4. *Acanthodasys thrinx* Ruppert, 1978 (Figs. 7; 9A, B)

The genital system of *Acanthodasys* consists of paired, lateral testes extending from the pharyngeointestinal junction to the caudal organ located posterior to the gut, an ovary located dorsal to the caudal organ and gut, and a frontal organ system extending from the larger oocyte to the pharyngeointestinal junction (Fig. 9A, B).

The testes are bounded anteriorly by large "cap" cells of unknown function and posteriorly by the caudal organ. The vasa deferentia appear to consist of germinal cells and perhaps a very thin bounding epithelium. Spermatogonia or primary spermatocytes are located posteriorly in both testes, and, spermatids are anteriormost. Spermatozoa extend along the entire length of the vasa deferentia in mature individuals and enter the proximal part of the caudal organ posteriorly.

The caudal organ is a long, glandulomuscular canal consisting of an inner secretory epithelium and an outer sheath of circular or spiral muscles. The inner wall of this organ forms a suspended tube near the terminal, midventral opening. The

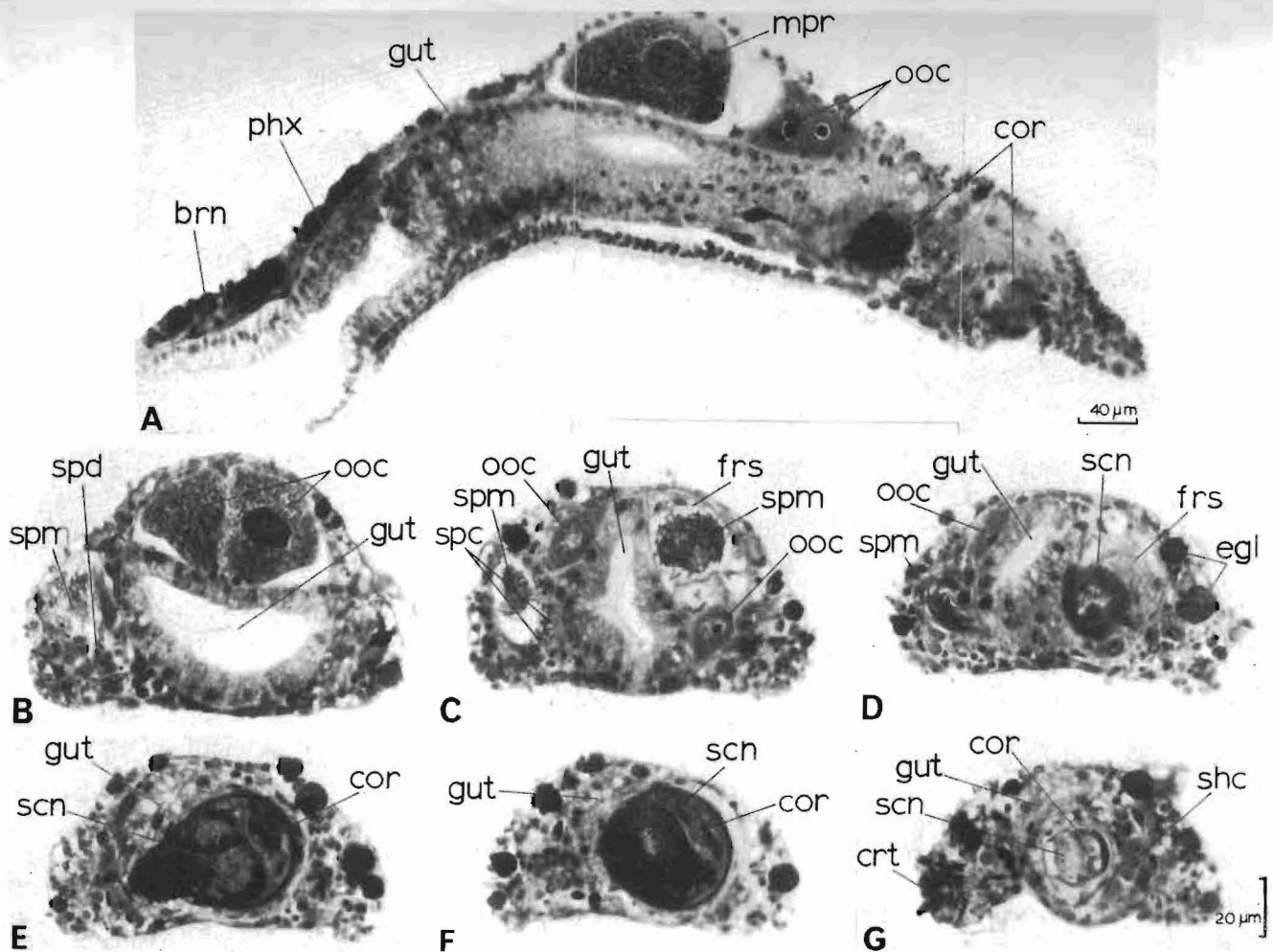


Fig. 5. *Platydasys* cf. *ocellatus*, photomicrographs of histological sections. — A, parasagittal sections through the body. — B–G, transverse sections anterior to posterior; B, level of anterior most oocytes;

C, level of frontal sac; D, posterior end of frontal sac; E, anterior portion of caudal organ; F, section through "body" of caudal organ; G, distal end of caudal organ.

cells forming the inner wall are rich in basophilic secretory granules (Fig. 7H, I).

The ovary is located dorsal to the caudal organ and posterior portion of the gut. In mature specimens, there is a progressive increase in size and yolk content of the oocytes from posterior to anterior (Fig. 7F). A mitotic figure was observed in the ovary of one juvenile specimen. An epithelium consisting of flattened cells was observed surrounding all the oocytes except the largest. A few nuclei, perhaps associated with a greatly flattened epithelium, were noted in some sections through the largest oocyte.

A simple tissue connection of oviductal cells is present on the middorsal line in front of the mature ovum. This "pore", presumably related to oviposition, can be observed externally as a middorsal discontinuity in the cuticular spines (Fig. 1B for *A. tetranchyrodermatoides* Ruppert, 1978). The circular muscles of the central body chamber (Rieger et al. 1974; Teuchert 1974) are strongly developed immediately anterior to the middorsal "pore" forming a sphincter muscle. This sphincter may function in oviposition (Fig. 9A, B).

A cellular sac containing a cluster of spermatozoa communicates with the largest oocyte by a short posterior opening formed by 4–5 small cells arranged in a ring. This dorsally located sac consists of more than one layer of squamous epithelial cells that may be continuous with the oviduct posteriorly and join the compact band of cells anteriorly. The

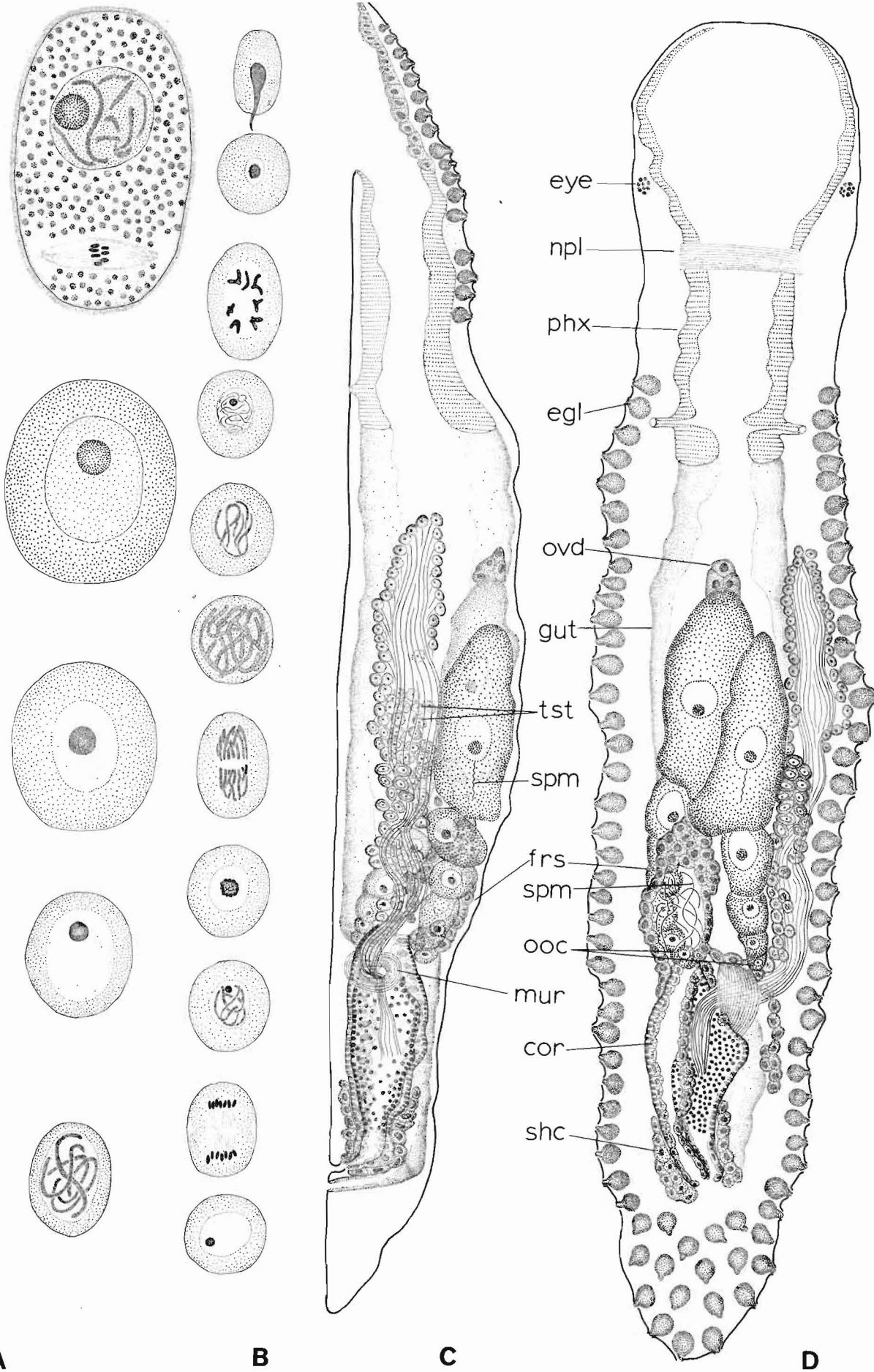
frontal sac ends blindly at its anterior end but it is in intimate contact with a compact band of cells (Fig. 7C).

The compact band of cells consists of large, strongly basophilic cells which resemble Y-cells, e.g. *Neodasys*, in their staining characteristics (Fig. 7B). This band shifts from dorsal to the gut to dorsolateral as it approaches the pharyngo-intestinal junction. It joins a short, cuticle-lined canal surrounded by a rosette of gland cells on the left side of the body. The canal opens to the exterior via a permanent pore on the left side of the body (Fig. 7A).

3.5. *Diplodasys ankei* Wilke, 1954 (Figs. 1A, E; 8; 9C, D; 12F; 14D)

The genital system of *Diplodasys* consists of paired testes located in the lateral region of the body, an ovary located dorsal to the caudal organ and gut, a caudal organ found posterior to the gut, and, a frontal organ system in the central body region extending from the largest oocyte to the pharyngo-intestinal junction (Fig. 9C, D).

The lateral testes extend from just behind the pharyngo-intestinal junction to the caudal organ. The walls of the vasa deferentia contain, from posterior to anterior, spermatogonia, spermatocytes and spermatids. Spermatozoa are located along the length of the testes. They converge on the midline of the body posteriorly to enter the proximal portion of the caudal organ (Fig. 8F, G). The terminal parts of the vasa



A

B

C

D

Fig. 6. *Platydasya* cf. *ocellatus*. — A, bottom to top, stages in growth and vitellogenesis of oocytes. — B, bottom to top, observed stages of spermatogenesis. — C-D, lateral and dorsal views of the

genital system based on reconstructions after serial transverse sections.

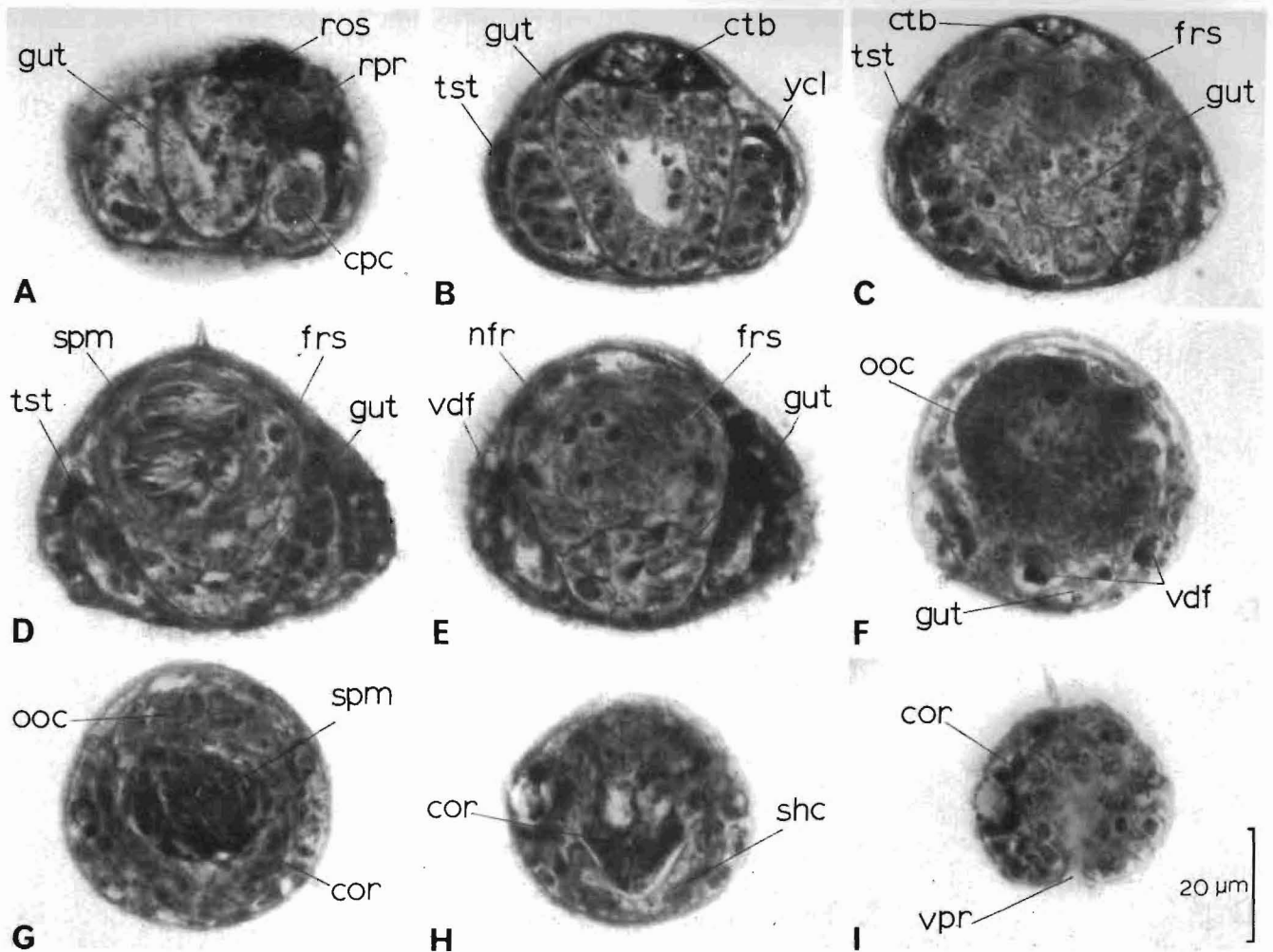


Fig. 7. *Acanthodasys thrinax*, photomicrographs of transverse histological sections (A-I) anterior to posterior. —A, level of rosette pore. —B, middle of compact tissue band. —C, anterior end of frontal sac. —D, middle of frontal sac. —E, posterior portion of frontal

sac. —F, level of anteriormost oocyte. —G, proximal end of caudal organ. —H, distal portion of caudal organ. —I, ventral opening of caudal organ.

deferentia consist of gland cells that surround the spermatozoa before and after they enter the caudal organ (Fig. 8E-G). There are several "cap" cells at the anterior ends of the vasa deferentia.

The caudal organ abuts the termination of the gut and continues posteriorly to a midventral opening. This organ is built of an inner layer of secretory epithelial cells surrounding a central lumen, and an outer sheath of circular or spiral muscles. The inner wall of the organ is folded near the ventral pore forming a suspended tube within the organ (Fig. 8H, I).

A single, dorsal row of oocytes grows anteriorly from a position at the anterior end of the caudal organ to the posterior third of the trunk. The small oocytes were observed to be encased in a very thin layer of cells, the oviduct. A bounding epithelium was not observed around the larger oocytes. No mitotic figures were observed in the oocytes. The largest oocyte in several specimens was rich in yolk granules, contained a prominent germinal vesicle and a sperm amphiaser ($n=8$) (see Fig. 14B, Ruppert 1977). A thin, weakly staining primary egg envelope was present. No modifications of the dorsal body wall related to oviposition were seen.

A cellular, sac-like structure containing a tangled cluster of spermatozoa is located immediately anterior to the largest oocyte. The flattened cells of this structure continue posteriorly as a neck-like process ventrolateral to the largest oocyte (Fig. 8C). Furthermore, these cells may be continuous

with a true oviduct. A compact band of large, strongly basophilic cells is continuous with the sac anteriorly. The compact band extends frontally, dorsolateral to the gut, to a position just behind the pharyngo-intestinal junction. At this point, the band joins a short cuticle-lined canal derived from the body wall that is surrounded by a rosette of gland cells (Fig. 8B). The canal and rosette open laterally on the left side of the body.

4. Ultrastructural observations

4.1. *Thaumastodermatinae* subfam. n.

The caudal organ of *Tetranchyroderma* sp. 1 is an active secretory epithelium. Five to eight cells with basally located nuclei are visible in transverse sections through the middle of the organ. Rough endoplasmic reticulum (RER) with swollen cisternae is particularly well developed. Large, electron dense secretion granules are clustered about the center of the organ. These membrane bound granules are produced by dictyosomes which, in turn, are topographically related to the RER; the latter sometimes forming whorls about the dictyosomes. The granules are uniformly dense with no apparent substructure. In *Tetranchyroderma* sp. 2 similar granules are located in the center of large vesicles which also contain loosely organized filamentous material. The cytoplasm of the caudal organ cells is rich in free ribosomes. The lumen is

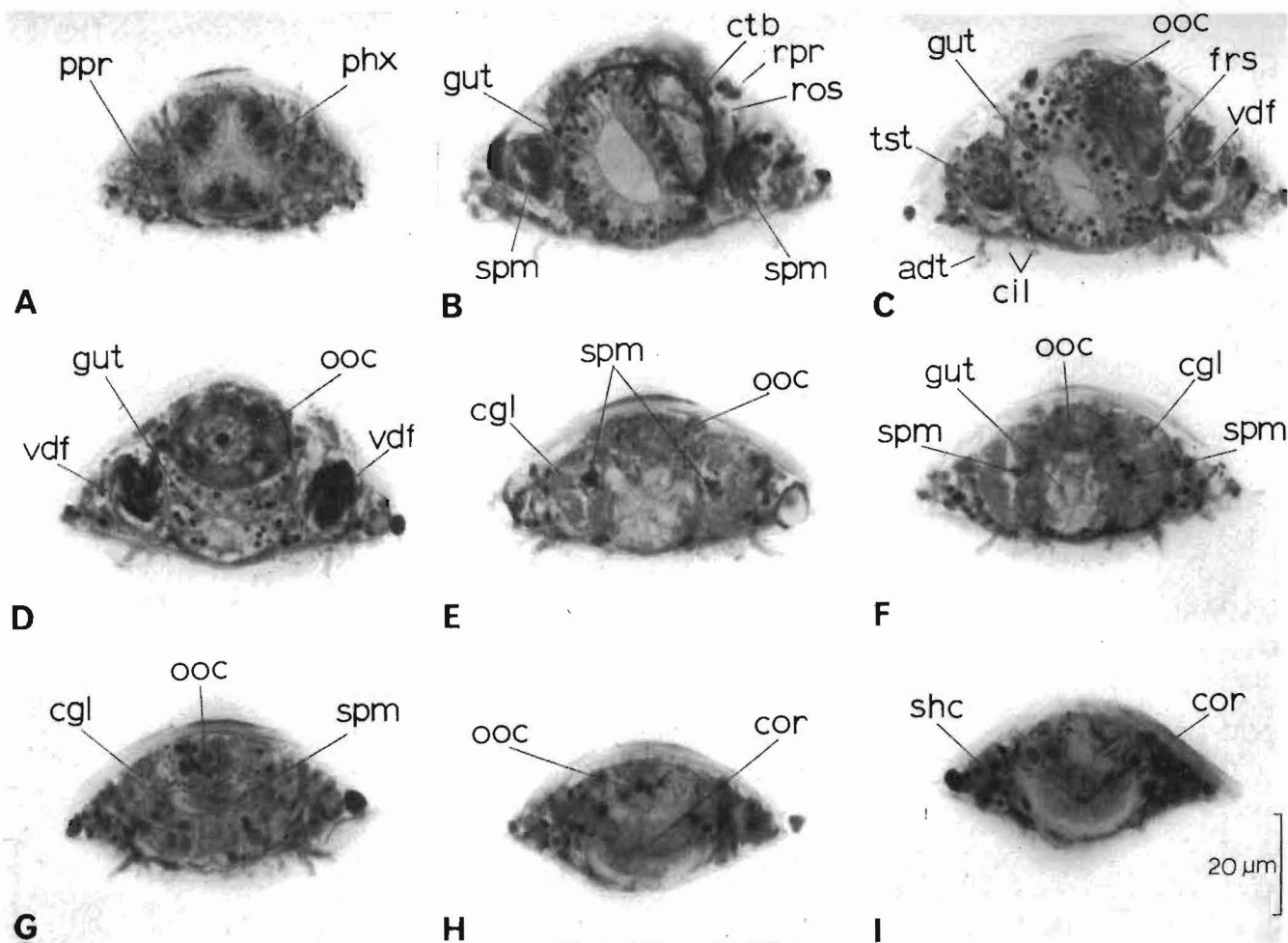


Fig. 8. *Diploasys ankeli*, photomicrographs of transverse sections (A-I) anterior to posterior. — A, level of pharyngeal pores. — B, rosette pore. — C, posterior end of frontal sac. — D, anteriormost

oocyte. — E, F, posterior ends of vasa deferentia. — G, rostral end of caudal organ. — H-I, distal portions of caudal organ.

occluded while the organ is "at rest", although a few microvilli, that extend longitudinally through the organ, are visible in transverse sections of *Tetranychroderma bunti*. These elongated microvilli arise from the luminal surface of the epithelial cells near the proximal opening of the caudal organ. Groups of tonofilaments, anchoring the microvilli, pass from the bases of the microvilli to hemidesmosomes on the basal plasmalemma near the proximal opening of the organ (Fig. 11C, D). Microvilli are absent from the caudal organ of *Tetranychroderma* sp. 2. A well developed basal lamina is present peripheral to the epithelial cells (Figs. 10B; 11F). The entire organ is ensheathed in a layer of circular or spiral muscle cells which forms a sphincter at both proximal and distal openings of the organ in all the species investigated (Fig. 11C, D).

The proximal neck of the caudal organ extends into the frontal sac in *Tetranychroderma*. In *T. bunti*, *T. sp. 2*, the sac consists of flattened, irregular cells peripherally and cell fragments centrally. The central mass contains sperm and scattered mitochondria, pieces of membranes, small granules and some glycogen particles (Figs. 10A; 11C). In addition, there are few to several large, membrane bound granules containing small vacuoles, membranes and irregularly distributed rod-like crystalline structures. The granules, perhaps lysosomes, are electron dense. The granules correspond structurally to the secretory products of the paired gland cells opening at the distal neck of the caudal organ. The peripheral

cells of the frontal sac are continuous anteriorly with oviductal cells bounding the larger oocytes.

Paired caudal gland cells open on each side of the mid-ventral pore of the caudal organ via a short, cuticle-lined neck. RER with swollen cisternae is well developed (Fig. 11H). Large, dense, membrane bound granules are present and are derived, in part, from the dictyosomes. These granules contain numerous, irregularly distributed, rod-like crystalline bodies.

In *Tetranychroderma*, the terminal portion of the vas deferens forms a narrow tube. Centrally located sperm are wrapped in what appears to be a single cell in transverse sections (Fig. 11E). A thin, basal lamina separates this cell from a muscular sheath that may be derived from muscle cells of the longitudinal body muscles. The myofilaments in this sheath run mostly in a circular direction. Transverse sections through the testis of *Thaumastoderma* at the level of the spermatids reveal an extremely flattened epithelium bounding the germinal cells (Fig. 11A). This epithelium clearly separates the spermatids, and central sperm, from the peripheral muscle cells, and, should be considered as forming a structurally distinct vas deferens.

Transverse sections through the largest oocyte of *Thaumastoderma* reveal a cell packed with yolk, lipid spheres and free ribosomes (Fig. 11B). Mitochondria, dictyosomes and some fragments of RER are also present. Microvillar extensions of the oolemma are absent, but small invaginations that

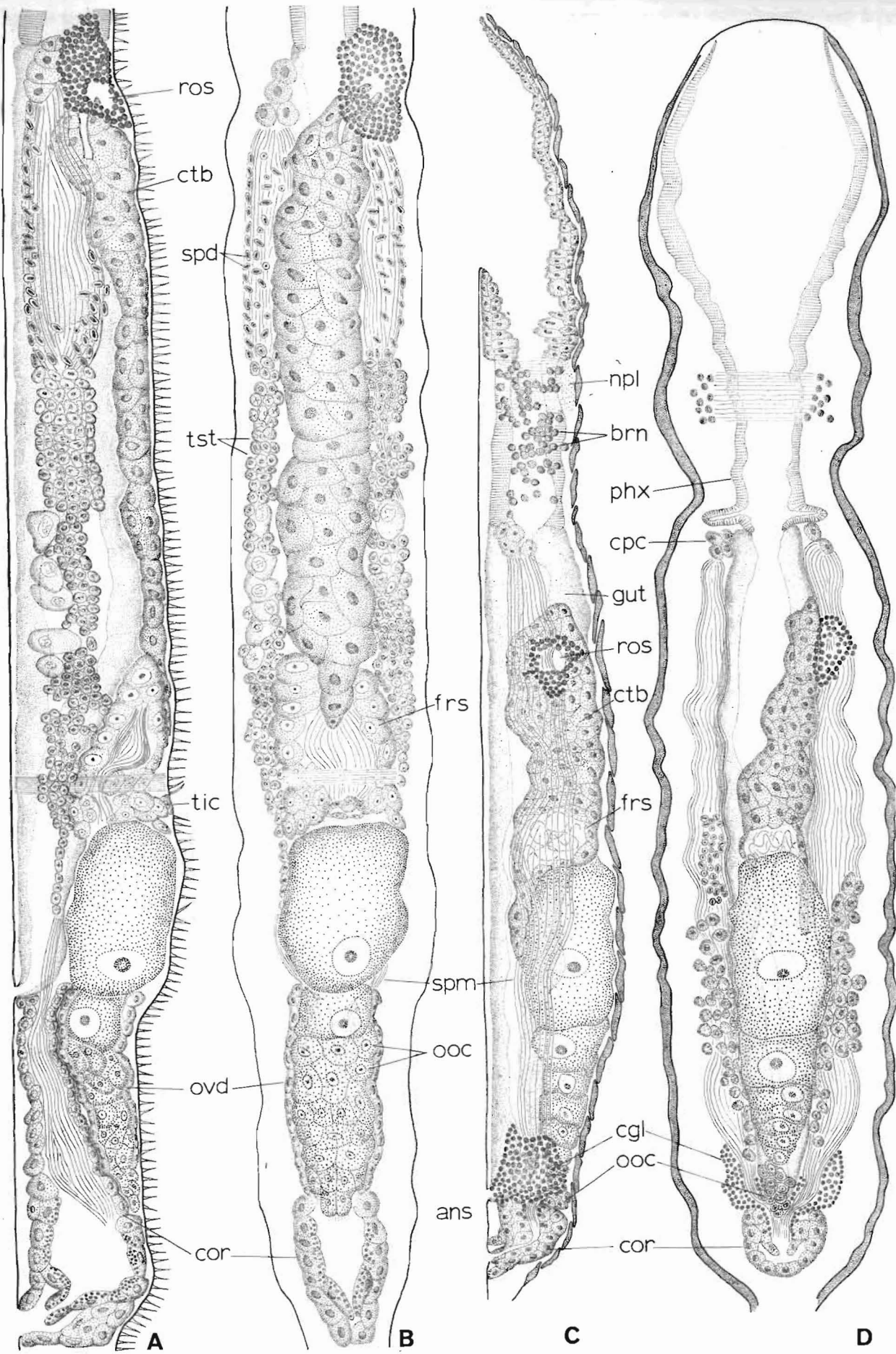


Fig. 9. Reconstructions of the genital systems of *Acanthodasyis thrinax* and *Diplodasyis ankei* after serial transverse sections. — A-B, *A. thrinax*, lateral and dorsal views. — C-D, *D. ankei*, lateral and dorsal views.

Note: the rosette organs should open on the left side of the body.

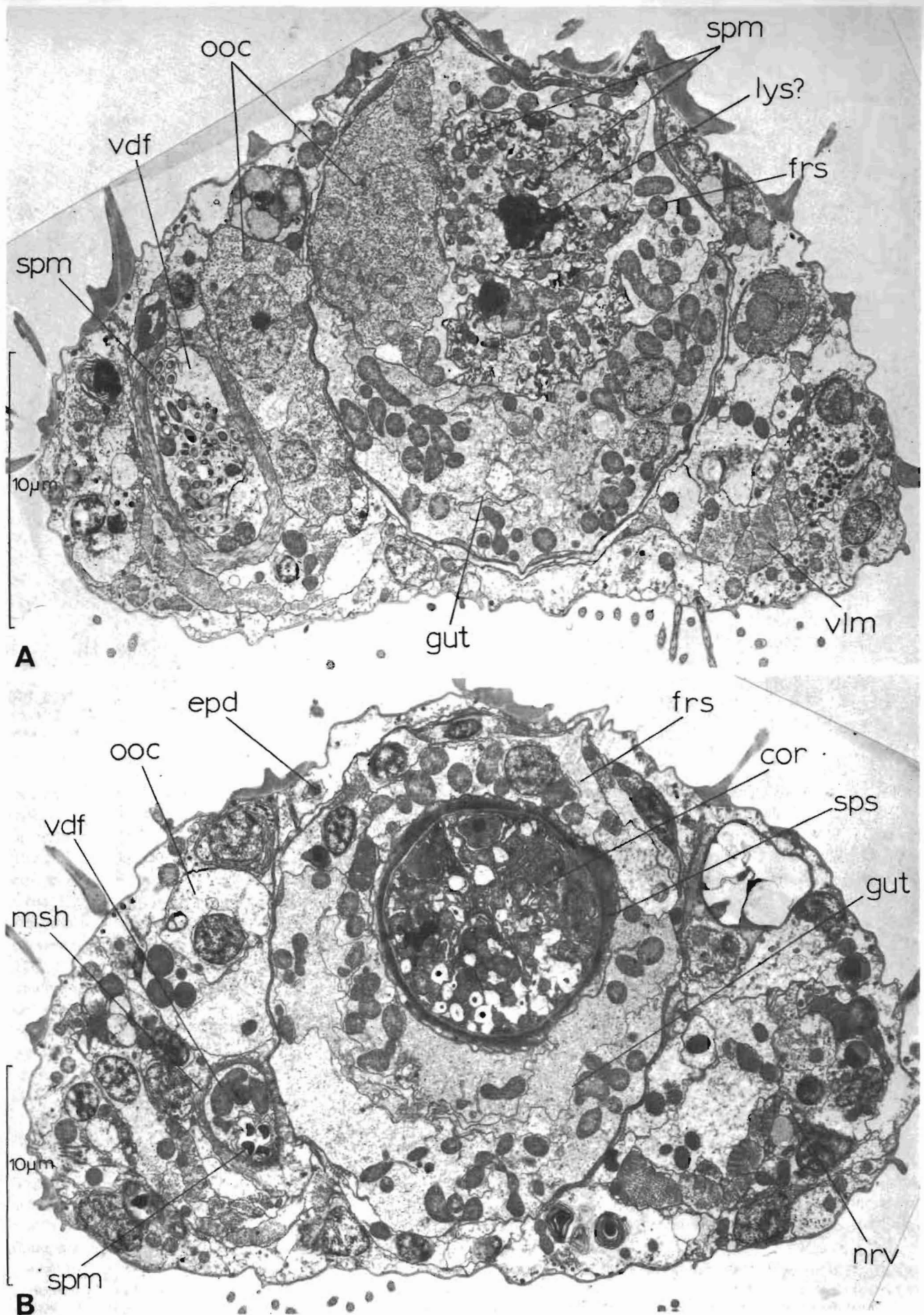


Fig. 10. TEM transverse sections through the posterior portion of the body of *Tetranchyroderma* sp. 2. — A, level of frontal sac. — B, level of proximal portion of caudal organ.

appear to form irregularly shaped vesicles occur along the oolemma. The egg envelope consists of a thin, inner layer of densely packed microfilaments that is continuous with an outer layer of loosely organized filaments. An extremely thin oviduct consisting of a single layer of cells surrounds the oocyte (Fig. 11B). The oviduct separates the oocyte from the gut ventrally and the muscle layer dorsally and laterally. This layer contains RER, glycogen granules, some small vesicles, and a few mitochondria. An invagination into the ventral side of the oocyte was also observed. A portion of oviductal tissue extends into this invagination and is particularly rich in RER and vesicles. No cytoplasmic connection with the oocyte was observed but serial sections were not obtained through this region.

4.2. *Diplodasyinae subfam. n.*

The caudal organ of *Acanthodasys* sp. 4 consists of an inner epithelium rich in dictyosomes and RER. The proximal part of the organ contains sperm. Vesicles containing electron dense granules and loosely organized filamentous material are found in the epithelial cells at the anterior end of the organ. These granules are similar to those found in the caudal organ of *T. sp. 2*. Gland cells with elongated necks extending to the midventral pore are located in the posterior walls of the caudal organ of *Acanthodasys* sp. 4. These gland cells produce spherical to ellipsoidal, dense, secretion granules. The gland necks also contain longitudinally oriented microtubules. A thin basal lamina separates the epithelial layer from several longitudinal muscle bands and an outer sheath of circular muscle cells. The muscle layer of the caudal organ is derived from the circular and longitudinal muscles found anteriorly around the gut. Although of basically similar construction, the epithelial cells of the caudal organ of *Acanthodasys vermiformis*, contain only one type of granule and it is structurally distinct from either of those found in *Acanthodasys* sp. 4. These membrane bound granules contain whorls of coiled, tubular structures, each "tube" with an hexagonal cross section (Fig. 14B, E, F). These will be designated as paracrystalline granules. Quite similar granules are known from the spermatids of the acoel *Childia* (Henley 1974), from the penis epithelium in austrognathiid Gnathostomulida (Dr Marlene Mainitz, Universität Wien, personal communication) and from the juxttaglomerular apparatus of the primate *Tupaia* (Forssmann & Taugner 1977). Identical granules are produced by cells surrounding sperm as they enter the caudal organ of *Diplodasys*, and, by at least some of the inner cells of the caudal organ itself (Fig. 14D).

There is a cellular oviduct in *Acanthodasys* that extends frontally from the rostral end of the caudal organ and is located dorsal to the gut. The oviduct contains the growing oocytes. In *Acanthodasys* sp. 4, the mid-dorsal pore, which consists only of a connection of oviductal tissue to the dorsal body wall, is located immediately in front of the rostral end of the caudal organ. The oviduct is continuous anteriorly with the frontal sac. The frontal sac of *Acanthodasys vermiformis* is constructed of 4–5 extremely flattened layers of oviductal cells that surround a cluster of sperm and cellular debris, mostly membrane fragments. Large, irregular granules are also present. The frontal sac is continuous with a compact band of tissue anteriorly.

The compact tissue band, interpreted as the vaginal canal (Fig. 15D), consists of large, irregular cells with incomplete plasma membranes (Fig. 12A, B). There are few organelles

present except scattered mitochondria and halos of discharged or extracted secretion products. Some of these structures contain fragments of tubular structures. This tissue band, separated from the gut by the basal lamina of the gut and 2 bundles of longitudinal muscle cells, extends anteriorly to the rosette organ.

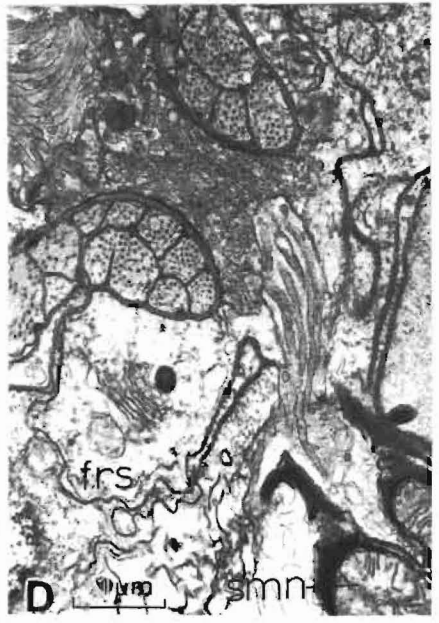
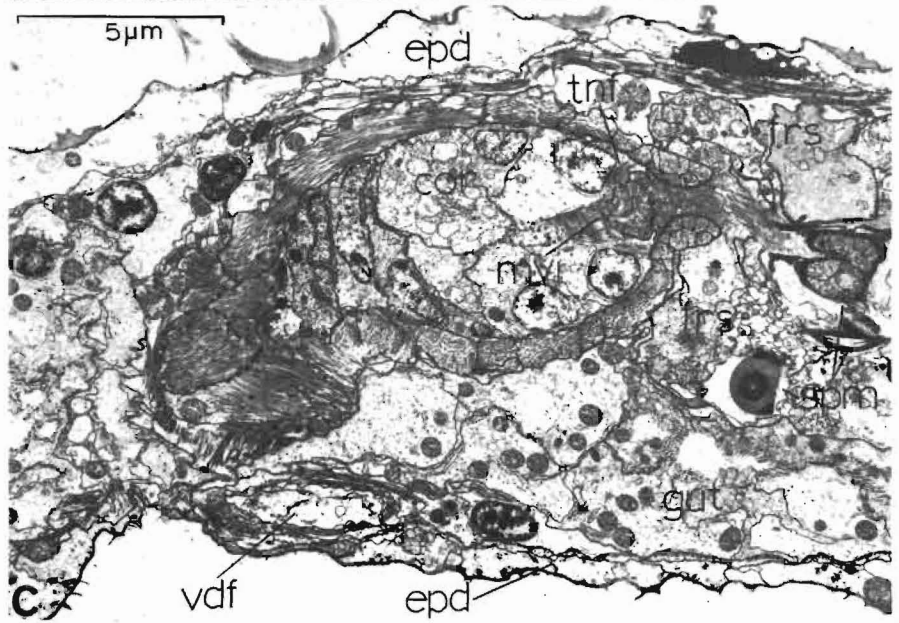
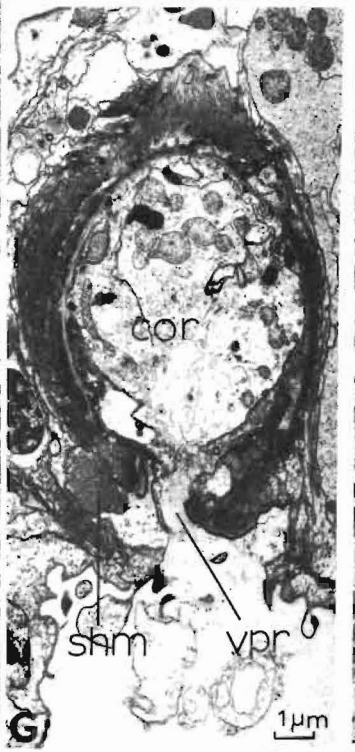
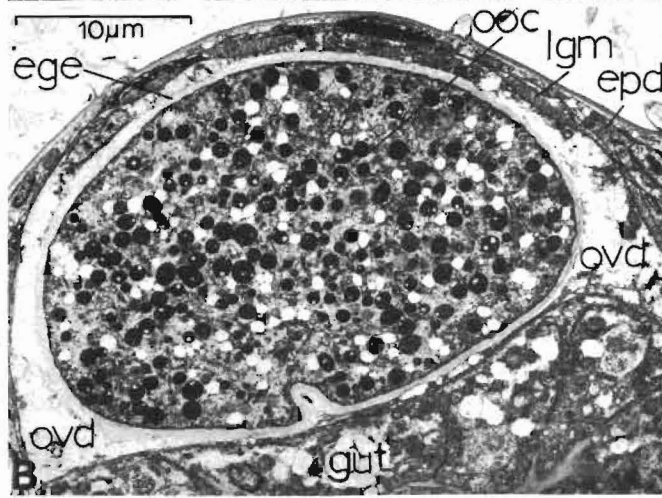
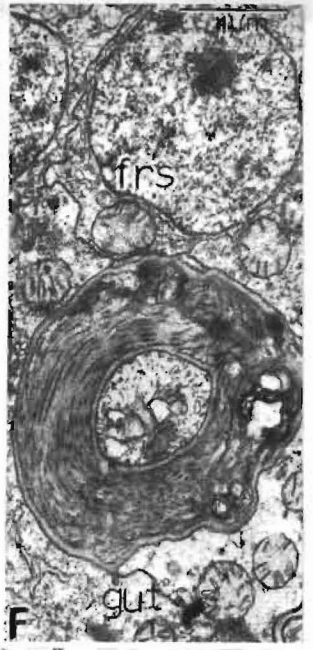
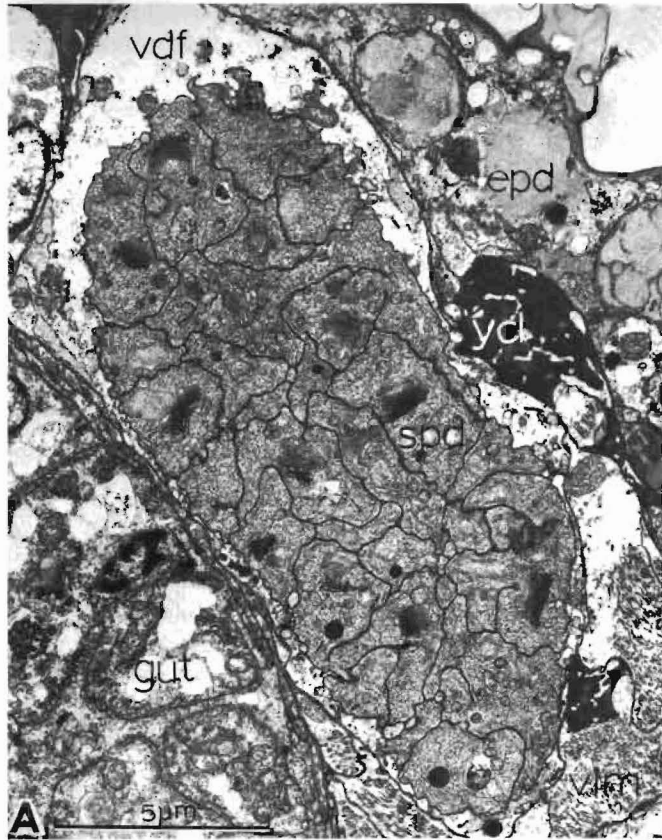
The rosette organ, interpreted as the female gonopore, is formed by several gland cells located in the epidermis. The gland cells are packed with large secretion products. These appear opaque, vesiculated, electron lucent or irregularly stained (*A. vermiformis*) depending on the stage of development and possibly the species involved. They are uniformly dense and only slightly stained in *Diplodasys ankei* and *Acanthodasys* sp. 4. These cells discharge into a folded, cuticularized canal that extends from the compact tissue band, through the muscle layer, to the dorsolateral pore on the left side of the body (Fig. 12A, D–F).

There are vasa deferentia in *Acanthodasys* consisting of a single cell, as seen in transverse sections, located lateral to the male germinal cells anteriorly and completely surrounding sperm posteriorly (Fig. 14C). In typical cross sections, the male tissue and the cells of the vasa deferentia are located lateral to the gut. They are bounded laterally and ventrally by longitudinal muscle cells (*musculi principalis*) and some Y-cells; dorsally by the cytoplasmic parts of circular muscle cells about the gut and oviduct; and, medially by the contractile parts of the circular muscle cells about the gut. The cells of the vasa deferentia move inside of the circular muscle layer at the level of the rostral end of the caudal organ (Figs. 12C; 13A, B). At this point, they are lateral to the gut cells and ventrolateral to the oviduct. The position previously occupied by the cells of the vasa deferentia is taken by the cytoplasmic parts of the circular muscle cells. The two bands of vasa deferentia cells join the rostral portion of the caudal organ located dorsal to the gut.

5. General discussion

It has been assumed from the beginning of this series on the analysis of reproduction in Gastrotricha that the caudally located accessory reproductive organs, the caudal organs, were homologous structures throughout the Macrodasysida (Ruppert & Shaw 1977). This assumption, that caudal organs are strictly comparable and have a common structural and functional basis, is still maintained. The proof of the homology of caudal organs in Macrodasysida (and *Neodasys*) will be the demonstration of recurrent correlated characters in the caudal-frontal organ systems throughout the group. It has already been shown (Ruppert 1978a), for example, that there is a common structural basis for accessory reproductive organs in *Turbanella*, *Dactylopodola* and *Macrodasys* despite what appear to be considerable functional modifications to this system. In those examples, it was argued that the caudal organ was either male in function (*Macrodasys*, input-output of autosperms) or that it no longer functioned in sperm transfer; that it might be vestigial.

The paradox of the Thaumastodermatidae is that the caudal organ is male in function (a penis) in *Acanthodasys* and *Diplodasys* and female in function (a bursal organ) in *Tetranchyroderma*, *Thaumastoderma* etc. The caudal organ of *Platydasys* is even more puzzling in being both a penis and a bursal organ. If it is assumed that what was once a penis cannot be transformed into a bursa and vice versa, then within the



Thaumastodermatidae either 1) the caudal organs are not homologous structures and therefore the family may be polyphyletic in origin, or 2), they are homologous structures and there is not yet a complete understanding of the structural and functional ground plans of the caudal organ, or more generally, the caudal-frontal organ system.

What is the possibility that genera of Thaumastodermatidae do not form a natural (monophyletic) group? One must answer immediately that the possibility of polyphyly is remote. Monophyly in this family is supported by common occurrence of a complex cuticle that is strikingly uniform throughout the group even at the level of ultrastructure (see Rieger & Rieger 1977 for additional data and discussion). Figure 1 depicts the common occurrence of 4-symmetry in the cuticular spines and scale-plates in several genera of Thaumastodermatidae. The general and detailed construction of the pharynges with reduced radial musculature and small pharyngeal pores is another common feature in the family. Thaumastodermatids uniformly lack circular muscles in the lateral body regions. There is generally an internal connection of the vasa deferentia or vas deferens to the caudal organ, a feature known from only one other, clearly independent line of Macrodasysida (*Mesodasys*). It is also known that all thaumastodermatids have multiciliated epidermal cells (Rieger 1976). In short, the Thaumastodermatidae is a uniform, well defined family. In fact, the Thaumastodermatidae is unique in Macrodasysida in not having some genera provisionally attached to it. It is reasonable, therefore, to assume monophyly for the Thaumastodermatidae and to reject the possibility that the caudal organs, or the caudal-frontal organ systems, are independently derived in the family. We must adopt the second statement listed above and attempt to arrive at a refined interpretation of the primitive structure and function of accessory reproductive organs in the family.

What then are the unifying and general features of the caudal-frontal organ systems of Thaumastodermatidae that will permit the identification of the common basis for the observed variations? The most striking feature is the internal connection of the vasa deferentia to the caudal organ. In addition, the caudal organs are located posteriorly near the anus and the frontal organs are anterior and dorsal in position. There is also cellular continuity between the caudal and frontal organs. In *Platydasys* and the remaining Thaumastodermatinae, there is not only cellular continuity between caudal and frontal organs, but the lumen of the caudal organ is continuous with the lumen of the frontal organ. I have argued previously, however (Ruppert 1978a), that for gastrotrichs in general the caudal organs and frontal organs are in cellular continuity but their lumina are never confluent. What is the explanation for this exception in Thaumastodermatinae?

The explanation is that the caudal organ of *Platydasys* is not a single organ but it is *two* organs located side by side and enclosed in a common sheath. The canal on the left side of the caudal organ leads directly to the frontal sac. Both this canal and the frontal sac should be designated as parts

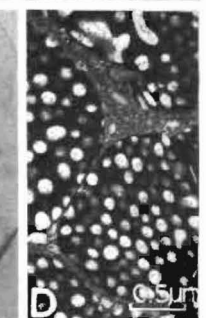
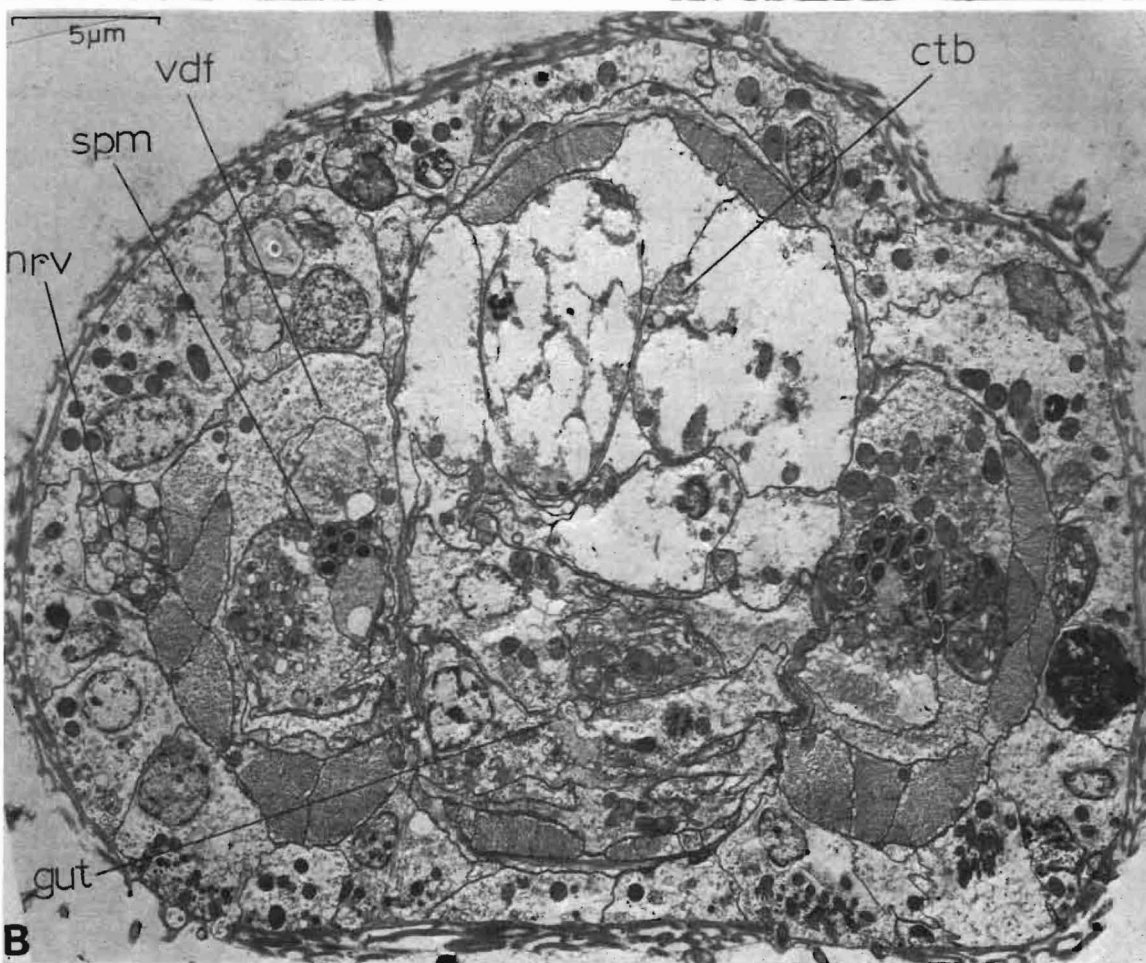
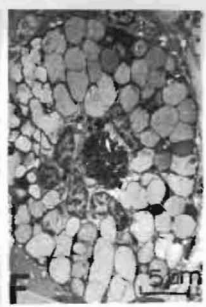
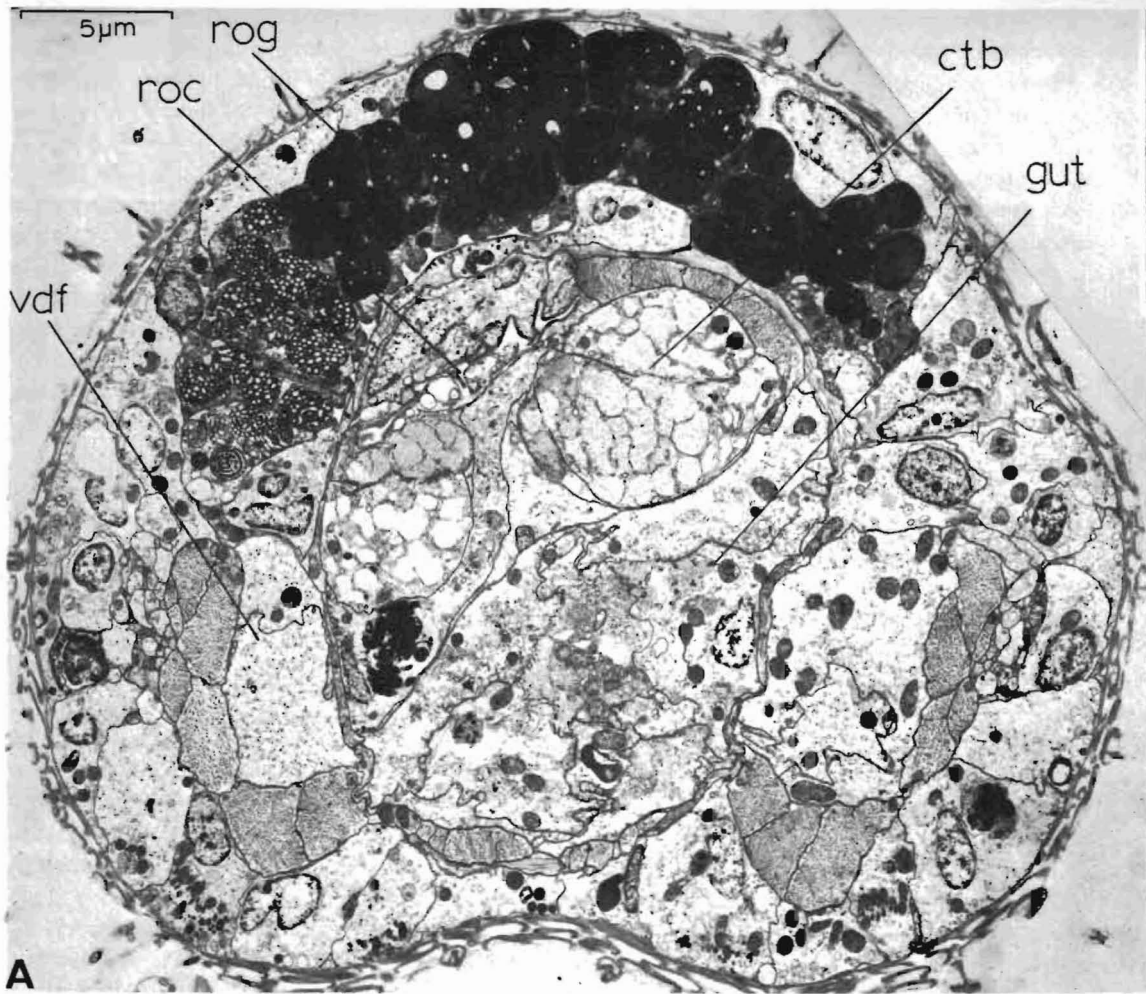
of the female accessory organ. The canal on the right side of the caudal organ receives autosperms and is clearly the male accessory organ. The term "caudal organ" applied to *Platydasys* arbitrarily designates the posterior portions of *both* male *and* female accessory organs. The term "frontal organ" designates only the sperm storage part of the female accessory organ. If this new interpretation of accessory male and female organs is extended from *Platydasys* to the remaining Thaumastodermatinae, then the terminal portion of the "vas deferens" in *Thaumastoderma*, *Tetranchyroderma* etc. should be recognized as the male accessory organ or the male portion of the "caudal organ". With respect to *Platydasys*, the remaining Thaumastodermatinae have reduced the male accessory organ and have increased the degree of development of the female accessory organ. Conversely, the Diplodasyinae can be interpreted as having developed predominantly the male accessory organ. The original female accessory organ is lost in Diplodasyinae and then re-evolved as the rosette organ. Figure 15 depicts diagrammatically these features. The phylogenetic consequences of this interpretation of the accessory reproductive organs suggest that *Platydasys* (Fig. 15D3) is an early evolutionary line in the Thaumastodermatinae, a line that culminates with such a species rich genus as *Tetranchyroderma* (Fig. 15D2). A very early split must be recognized as separating the two subfamilies. The Diplodasyinae (Fig. 15D1) can be considered to have diverged farthest in terms of the original construction of accessory reproductive organs if the original construction is assumed to be similar to that found in *Platydasys*.

Figure 15D3 depicts the organization of accessory reproductive organs in one species of *Lepidodasys*, a genus that may have some relationship to the Thaumastodermatidae (see systematics discussion and Rieger & Rieger 1977). I am aware that accessory reproductive organs in this genus are quite variable (perhaps indicating that the genus is defined too broadly) but a short discussion of the anatomy of the accessory organs, compared with those of Thaumastodermatidae, may enhance our understanding of these organs in gastrotrichs in general. The caudal organ of this undescribed species of *Lepidodasys* consists of a blind glandulomuscular sac *and* a weakly developed canal leading to a sperm storage organ. The glandulomuscular organ and the canal share a common ventral opening near the anus. The glandulomuscular organ may be the male accessory organ and the canal apparently represents the input part of the female accessory organ. This construction is basically similar to that of *Platydasys* (Fig. 15D4) except that the vasa deferentia of *Lepidodasys* do not internally join what we have interpreted as the male accessory organ. They open instead at paired ventral pores located anteriorly, a condition similar to most Macrodasysida exclusive of the Thaumastodermatidae.

The "caudal organ" of the genus *Dactylopodola* has been described previously (Ruppert 1978a) as consisting of a blind, glandular sac *and* a canal leading internally to compact tissue near the ova. Again, both these structures open by a common ventral pore near the anus and again the vasa deferentia are structurally independent of this "caudal organ".

The male *and* female character of the "caudal organs" in these examples plus the frequent observation in Macrodasysida that the vasa deferentia are not associated with a copulatory organ suggest that the "caudal organ" of Macrodasysida was originally two intimately associated organs, one male (input-output of autosperms) and one female (input of allo-

Fig. 11. TEM sections of species of Thaumastodermatinae. — A, *Th. heideri*, transverse section through the anterior end of the testis. — B, *Th. heideri*, transverse section through the largest oocyte. — C–D, *T. bunti*, oblique sagittal section through the caudal organ and frontal sac; enlargement of proximal portion of caudal organ. — E–H, transverse sections of *T. sp. 2*; E, vas deferens; F, anterior "neck" of caudal organ; G, ventral opening of caudal organ; H, caudal gland cell.



sperms). The last paper in this series will test the validity of this hypothesis in Macrodasysida and *Neodasys*.

6. Systematics discussion

Three comparative anatomical investigations have been made recently of Gastrotricha. These were an examination of ciliated epidermal cells (Rieger 1976), cuticle ultrastructure (Rieger & Rieger 1977) and now, the structure and function of reproductive organs. The new information derived from these investigations suggests that major taxonomic revisions are necessary in the Gastrotricha. The intention of this paper, however, is not to enter into a detailed discussion of systematics but to uncover some facts about the reproductive system of Thaumastodermatidae and to attempt to form some generalizations, first in the family, then in the Gastrotricha. Nevertheless, the anatomical patterns of the genital organs of Thaumastodermatidae demand the definition of new groups in the family. After a short discussion of *Lepidodasys*, a revised system of the Thaumastodermatidae will be given in diagnosis form.

Ironically, the genus *Lepidodasys* can no longer be aligned with the Lepidodasyidae (see Remane 1936) because it is now certain that the oocytes grow from posterior to anterior and become located dorsal to the gut. The family definition requires the opposite direction of growth. Also, *Lepidodasys* has two characteristics that are, to my knowledge, unique in Macrodasysida. The first is the absence of pharyngeal pores. The second is the presence of a non-striated pharynx myoepithelium. Both features are unknown elsewhere in Macrodasysida but are similar to pharynx constructions of Chaetonotida as well as Nematoda and Tardigrada. *Lepidodasys* has a complex cuticle as do the genera of Thaumastodermatidae but the fine structure of the scales of *Lepidodasys* does not resemble closely that of thaumastodermatids (Rieger & Rieger 1977). There are some features of *Lepidodasys*, however, that appear to be shared uniquely with the Thaumastodermatidae. The first is the absence of circular muscles from the lateral regions of the body (also true of *Neodasys* and Chaetonotida although the latter can have dorsoventral muscles located laterally e.g. *Draculiciteria*). The second is the occurrence of myofilaments in the Y-cells (Fig. 13E, F for *Acanthodasys*; unpublished data for *Lepidodasys*). If *Lepidodasys* is to be aligned at all with the Thaumastodermatidae, then the genus must be viewed as a very early divergence from the main line of evolution in that family. This suspicion will be given no formal taxonomic recognition at the present time.

7. Diagnoses

Lepidodasys Remane 1926, emended diagnosis

Mostly elongate Macrodasysida, nearly circular in transverse section with small nearly terminal mouth opening and no head

Fig. 12. TEM sections of species of Diplodasyinae. — A–D, *Acanthodasys vermiformis*; A, transverse section through the body immediately posterior to the rosette pore; B, transverse section through the body at the level of the compact tissue band; C, transverse section showing the transition of the vas deferens from the lateral to central body "chamber"; D, enlargement of rosette "gland" secretions — E, *Acanthodasys* sp. 4, sagittal section through rosette pore (courtesy of Dr R. M. Rieger) — F, *Diplodasys ankei*, frontal section through rosette organ.

delimitation. Cuticle elaborated as flat-scales, ribbed-scales or hat-shaped scales (see Rieger & Rieger 1977) often organized in crossed helical patterns. Multiciliated epidermal cells; ventral cilia in two longitudinal rows, often partially reduced. Epidermal glands with granular or fibrous inclusions, sometimes extremely well developed. Adhesive tubes in a semi-circle or two groups anteriorly; arranged marginally around the blunt posterior end; in ventrolateral and dorsolateral rows along the body. Sphincter muscle developed around mouth opening; powerfully developed radial pharyngeal musculature; lacking striations; pharyngeal pores absent. Circular muscles absent from lateral regions of the body. Y-cells contain myofilaments. Gonads paired; male anterior, female posterior; male and female gametes mature posterior to anterior; ova enter the central body region, dorsal to the gut, immediately anterior to the seminal receptacle. Male pores paired or single located anterior to the caudal organ; caudal organ with two canals sharing common ventral opening in front of the anus; one weakly developed canal leads into the seminal receptacle; the other is a blind, glandulomuscular sac. An oviduct is present. Mostly subtidal in distribution; fine to coarse sand.

Thaumastodermatidae Remane 1936, emended diagnosis

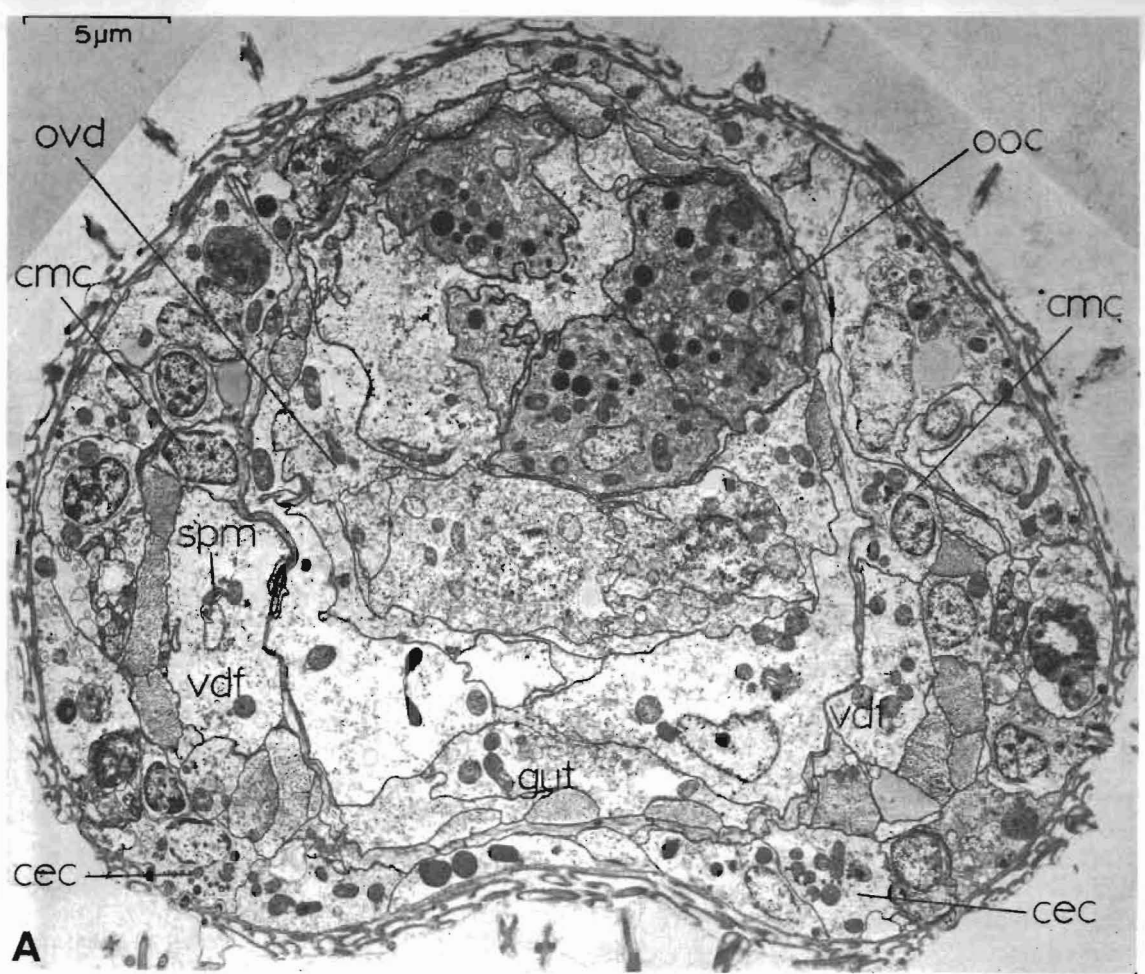
Macrodasysida of variable body form with two adhesive pedicles posteriorly; lateral adhesive tubes mostly ventrolateral in position. The complex cuticle forms spines, plates, bowl-shaped scales, multi-spined scales, stalked scales, etc., usually showing some evidence of 4-symmetry (Fig. 1 and see Rieger & Rieger 1977). Multiciliated epidermal cells; radial pharyngeal musculature reduced; pharyngeal pores small, located at the posterior end of the pharynx. Circular muscles absent from lateral regions of the body; Y-cells contain myofilaments. Male and female gametes mature posterior to anterior in one or two gonads. Well developed, glandulomuscular caudal organ near the anus; vasa deferentia internally join the male portion of the caudal organ. An oviduct is present. Very diverse in coarse, shelly subtidal sands; *Amphioxus* sand. Numerically abundant in medium to fine intertidal sand.

Thaumastodermatinae subfam. n. (Type genus *Tetranchyroderma*) Remane, 1926

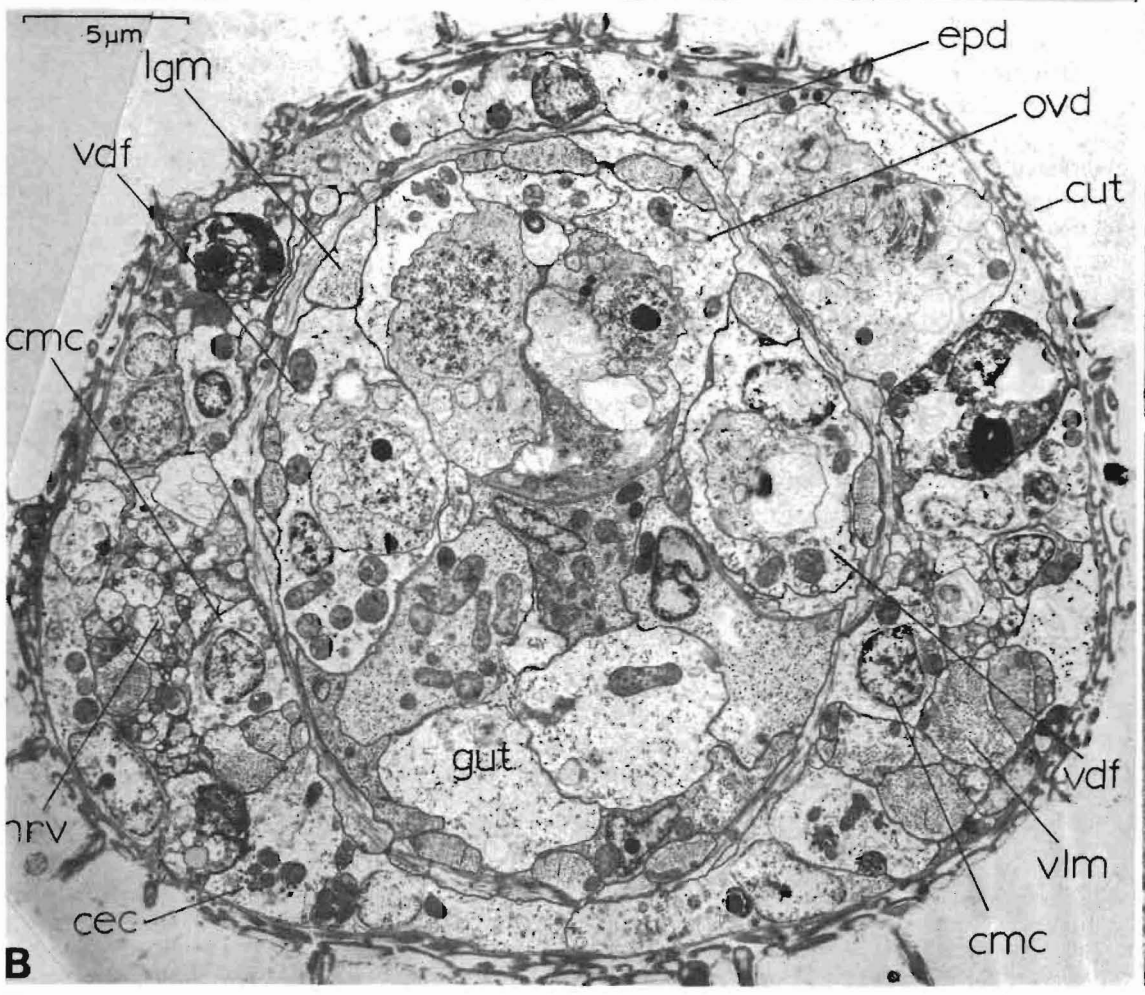
Thaumastodermatidae with reduced left gonad; spermatogonia located entirely in the right gonad; vas deferens joins

Fig. 13 (p. 110). TEM sections of *Acanthodasys vermiformis*. — A, transverse section through caudal portion of oviduct showing vasa deferentia in lateral body "chambers". — B, transverse section through the terminal part of the oviduct showing vasa deferentia in central "chamber". — C, detail of one bundle of radially organized tonofilaments anchoring the axial "visceral mass" to the body wall. — D, longitudinal section through a dorsolaterally located epidermal gland. — E, transverse section through the principal ventrolateral longitudinal muscle bundle, showing Y-cells. — F, detail of Y-cell and longitudinal muscle cell.

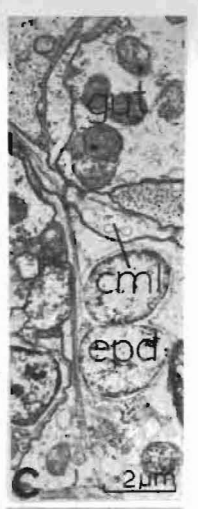
Fig. 14 (p. 111). TEM sections of species of Diplodasyinae. — A–C, *Acanthodasys vermiformis*; A, transverse section through the body at the terminal portion of the oviduct; B, transverse section through the body at the proximal end of the caudal organ, immediately behind the anus; C, transverse section through the vas deferens. — D, *Diplodasys ankei*, paracrystalline body from the terminal parts of the vasa deferentia. — E, *A. vermiformis*, paracrystalline bodies from the caudal organ showing relationship to the dictyosome. — F, *A. vermiformis*, detail of paracrystalline body.



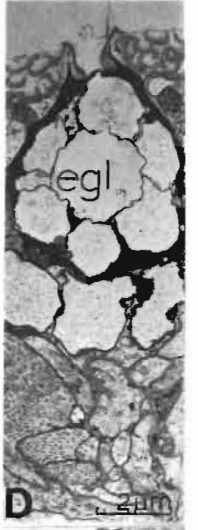
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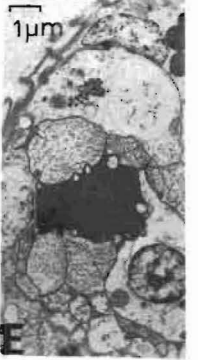
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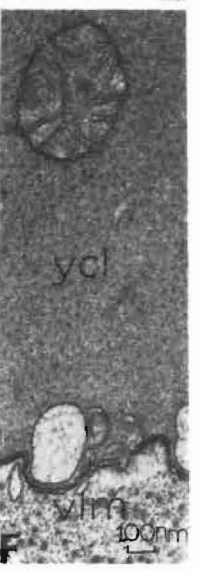
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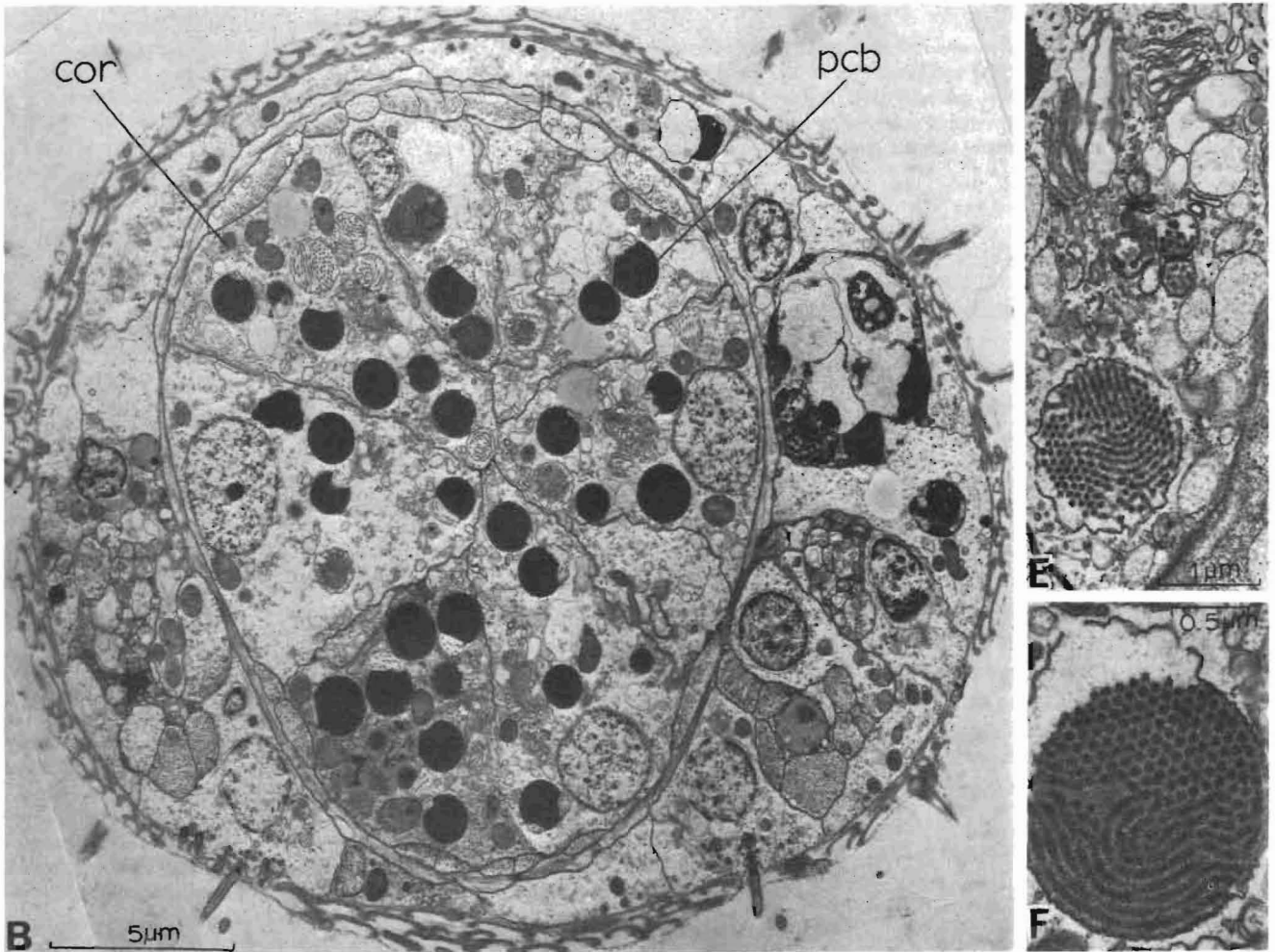
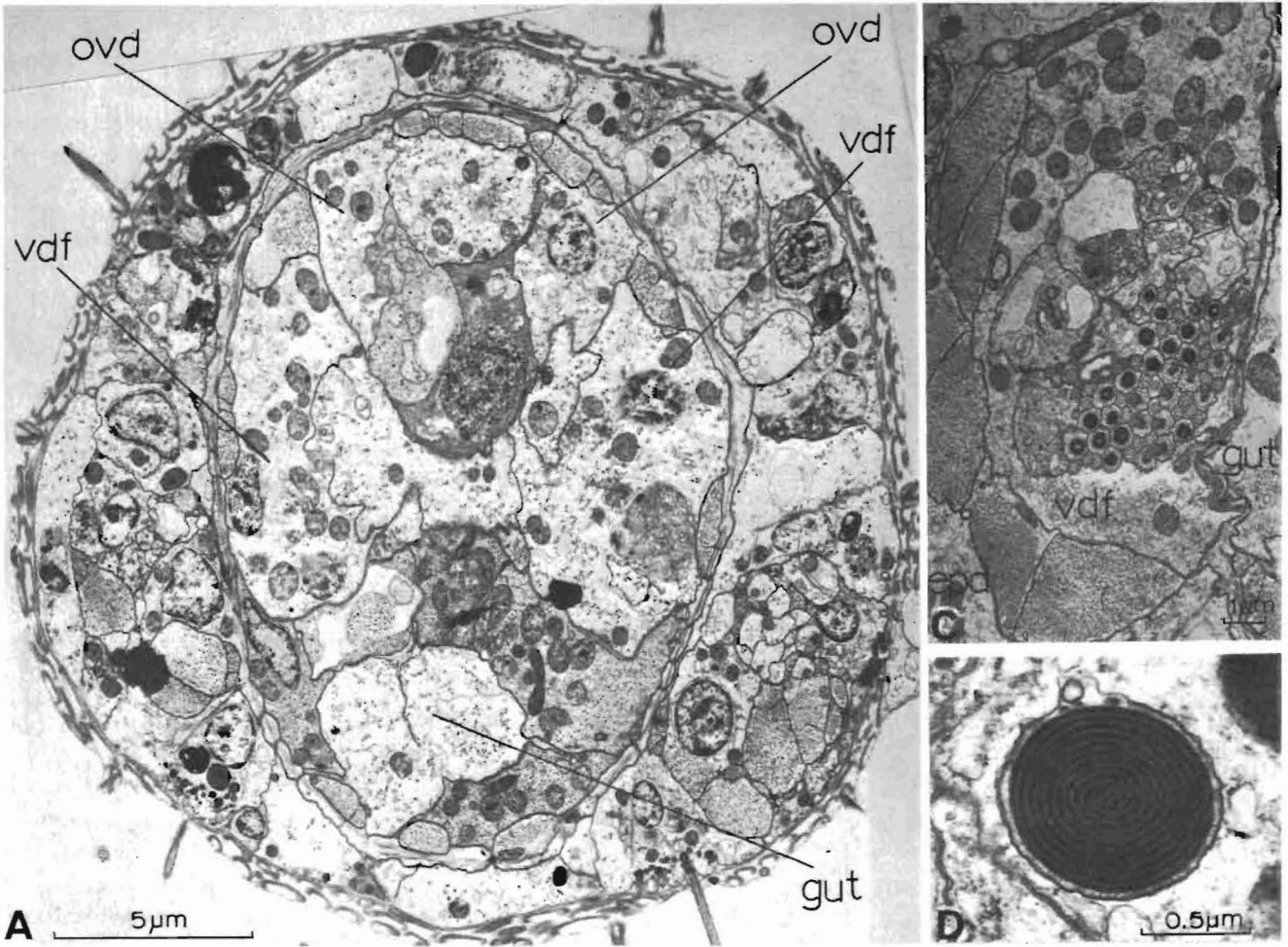
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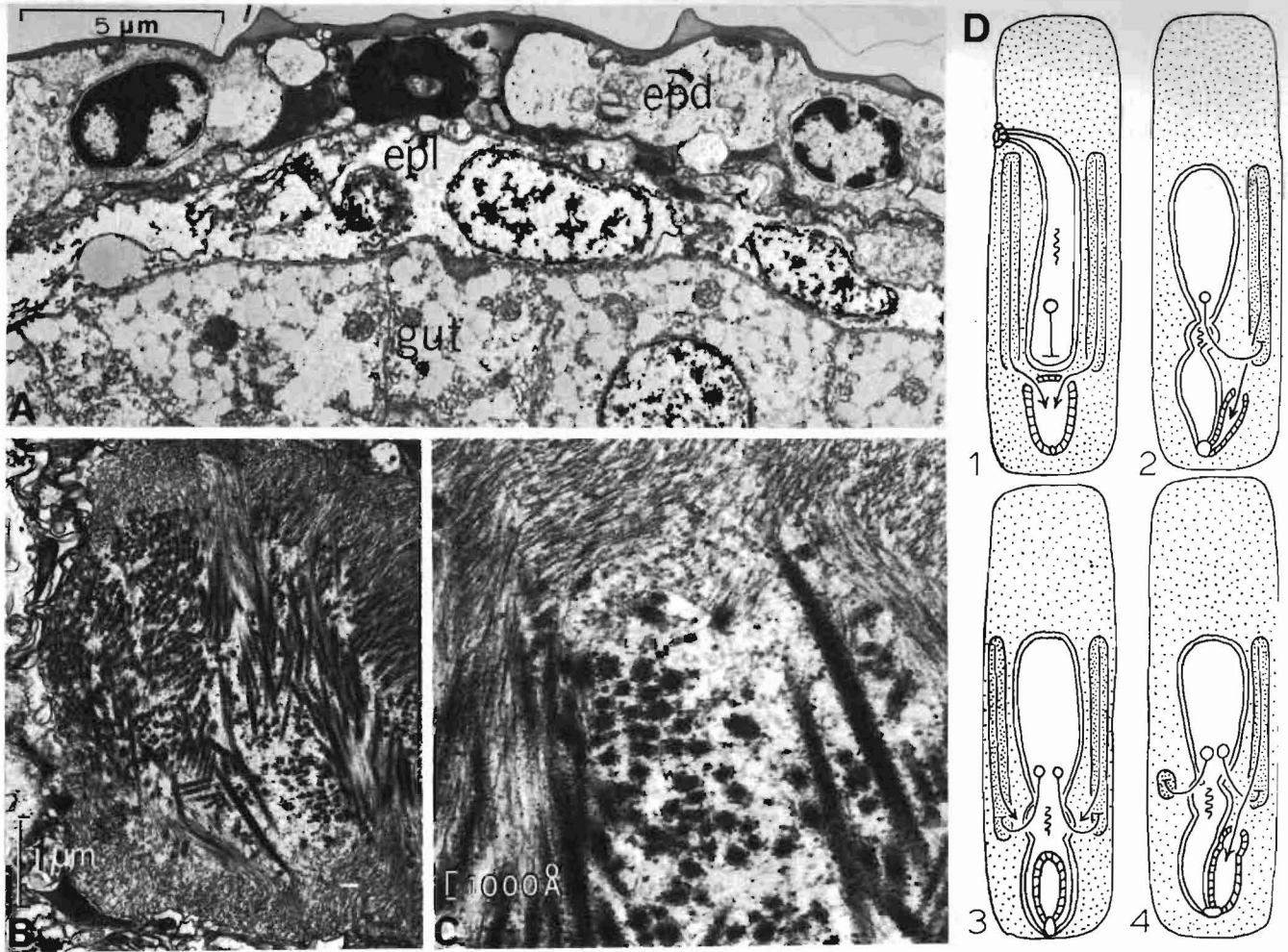


Fig. 15. TEM sections of *Platydasys* and summary of reproductive anatomy of Thaumastodermatidae and *Lepidodasys*. — A, transverse section through the body wall at midbody level showing absence of circular muscles and the occurrence of a bounding epithelium. — B, transverse section of the principal ventrolateral longitudinal muscle

cell. — C, enlargement of same, showing thick, paramyosin-like filaments. — D, diagram indicating the organization and homologous parts of genitalia in Thaumastodermatidae and *Lepidodasys* 1) *Diplodasyinae*, 2) *Thaumastodermatinae*, 3) *Platydasys*, 4) *Lepidodasys* sp.

right half on the caudal organ; left half of caudal organ extends to a seminal receptacle; caudal organ with a single ventral opening. Cuticle usually elaborated as multispined scales. Gland cells well developed on each side of the ventral opening of the caudal organ. Ventral cilia in transverse rows. Body form variable, from elongate and circular in cross section to short and flattened in cross section.

Platydasys Remane, 1927

Large Thaumastodermatinae with a large mouth. Cuticle thick with irregularly distributed, small spines hat-shaped scales, cuticularized gland necks and toothed scales. Numerous epidermal glands present, probably several types. Vas deferens joins male portion of the caudal organ; male and female portions of the organ are about equally developed; ovaries are paired. Circular muscles are absent from the central as well as the lateral regions of the body; ventrolateral longitudinal muscles are paramyosin type. *Platydasys* differs from the other more uniform genera in the subfamily in a number of characters, e.g. muscle organization, structure of the caudal organ, cuticle. These differences would seem to set *Platydasys* aside as a distinct early evolutionary line in the subfamily. This fact is not being formally recognized to avoid further complicating the taxonomy of the group.

P. maximus Remane, 1927; *P. brachycephalus* Levi, 1954; *P. tentaculatus* Swedmark, 1956; *P. ruber* Swedmark, 1956; *P. styliferus* Boaden, 1965; *P. phacellatus* Clausen, 1965; *P. mastigurus* Clausen, 1965; *P. ocellatus* Clausen, 1965; *P. pacificus* Schmidt, 1974.

Tetranchyroderma Remane, 1926

Large or small Thaumastodermatinae mostly with large mouth opening. Cephalic sensory organs with 0–1 pairs of soft, palp-like organs, and one pair of “cirri”; dorsolateral cirri present in some species. Cuticle as triancres, scaled triancres, tetrancres, pentancres or hexancres; often there is asymmetry or special modification of these basic scale types.

T. hystrix Remane, 1926; *T. polyacanthus* (Remane, 1927); *T. apus* Remane 1927; *T. megastoma* (Remane, 1927); *T. dendricum* Saito, 1937; *T. cirrophora* Levi, 1950; *T. papii* Gerlach, 1953; *T. vera* Wilke, 1954; *T. massiliense* Swedmark, 1956; *T. suecica* Boaden, 1960; *T. coeliopodium* Boaden, 1963; *T. thysanogaster* Boaden, 1965; *T. tribolosum* Clausen, 1965; *T. dragescoi* Swedmark, 1967; *T. indica* Rao & Ganapati, 1968; *T. swedmarki* Rao & Ganapati, 1968; *T. bunti* (= *Thaumastoderma bunti*) (Thane-Fenchel, 1970); *T. antennatum* Luporini et al., 1970; *T. hirtum* Luporini et al., 1970; *T. paradoxa* Thane-Fenchel, 1970; *T. polyopodium* Luporini et al., 1971; *T. boadeni* Schrom, 1972; *T. sp. 1* (Schrom 1972); *T. sp. 2* (Schrom 1972); *T. sp. 3* (Schrom 1972); *T. pacificum* Schmidt, 1974.

Thaumastoderma Remane, 1926

Small Thaumastodermatinae with a small mouth opening. Cephalic sensory organs as at least 2 pairs of soft, palp-like organs and one pair of short "cirri"; dorsolateral rows of cirri present. Cuticle elaborated as tetrancres or pentancres. Uptake portion of caudal organ, large.

Th. heideri Remane, 1926; *Th. mediterranea* Remane, 1927; *Th. swedmarki* Levi, 1950; *Th. cantacuzeni* Levi, 1958; *Th. ramuliferum* Clausen, 1965; *Th. arcassonnense* d'Hondt, 1965.

Pseudostomella Swedmark, 1956

Small Thaumastodermatinae with prebuccal apparatus (see Ruppert 1970). Cuticle as scaled triancres, tetrancres or pentancres.

Ps. roscovita Swedmark, 1956; *Ps. malayica* Renaud-Mornant, 1967; *Ps. indica* Ganapati & Rao, 1970; *Ps. sp.* (Luporini et al. 1970).

Ps. plumosa, *Ps. cataphracta* too!

Ptychostomella Remane, 1926

Small Thaumastodermatinae with a large mouth. Cuticle thick; scales and spines absent. Mostly subtidal in distribution, often with *Platydasys*.

Pty. pectinata Remane, 1926; *Pty. ommatophora* Remane, 1927; *Pty. mediterranea* Remane, 1927; *Pty. helena* Roszczac. 1939; *Pty. sp.* (Fornieris 1961).

Diplodasyinae subfam. n. (Type genus *Acanthodasys*)

Remane, 1927)

Thaumastodermatidae with paired, hermaphroditic gonads. Vasa deferentia join proximal end of the caudal organ which functions entirely as a penis. Caudal organ opens behind the anus. Oviduct continues anterior to the oocytes to join a rosette organ on the left side of the body that opens dorso-laterally or laterally near the pharyngo-intestinal junction. Ovary dorsal to or immediately in front of caudal organ. Ventral cilia in 2 longitudinal rows. Diverse in coarse, shelly subtidal sediments; *Amphioxus*-sand. Also present in medium to fine intertidal sands esp. *Acanthodasys*.

Acanthodasys Remane, 1927

Elongate Diplodasyinae, nearly circular in transverse section (some exceptions) with small mouth. Cuticle has a thick layer of scales and spines.

A. aculeatus Remane, 1927; *A. diploāsyooides* Ruppert, 1978b; *A. tetranchyrodermatoides* Ruppert, 1978b; *A. vermiformis* Ruppert, 1978b; *A. thrinax*, Ruppert, 1978b; *A. platydasyoides* Ruppert, 1978b.

all nonona mude

Diplodasys Remane, 1927

Short, blunt, dorsoventrally flattened Diplodasyinae with extremely large subterminal mouth. Dorsal and ventral cuticle as large flat scales, often with a raised cross in the center. Four angled spines occur laterally. Glands present around terminal parts of the vasa deferentia.

D. platydasyoides Remane, 1927; *D. minor* Remane, 1936; *D. ankei* Wilke, 1954; *D. ankei* ssp. *pacificus* Schmidt, 1974; *D. remanei* Rao & Ganapati, 1968.

Two additional genera must be included in the family. These are *Hemidasys* Claparede, 1867 and an unnamed genus (Remane 1926). These forms are adequately discussed by Remane (1936).

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Abbreviations in the figures

<i>adt</i>	adhesive tube	<i>npl</i>	neuropile
<i>ans</i>	anus	<i>nrv</i>	nerve
<i>brn</i>	brain	<i>ooc</i>	oocyte
<i>cec</i>	ciliated epidermal cell	<i>ovd</i>	oviduct
<i>cgl</i>	caudal gland cell	<i>pcb</i>	paracrystalline bodies
<i>cil</i>	cilium	<i>phx</i>	pharynx
<i>cmc</i>	circular muscle cell	<i>ppr</i>	Pharyngeal pore
<i>cml</i>	circular muscle layer	<i>roc</i>	rosette canal
<i>cor</i>	caudal organ	<i>rog</i>	rosette glands
<i>cpc</i>	"cap" cell	<i>ros</i>	rosette organ
<i>crt</i>	"cirri" rootlets	<i>rpr</i>	rosette pore
<i>ctb</i>	compact tissue band	<i>scn</i>	sperm canal
<i>cut</i>	cuticle	<i>shc</i>	sheath cells
<i>ege</i>	egg envelope	<i>shm</i>	sphincter muscle
<i>egl</i>	epidermal gland	<i>smn</i>	sperm mitochondrion
<i>epd</i>	epidermis, epidermal cell	<i>spc</i>	spermatocyte
<i>epl</i>	epithelial layer	<i>spd</i>	spermatid
<i>eye</i>	eye	<i>spm</i>	sperm
<i>frs</i>	frontal sac	<i>sps</i>	spiral muscle sheath
<i>gut</i>	gut, intestine	<i>tic</i>	tissue connection
<i>lgm</i>	longitudinal muscle	<i>tnf</i>	tonofilaments
<i>lys</i>	lysosome	<i>tst</i>	testis
<i>mpr</i>	male pore	<i>vdf</i>	vas deferens
<i>msh</i>	muscle sheath	<i>vlm</i>	ventrolateral longitudinal musc.
<i>mur</i>	muscle ring	<i>vpr</i>	ventral pore
<i>mvi</i>	microvilli	<i>ycl</i>	Y-cell
<i>nfr</i>	"neck" of frontal sac		

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