



Male Genital Tract and Spermatogenesis in Nematodes

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ABSTRACT

The male reproductive system of nematodes is composed of three parts, testis, seminal vesicle and vas deferens. The genital tract is short and uncoiled in plant-parasitic nematodes. It is long and coiled in animal-parasitic nematodes. A single testis is present in secernentian nematodes and two testes are present in adenophorean nematodes. However, there are few exceptions to this monorchic and diorchic conditions in the same family. Spermatogenesis is confined to the distal end of the testis, a condition known as telogonic gonads. The morphogenesis of the nucleus during the meiosis and other changes occurring in the various stages of developing male gametes studied in various nematodes were studied by different workers.

Keywords: Nematode male reproductive system, Monorchic and diorchic conditions, Telogonic gonads, Spermatogenesis and meiosis, Plant vs. animal parasitic nematodes

INTRODUCTION

Gonads of nematodes are tubular structures that lie in conformity with their ducts. Therefore, the gametes are not released into the body cavity, pseudocoelom (Bird and Bird, 1991). Male genital organs include testes, seminal vesicle, vas deferens, ejaculatory duct and accessory genital organs like the copulatory bursa, genital alae and spicule. The tubular testes are lined with epithelium and glandular tissue. The spermatozoa are produced at the distal end of the testis and become mature during the passage through the parts of the genital ducts. The lumen of solid testis is completely occupied by spheroidal primordial germ cells. A central branching core called rachis is associated with the primordial germ cells. The primordial germ cells undergo rapid mitotic divisions to form spermatogonia which pass through the various stages of spermatogenesis to produce mature functional spermatozoa. The succeeding part of male genital tract is slightly larger than the testis and has a thin epithelial lining.

The developing germ cells are loosely placed in the lumen of vas deferens. The large sized germ cells are not attached to the rachis. The seminal vesicle leads into the next part of the genital duct, the vas deferens. The lining of seminal vesicle is thick than the previous counterparts. The ejaculatory duct open to outside through cloacal aperture (Basyoni and Rizk, 2016).

Male members of the nematode genera have copulatory bursae with spicules. The spicules act as sensory probe during the act of copulation. The structure of copulatory bursae of *Oesophagostomum columbianum* and *Haemonchus contortus* were discussed in detail by Johal (1988) and Singh (2015a). Vongandy *et al* (2020) compared the gubernaculum length and left spicule barb length of *Haemonchus contortus* from Thailand and Lao PDR.

Spermatogenesis in nematodes starts in the germinal zone at the distal end of testis i.e. telogonic. In some groups of nematodes like trichurids, the germ-cell formation occurs throughout the length of the testis, a condition known as hologonic. The testis, in case of telogonic species of nematodes, can be divided into germinal and growth zones. The spermatids produced in the testis are stored in the seminal vesicle. The spermatids develop into spermatozoa in the male genital tract or in the female genital tract during copulation.

MALE GENITAL TRACT

The structure of the bounding epithelia of testis and seminal vesicle in *Nematodirus battus* (Maritn and Lee, 1980). It was reported to be composed of a single layer of greatly elongated spindle shaped epithelial cells containing nuclei, many mitochondria and granular as well as rough endoplasmic reticulum. Bird and Bird (1991) observed that a continuity existed in the epithelium of testis and that of gonoduct.

According to Wright and Sommerville (1985a), The testis could be divided into four developmental zones, a zone of division of spermatogonia, a zone of growth of spermatocytes, a zone in which meiosis occurs and a zone of differentiation and formation of sperms. Bird and Bird (1991) observed the merger of the growth zone of testis into the seminal vesicle via a duct called the vas efferens. The vas deferens was found to be bounded by a layer of columnar glandular epithelium surrounded by a network of muscles. Furthermore, they reported the division of vas deferens into an anterior glandular and a posterior non-glandular portion. Earlier, even a sphincter with a nucleus was reported at that point by Magath (1919) and Musso (1930). In *Rhabditis strongyloides*, Schendier (1866) observed lateral pouches extending anteriorly on both sides of the vas deferens. Almost similar but incompletely separated glands known as ejaculatory

glands were also reported in *Ancylostoma* by Looss (1905). According to him, the adhesive secretion of the ejaculatory glands helped to hold male and female together during copulation. However, Baker (1936) in *Heterakis* and Sommerville and Weinstein (1964) in *Nematospiroides dubius* could not obtain any evidence of such adhesive secretion.

Chitwood and Chitwood (1950) reviewed the structure and modification in the arrangement of rays, their nerve innervation and the presence of sensory papillae in the male bursa of strongylids. The structural variation in bursa at species level was also discussed by Sommerville and Weinstein (1960), Green (1966), Jones (1966), Levine (1968), Croll and Wright (1976), Ohmori *et al.* (1976), Dvoinos and Kutimov (1979), Gibbons (1980), Johal (1988) and Singh (2015). Marchant (1970) stated that the bursa in the strongylids appeared to be an extremely sensitive structure as it generally flared up in the presence of a substance emitted by the female vulva. Chitwood and Chitwood (1950) described in detail the shape and structure of spicules, a characteristic feature of male nematodes. They proposed that the number, variation in size and shape of the spicules could be used as a diagnostic character in nematode taxonomy. Earlier, Seurat (1920) described that the presence of single spicule characterized the families Trichuroidea, Dioctophymatoidea, Oxyuridae and Thelostomatidae. The structure and size of the spicules along with gubernaculum were described in detail by Chitwood and Chitwood (1950) and Bird and Bird (1991) in different nematodes. Gomes *et al.* (1992) while working on *Trichuris travassosi* proposed the term spicular prepuce to designate the structure previously known as the spicular sheath. The term spicular sheath should now be used to refer to cuticle that covers the spicule.

In case of *Haemonchus contortus*, a long coiled tubular testis is present which is divided into a germinal and a growth zone. The testis is followed by a dilated seminal vesicle and a glandular vas deferens opening into the cloaca. The epithelial lining of seminal vesicle is markedly thickened near the posterior end. The lining of vas deferens consists of a unique epithelium in its initial part which subsequently change into a glandular one. Some accessory copulatory structures are associated with the cloacal region i. e., a single median gubernaculum, a large sized copulatory bursa and a pair of spicules (Figs. 1-8) (Singh 2001 and 2015a).

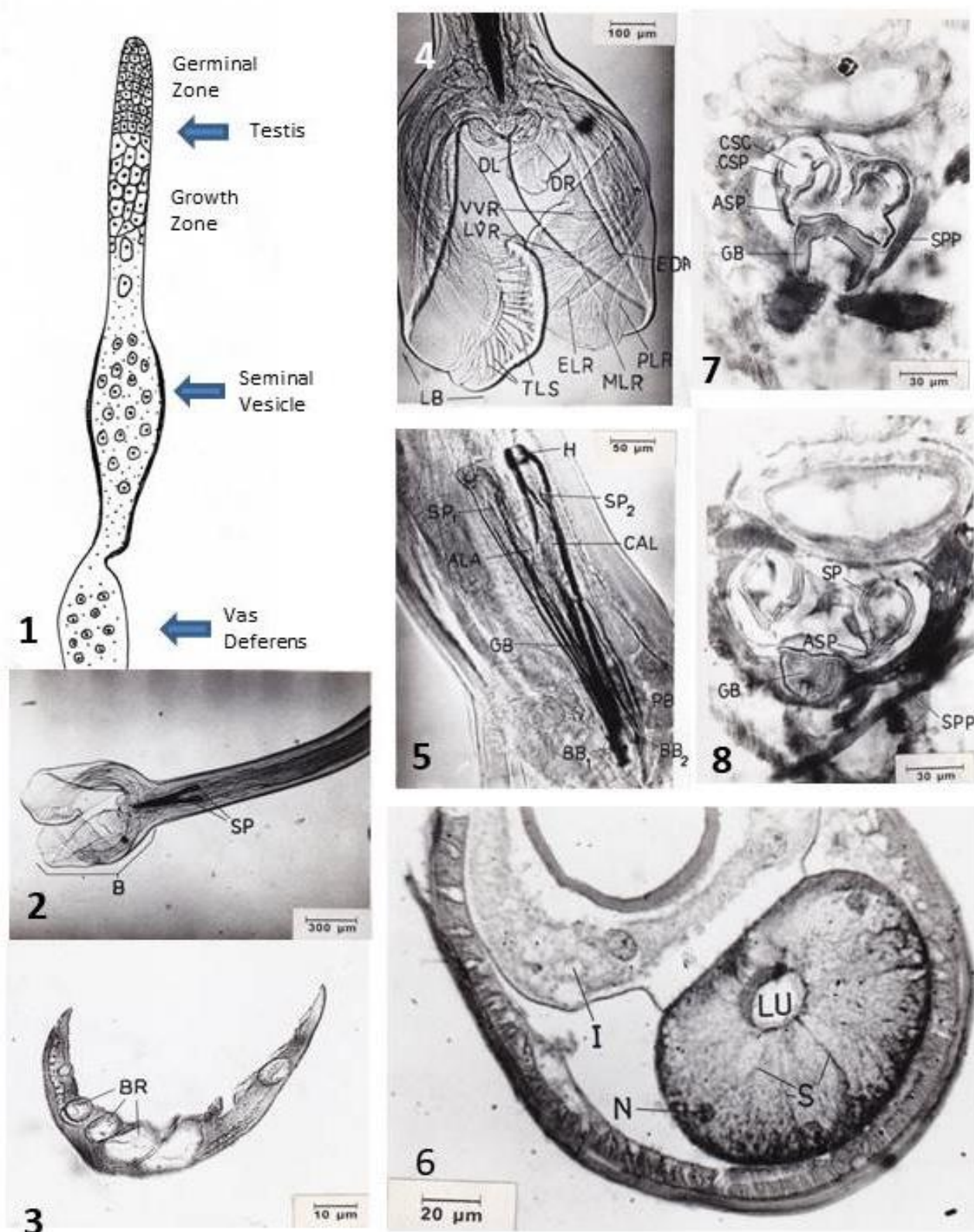


Fig.1: A diagrammatic representation of germinal and growth zone of testis, seminal vesicle and vas deferens of male nematode. **Fig. 2:** Posterior end of male showing copulatory bursa. **Fig. 3:** T.S. of bursa of male. **Fig. 4:** Detailed structure of bursa of male. **Fig. 5:** Posterior end of male showing spicules. **Fig. 6:** T.S. of male showing vas deferens. **Fig 7 & 8:** T.S. through the cloacal region of male. {*Haemonchus contortus*; Haematoxylin-Eosin staining}

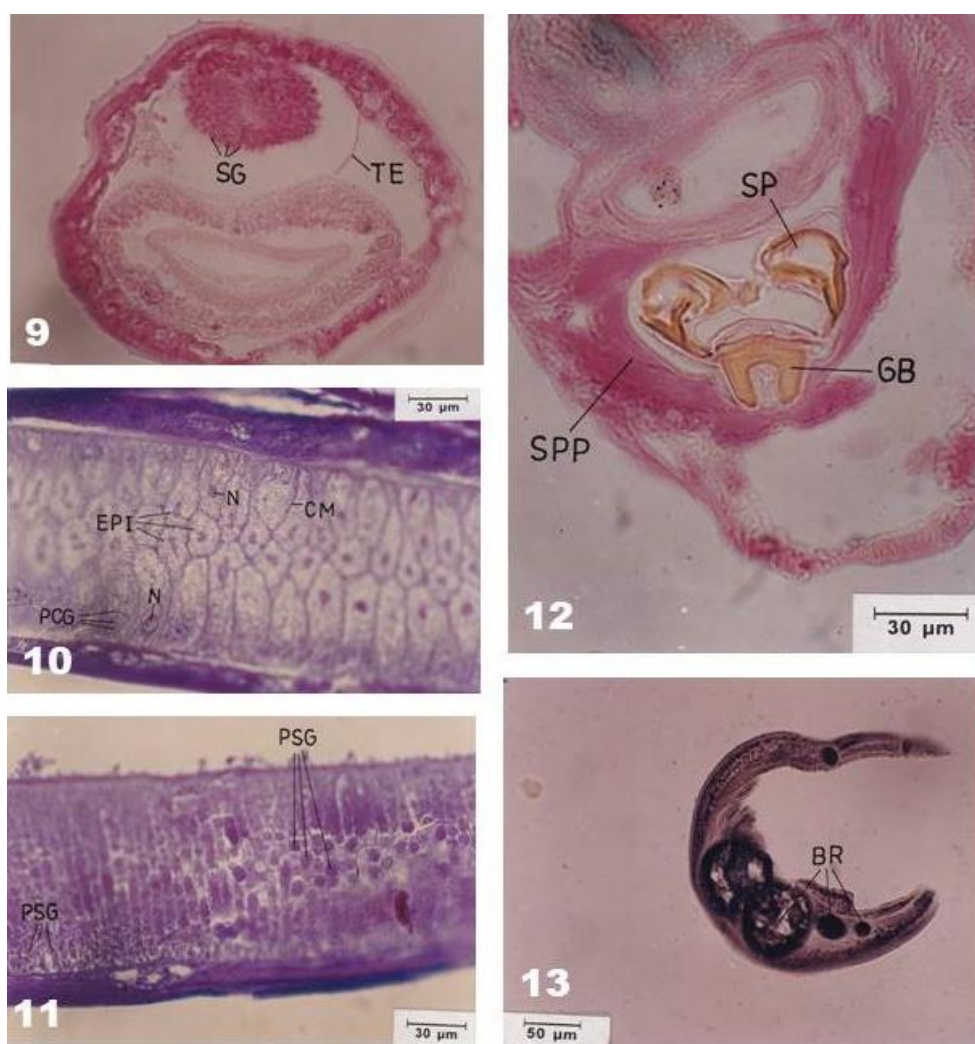


Fig.9: T.S. of male through testis showing concentration of glycogen.[Best's Carmine staining] **Fig. 10 & 11:** L. S. of Male through vas deferens showing concentration of proteins [Mercuric Bromophenol Blue staining]. **Fig. 12:** T. S. through the cloacal region of male showing distribution of proteins [Ninhydrin Schiff's staining]. **Fig. 13:** T. S. through bursa of male showing distribution of lipids [Sudan Black B staining]{*Haemonchus contortus*}

Lee (1960) performed a histochemical analysis on male reproductive organs of *Thelastoma bulhoesi* and found that the testicular epithelium was rich in glycogen while developing germ cells in the germinal as well as the growth zone and also the mature spermatozoa were glycogen free. However, small quantities of glycogen were observed in the glandular wall of the seminal vesicle and the upper regions of the vas deferens. Johal (1988) reported that the testicular epithelium of *Oesophagostomum columbianum* was totally free from glycogen and only the spermatocytes, cytoplasmic strands connecting the spermatocytes to the rachis and the spermatids lying in the seminal vesicle were found positive for the presence of glycogen. No evidence of mucopolysaccharides was

seen in the male reproductive system in *Diplotrriaena tricuspis* (Wajihullah and Ansari, 1981).

The presence of fat in the male reproductive system of *Ancylostoma caninum* was restricted to the bursa (Giovannola, 1936). In *Thelastoma buhoesi*, Lee (1960), reported the total absence of lipid in the male reproductive system. Nath *et al* (1961) detected the presence of groups of phospholipids in the spermatid just before the development of the refringent body in *Porrocaecum*. In *Oesophagostomum columbianum*, Johal (1988) described the presence of lipid not only in the epithelium of testis but also in protoplasmic part of spermatocytes and the protoplasmic strands connecting them to the rachis.

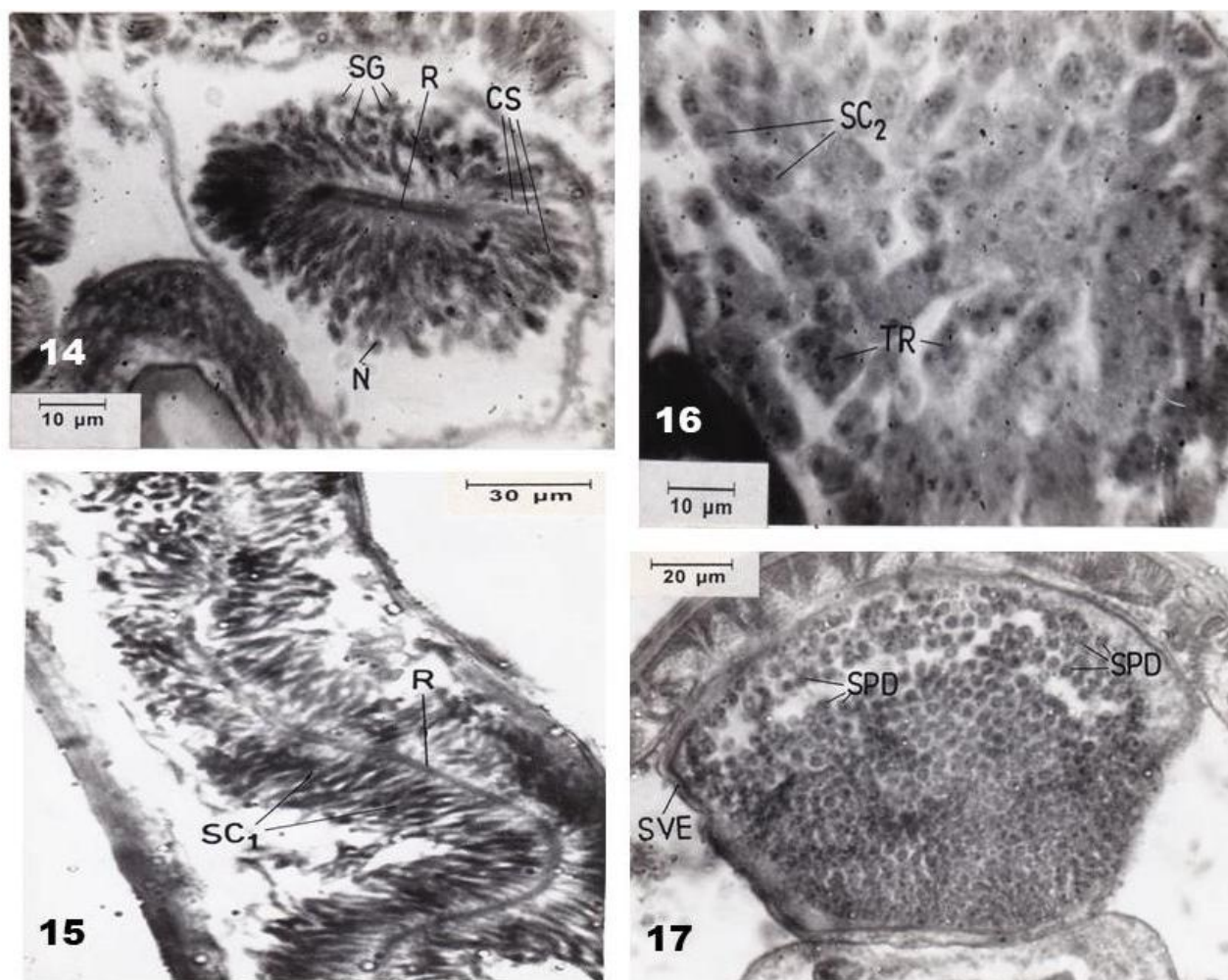


Fig.14: T. S of male showing germinal zone of testis. **Fig. 15:** L. S. through testis showing primary spermatocytes. **Fig.16:** T.S. of testis showing meiotic division in secondary spermatocytes. **Fig.17:** T.S. through the seminal vesicle showing spermatids. {*Haemonchus contortus*; Haematoxylin-Eosin staining}

(Abbreviations used in Figures: ASP: Ala of spicule; B: Bursa; BR: Bursal rays; CAL: Calamus; CC: Central core; CM: Cell membrane; CO: Corpus; CS: Cytoplasmic strands; CSC: Central soft core; CSP: Cuticularized wall of the spicule; DL: Dorsal lobe; DR: Dorsal ray; EDR: Externo dorsal ray; ELR: Externo lateral ray; EPI: Epithelium; GB: Gubernaculum; I: Intestine; LB: Lateral lobe; LU: Lumen; LVR: Latro ventral ray; MLR: Medio lateral ray; N: Nucleus; PSG: Proteinaceous secretory granule; PCG: Proteinaceous cytoplasmic granule; PLR: Posterolateral ray; R: Rachis; SG: Spermatogonium; SC1: primary spermatocyte; SC2: Secondary spermatocyte; SPD: Spermatid; SP1:First spicule; SP2:Second spicule; SPP:Spicular pouch; TE: Testicular epithelium; TLS:Tube like extensions; VVR: Vento ventral ray.

Lee (1965) described the presence of protein granules in the spermatozoa of several Ascarids in the form of the ascaridine and stated that these granules fused to form the central refringent body in spermatozoa which subsequently play an important role in the synthesis of RNA in male pronucleus. The presence of nucleoproteins in the refringent body of spermatozoa was also reported by Nath *et al* (1961).

According to Kankal (1989) the protein formed the main structural component in the testis of *Tanqua*

anomala. Protein was detected in the male genital epithelium and nuclei of spermatogonia and spermatids in *Oesophagostomum columbianum* (Johal, 1988). Mansir and Justine (1995) made the immunolocalization of tubulin around the nucleus and in the elongating part of the cytoplasm during the spermatid formation in *Heligmosomoides polygyrus*. The same authors in the years 1996 and 1999 detected the presence of actin and major sperm protein (MSP) in the spermatozoa of *Heligmosomoides polygyrus* and *Graphidium strigosum* respectively. Rudall (1955)

stated that the proteins similar to those present in the cuticle were also seen in the spicules of nematodes. Johal (1988) determined the proteinaceous nature of the spicular pouch and spicular sheath in *Oesophagostomum columbianum* and she also suggested that the spicular proteins appeared to be different from the outer cuticular proteins.

The presence of DNA in the spermatids of *Parascaris equorum* was detected by Nigon and Boret (1955) and they further reported the twenty time increase in DNA in the sperm pronucleus after fertilization. Wajihullah and Ansari (1981) described that the male reproductive system of *Diplotrinaena tricuspidis* gave only a slight response for RNA and DNA. Whereas, Johal (1988) reported the intense activity of both RNA as well as DNA in the developing spermatocytes.

The testicular epithelium and developing gametocytes of *Haemonchus contortus* contain a fair amount of glycogen. A rich quantity of carbohydrates and lipid alongwith a moderate quantity of protein is present in the testicular epithelium. The spermatozoa contain a substantial amount of glycogen, protein and lipids. The vas deferens contain structural proteins and protein positive secretory granules in the succeeding part. The specular pouch and bursal rays are highly lipoidal in nature and lipid alongwith scleroprotein constitutes the spicule and gubernaculum (Figs. 9-13) (Singh, 2015b).

SPERMATOGENESIS

Von Beneden (1883) was the pioneer worker who studied spermatogenesis in *Parascaris equarum* and described the meiotic division for the first time. Subsequently, a host of workers studied the process of spermatogenesis in various nematodes such as Taylor (1960) in *Litomosoides carinii* and *Dirofilaria immitis*, Nath *et al* (1961) in *Porrocaecum*, Jamuar (1966c) in *Nippostrongylus brasiliensis*, Foor (1970) in *Angiostrongylus cantonensis*, McLaren (1973b) in *Dipetolenema viteae*, Wright and Sommerville (1977 and 1985a) in *Nematospirioides dubius*, Ugwunna and Foor (1982) in *Ancylostoma caninum*. Adamson and Waerebeke (1985) in *Obainia petteri*, Waetebeke *et al.* (1990) in *Rhigonema madecassum*, Takahashi *et al.* (1994) in *Trichinella spiralis*, Cares and Baldwin (1994) in *Ekphymatodera thomasoni*, Johal (1995c) in *Oesophagostomum columbianum*, Mansir

and Justine (1995) in *Heligmosomoides polygyrus* and Mansir and Justine (1999) in *Graphidium strigosum*.

Rauther (1930), classified the testis into telogonic and hologonic types depending upon the location of the germinal area. Triantaphyllou and Hirschmann (1964) reported the commencement of spermatogenesis from the tip of the testis. The proliferating spermatogonia had large nuclei and indistinct walls. Martin and Lee (1980) reported the speratogonia of *Nematadoris battus* as hexagonal cells containing large nuclei, many small elongated mitochondria and a little endoplasmic substance. They further described the mature spermatocytes as large, spindle shaped cells membranous organelles lined with the electron dense fibrous substance in them. The spermatocytes at this stage were attached to the rachis by narrow cytoplasmic bridges. McLaren (1973) described that in *Dipetalonema viteae* too, the germ cells remained attached to the rachis until they had developed into secondary spermatocytes. He believed that the rachis was a continually elongating structure and seemed to play an important role in maintaining the synchronous maturation of the male gametes.

Wright and Sommerville (1985a and b) reported some transitional changes occurring in the spermatocytes prior to meiotic division in which the mitochondria and cup-shaped membranous organelles migrated to the periphery of the cells and the chromosomes came to lie free in the cytoplasm after the breakage of the nuclear envelope. Later, the second meiotic division resulted in the production of rounded spermatids. Favard (1961) in *Ascaris megalocephala*, Lee (1971) in *Heterakis gallinarum* and Beams and Sekhon (1972) in *Rhabditis pellio* reported a reduction in the cytoplasmic contents during this division.

The morphogenesis of the nucleus during the meiosis has drawn the attention of many workers. In ascarids, a non-membrane bound nucleus surrounded by an electron-dense layer and containing small spheres of varying density was reported by Favard (1961) and Clark *et al.* (1967). In filarial nematodes (Maeda, 1968 and McLaren, 1973), the chromosomes which appeared in the primary spermatocytes at the onset of meiosis remained as separate entities and got aggregated to reconstitute the nucleus in the last stages. In *Nippostrongylus brasiliensis* (Jamuar, 1966c), *Ancylostoma caninum* (Foor, 1970) and *Nematodirus battus* (Martin and Lee, 1980) though a typical

membrane bound nucleus was not reported in the spermatid, but the nuclear material did aggregate in a central fibrous mass which later condensed and got pushed out on one end of the cell to form a tail like portion. A comet like nuclear material was reported in *Aspiculuris tetraptera* and *Oesophagostomum columbianum* by Lee and Anya (1967) and Johal (1995) respectively.

In their intensive study on spermatozoa of Rhigonematid nematodes, Waerebeke *et al.* (1990) revealed that although the spermatozoa of all nematodes were aflagellate yet a considerable structural variation occurred from species to species. Interspecific variations were evident in size, shape and morphology of the main body of the spermatozoa, such as amoeboid (Chitwood, 1931 and Foor 1970), spheroid (Jamar, 1966), elongated (Martin and Lee, 1980 and Waerebeke *et al.*, 1990) and comet like (Lee and Anya, 1967 and Johal, 1995).

In *Haemonchus contortus*, spermatogenesis starts at the tip of germinal zone of monarchic and telogonic testis. All the four phases of spermatogenesis take place in the male genital tract. Numerous spermatogonia proliferated in the germinal zone of testis divide mitotically and arrange themselves around different cytoplasmic branches which aggregate to form a central nonnucleated cytoplasmic cord, the rachis. The spermatogonia increase in size and develop into primary spermatocytes. The rounded spermatids undergo cytoplasmic reduction before metamorphosing into spermatozoa (Figs. 14-17) (Singh and Johal, 1997).

Conflict of interest

The authors declare no competing interests.

Data Availability Statement: Not applicable.

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