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Development of Gonads in Plant and Soil Nematodes -A Review

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The article describes the comparatiye gonad development among different nematode groups. The monoprodelphic gonad of female develops from a single primordium which is oriented parallel to the longitudinal axis. The development starts with proliferation of somatic nuclei posteriad while the germinal nuclei remain at the anterior end of primordium. In the didelphic secernentea the gonad develops from a single primordium which may be longitudinally oriented in tylenchs or obliquely oriented in some rhabditids and diplogasterids. In didelphic Adenophorea the gonad develops either from a single longitudinally oriented primordium (e.g dorylaims) or two primordia oblique in position with each other (e.g. mononchs).

In Secernentean males the monorchic gonad develops as a result of anterior proliferation of somatic nuclei. The germinal nuclei thus remain at the posterior end. In diorchic condition which is exclusively found in Adenophorea the primordium elongates both in anterior and posterior direction to give rise to two opposed testes joined with a common vas deferens.

The ventral hypodermal chord nuclei play an important role in gonad development. In females they form a part of vagina while in males they form the supplements. The spicules develop from the dorso-lateral aggregates of cells known as spicular primordia.

Key Words: Gonad, Development, Nematodes, Primordium

Introduction

Study on the developmental biology of nematodes is important in understanding the sequences of development and also in determining of life span of economically important species to device appropriate control measures. Work on developmental biology was initiated as early as 1875 by Bütshli. Afterwards Boveri (1895) carried out extensive and highly significant work on nematode embryology and this was followed by other workers. Chitwood and Chitwood (1950) and de Coninck (1965) reviewed the early literature on reproductive biology. Till now, developmental biology of a number of species of soil-inhabiting nematodes including plant parasitic species has been studied. In the present article an attempt is made to compare patterns of gonad development in the different Orders of Secernentea and Adenophorea and to determine the inter-relationship between these diverse groups of nematodes.

Results

The comparative analysis of the data recorded revealed that the process of transformation of the first stage juvenile into the adult involves a sequence of post-embryonic cell lineages. Generally it was believed that the organs other than gonad show post-embryonic growth because of the cell enlargement and not by their proliferation. Recent findings (Nicholas 1984) have shown that during post-embryogenesis a few cells are added to the nervous system, musculature, hypodermal syncytium and intestine but growth in these organs occurs primarily due to cell enlargement. The gonads are formed as a result of rapid proliferation and multiplication of cells of the germinal primordium. The entire process is completed during a period of four moults and the reproductive system becomes functional only after the fourth moulting has been completed. The progenitor cells of the gonads are located in the germinal primordium. In the first stage juvenile, it consists of the primordial cells which give rise, to descendants responsible for gonad formation. The proliferation of primordial cells was considered to be restricted to the periods of moulting (Yuen 1965, Hirschmann & Triantaphyllou 1967), but in some nematodes the cells continue to divide throughout the post-embryological phase (Roman & Hirschmann 1967, Chin 1977). In tylenchs the primordium of the second stage juvenile is identical to that of the first stage because no division occurs in the primordial cells at the first moult (figure $1B_1$). The cephalobids viz. *Chiloplacus symmetricus* (Ahmad & Jairajpuri 1979) and *Acrobeles complexus* (Thomas 1965) also show unchanged primordium in the second stage but the division of the primordial cells starts right from the first moulting (figure $1B_2$) in *Teratorhabditis andrassyi* (Tahseen & Jairajpuri 1988). Similar observations were made on a didelphic rhabditid, *Caenorhabditis elegans* (Ehrenstein & Schierenberg 1980). The development follows two different lines after the second moulting depending on the sex of the developing juvenile. In this paper each one (i.e., female and male) has been dealt separately.

In the text the primordial structure is described in terms of nuclei because studies on gonad development were made on nematodes stained with nuclear dyes.

Female Gonad

The reproductive system of females can be categorised into monodelphic and didelphic types. The monodelphic gonad represents presence of one sexual branch while two sexual branches are present in didelphic type of gonad. The developmental patterns in females are different depending upon the type of the gonad.

Monodelphic gonad : The studies conducted so far on monodelphic species are mainly restricted to those with a mono-prodelphic gonad (anterior sexual branch). Important studies on monodelphic Tylenchida were made by Van Gundy (1958) on *Tylenchulus semipenetrans*, Hirschmann (1962) on *Ditylenchus triformis*, Anderson and Darling (1964) on *D. destructor* and Hechler and Taylor (1966) on *Seinura oxura, S. celeris, S. oliveirae* and *S. steineri*. Some other mono-prodelphic tylenchids include *Pratylenchus* sp. (Roman & Hirschmann 1969), *Criconema octangulare* (Knobloch 1978), *Aphlenchoides besseyi* (Gokte & Mathur 1989). Monodelphic cephalobid species that were studied include *Acrobeles complexus* and *Chiloplacus symmetricus* by Thomas (1965) and Ahmad and Jairajpuri (1979) respectively.

The basic pattern of development of mono-prodelphic gonad in species of various groups of nematodes is similar with only slight variations. The gonad develops from a single primordium located mid-ventrally and lying parallel to the longitudinal axis. The primordium generally contains a single germinal nucleus (that will give rise to the ovary) flanked by a somatic nucleus on each side (figure $1A_1$). However, in a rhabditid, *Teratorhabditis andrassyi*, Tahseen and Jairajpuri (1988) observed two germinal nuclei to be present instead of one (figure $1A_2$). During the second moulting development of female gonad progresses with the proliferation of posterior somatic nuclei while the germinal nuclei remain at the anterior end (figure $1C_1$, C_2). This stage marks the beginning of sex differentiation on the basis of primordial elongation (figure $1D_1$, D_2). The primordium elongates posteriorly and forms a narrow tubular somatic region (figure $1E_1$, E_2). The somatic nuclei differentiate into a cap nucleus present at the tip of ovary and epithelial

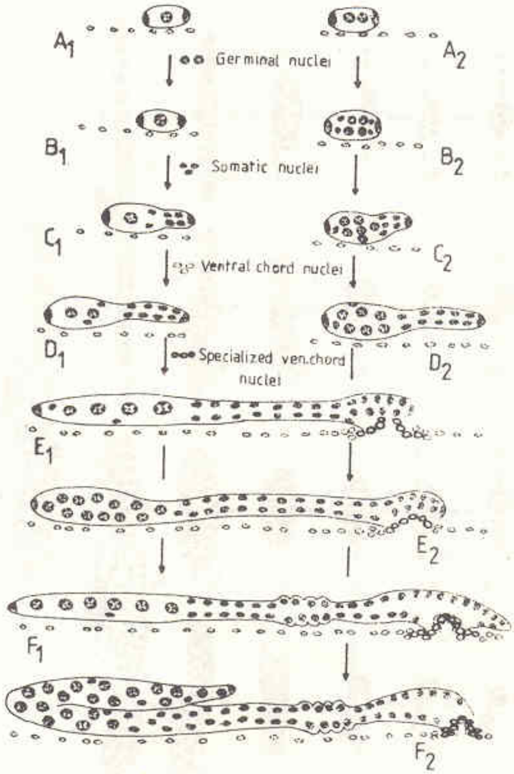

Figure 1 Development of monoprodelphic gonad **A_1 - F_1** monodelphic outstretched gonad; **A_2 - F_2** monodelphic reflexed gonad. **A,** First stage primordium; **B,** Third stage primordium; **D,** Third stage moulting primordium; **E,** Early fourth stage primordium; **F,** Late fourth stage primordium

nuclei which contribute to the formation of entire sexual branch except for the germinal cells. The somatic tube elongates posteriorly and with the advancement of development different parts of gonad such as oviduct, crustaformeria and uterus become differentiated. The vagina is formed by specialized nuclei which are modified ventral chord nuclei. In monoprodelphic species specialized ventral chord nuclei are located post-equatorially because of the posteriorly located vagina. The somatic tube joins the vagina, formed by the specialized ventral chord nuclei in the species without post-uterine extension (sac), e.g. in *T. andrassyi* (Tahseen & Jairajpuri 1988) but in species with post-uterine extension some somatic nuclei proliferate beyond the vaginal area and give rise to a sac as in *Seinura* spp. (Hechler & Taylor 1966) and *C. symmetricus* (Ahmad & Jairajpuri 1979). The germinal nuclei in the apical part of primordium also proliferate with few somatic nuclei in between which form the ovarian epithelium. The gonad is outstretched in tylenchs but may reflex in late fourth stage to form flexure(s) in rhabditid, cephalobid and diplogasterid nematodes belonging to class Secernentea. The flexure(s) develop(s) in the same way in Class Adenophorea also. The flexure contains germinal nuclei representing the ovary.

Didelphic gonad: The didelphic tylenchs in which the gonad development has been studied include *Radopholus similis* (Van Weerdt 1960) *Helicotylenchus vulgaris* (Yuen 1965), *Helicotylenchus dihystera* (Hirschman & Triantaphyllou 1967) *Rotylenchus robustus* (Rossner 1971), *Rotylenchulus reniformis* (Sivakumar & Seshadri 1971), *Rhizonema sequoiae* (Vera et al. 1984), and *Radopholus similis* (Rivas & Roman 1985). The gonad development in didelphic rhabditids, e.g., *Pelodera teres, Diploscapter coronata, Cylindrocorpus longistoma* and *Caenorhabditis elegans* were studied by Chuang (1962), Hechler (1968), Chin (1977) and Ehrenstein and Schierenberg (1980). Among adenophoreans the developmental studies carried out were mostly on mononchs, e.g., *Anatonchus amiciae* (Coomans & Lima 1965), *Miconchus studeri* (Khan & Coomans 1980) and *Parahadronchus shakili* (Ahmad & Jairajpuri 1982). The biology of *Aporcelaimellus* sp. and the female reproductive system in *Xiphidorus* spp. were further studied by Wood (1973) and Kruger and Heyns (1990) respectively. Shafqat et al. (1991) gave an account of the development of *Dorylaimus stagnalis.* Developmental sequences were also studied in the aerolaimid, *Plectus zelli* (Tahseen et al. 1992) and the enoplid, *Tobrilus paludicola* (Tahseen et al. 1992).

The didelphic gonad may develop from a primordium containing two germinal nuclei (figures $2A_1$, A_2, A_3) or from two primordia with one germinal nucleus each ($2A_4$). Generally in tylenchs two primordia have not been reported till date. In other secernenteans also the didelphic gonad is formed by a single primordium which may be oriented longitudinally or obliquely to the longitudinal axis. In adenophoreans the mononchs possess two primordia connected by a cellular strand, e.g. *A. amiciae* (Coomans & Lima 1965), *M. studeri* (Khan & Coomans 1980) and *P. shakili* (Ahmad & Jairajpuri 1982). The araeolaimid, *P. zelli* was also observed to possess paired primordia (Tahseen et al. 1992). Among others, *D. stagnalis* (Shafqat et al. 1991) and *T. paludicola* (Tahseen et al. 1992) possessed a single oval and broad primordium. The general primordium in tylenchs is more or less oval and parallel to the longitudinal axis (figures $2A_1$, B_1, C_1) while in the rhabditids, *D. coronata* (Hechler 1968) and *D. orientalis* (Tahseen et al. 1991) and the diplogasterid, *Mononchoides fortidens* (Tahseen et al. 1990) the primordium is spindle-shaped and placed obliquely to the longitudinal axis of body (figures $2A_2$, B_2, C_2).

The basic pattern of development in all didelphic species is similar with slight differences in the process of vagina formation. The proliferation of somatic nuclei results in an anterior and posterior elongation of primordium. In nematodes with paired primordia, the longitudinal and lateral growth results in formation of a single uniform structure (figure $2C_4$). The germinal nuclei occupy the two apical ends of the primordia while the somatic nuclei undergo proliferation and differentiation to form parts of genital tract such as oviduct, crustaformeria and the uteri. The number of somatic as well as germinal nuclei remains more or less the same in the two genital branches (figures $2E_1$, E_2, E_3, E_4). In tylenchs the

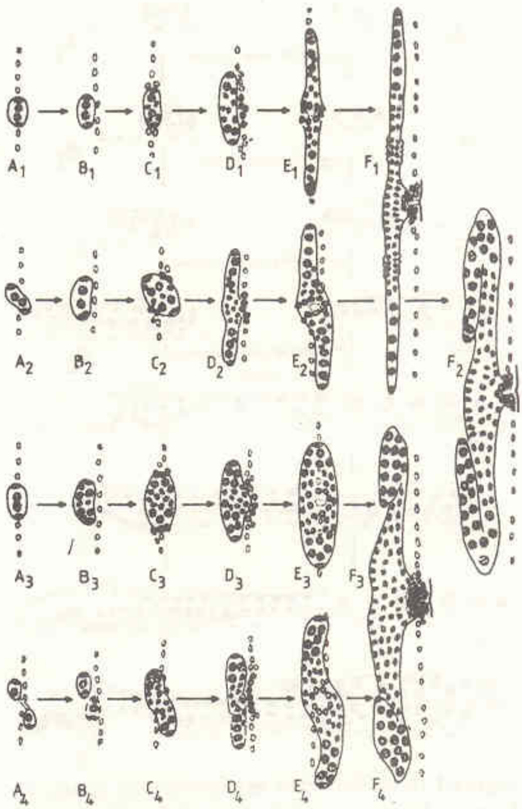

Figure 2 Development of didelphic gonad A_1 - F_1, didelphic outstretched gonad; A_2 - F_2, A_3 - F_3, A_4 - F_4, didelphic reflexed gonad. **A,** First stage primordium; **B,** Second stage primordium; **C,** Third stage primordium; **D,** Third stage moulting primordium; **E,** Early fourth stage primordium; **F,** Late fourth stage primordium

primordium shows a hollow invagination midventrally which is surrounded by specialized ventral chord nuclei to form vagina (figures $2E_1$, F_1). The vagina formation is sometimes initiated by a special nucleus called 'vaginal initial' or 'I' nucleus as in *H. dihystera* (Hirschmann & Triantaphyllou 1967) but this is not a common feature in all nematodes. An elongate nucleus has been observed in the vicinity of specialized ventral chord nuclei, in *M. fortidens* (Tahseen et al. 1990). In the adenophoreans with a single primordium, e.g., *D. stagnalis* (Shafqat et al. 1991) and *T. paludicola* (Tahseen et al. 1992) the vagina is formed by a mid-ventral conoid protrusion of the gonad as well as the specialized ventral chord nuclei (figures $2D_3$, F_3). Didelphic gonads may be outstretched as in tylenchs/with exception of some obese forms (figure $2F_1$) or reflexed as in rhabditids, diplogasterids (figure $2F_2$) and all adenophoreans (figure $2F_3$). The flexure of anterior part of primordium containing germinal nuclei develops in the latter groups in the late fourth stage (figures $2F_2$, F_3). In *Meloidogyne* spp. though the condition is didelphic-prodelphic but the primordium in the beginning is a butterfly-shaped structure. Later the two arms of primordium grow anteriorly instead of opposed direction.

Male Gonad

The males like females also possess two types of reproductive systems, the mononchic and the diorchic. The secernenteans are characterized by monorchic gonads while diorchic condition is restricted to the Class Adenophorea.

Monorchic gonad: The development starts from a single primordium (figure 3), either oriented parallel or obliquely (Tahseen et al. 1991) to the longitudinal axis. The pattern of development is by and large, similar in all secernenteans. The somatic nuclei divide and proliferate anteriorly producing a somewhat pear-shaped primordium in the second moult which marks the differentiated male primordium. The third stage male primordium has germinal nuclei placed posteriorly with somatic gonoduct anterior to them (figures $3C_1$, C_2). The somatic tube grows further anteriorly and reflexes over in third moulting stage in monorchic forms (figures $3D_1$, D_2) with an exception of *S. oliveirae* (Hechler & Taylor 1966). The reflexed part containing somatic nuclei elongates posteriorly up to the rectum and differentiates into the vas deferens, seminal vesicle, ejaculatory gland (in rhabditids) and the ejaculatory duct. The small germinal part elongates as a result of division of germinal nuclei and forms the testis (figure $3F_2$). In tylenchs the reflexed germinal part straightens and forms the outstretched testis at the anterior extremity of the gonad (figure $3F_1$). The ejaculatory duct joins the rectum to form a cloaca during the final moulting. The spicules and associated structures are formed by special cell aggregates, the spicular primordia on the dorso-lateral sides of rectum (figures $3F_1$, F_2). The cell aggregates become more compact in the fourth stage juvenile and later appear as refractory lines which become condensed to form the spicules in the adults.

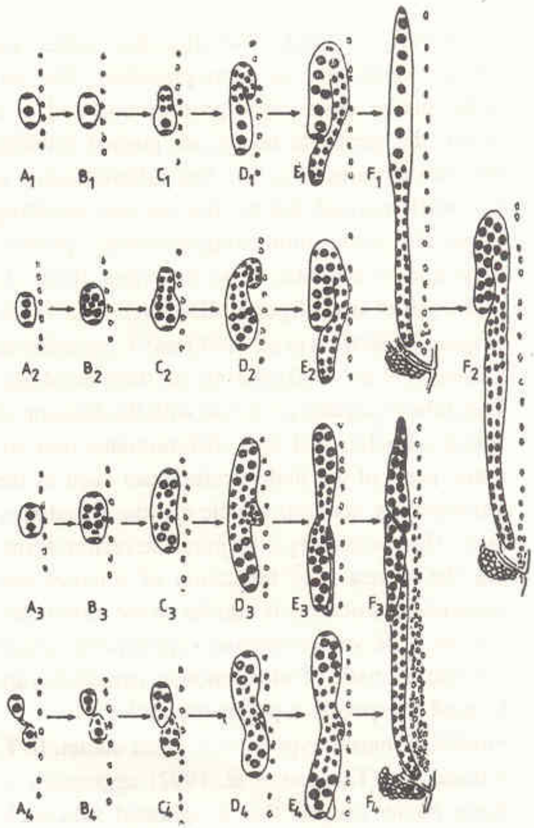

Figure 3 Development of male gonad **A_1 - F_1**, monorchic outstretched gonad; **A_2 - F_2**, monorchic reflexed gonad. **A_3 - F_3**,, **A_4 - F_4**, diorchic outstretched gonad; **A**, First stage primordium; **B**, Second stage primordium; **C**, Third stage primordium; **D**, Third stage moulting primordium; **E**, Early fourth stage primordium; **F**, Late fourth stage primordium

Diorchic gonad: The diorchic males are found exclusively in adenophoreans. The somatic nuclei show rapid proliferation and as a result, the germinal nuclei are pushed towards the ends (figures $3C_3$, C_4). Sex differentiation is not well marked during the second moulting stage. The primordium elongates anterio-posteriorly and a somatic tube emerges from its mid-ventral area (figures $2D_3$, D_4), e.g., in *D. stagnalis* (Shafqat et al. 1991) and *T. paludicola* (Tahseen et al. 1992) during the third moulting. This tube elongates posteriad with the division of somatic nuclei, and later differentiates into somatic parts of the male genital tract such as the vas deferens, seminal vesicle and the ejaculatory duct. The ejaculatory duct joins the rectum forming the cloaca. The formation of spicules and associated structures is similar to the monorchic species. The ventro-median supplements which are characteristic of adenophorean nematodes are formed by special supplement nuclei which are modified ventral hypodermal chord nuclei. In *T. paludicola* (Tahseen et al. 1992) aggregates of these nuclei around the invaginated subcuticle give rise to supplements. Shafqat et al. (1991) also reported multiplications of ventral chord nuclei to form the contiguous supplements in *D. stagnalis*.

Conclusion

Study of the developmental sequences in different groups of nematodes revealed that the general pattern of gonad development is determined mainly by the structure of primordium and the germinal nuclei contained in it. The basic developmental patterns of monodelphic and didelphic gonad(s) are same in all secernenteans. However, slight variations occur in the mode of development in some didelphic forms with reflexed gonad where the development starts with obliquely oriented primordium. For monorchic males the developmental sequences are similar in the entire Class Secernentea. In Adenophorea, the didelphic mononchs with paired primordia show a similar development as in the araeolaimids which also have similar primordial design. However, other didelphic species with single longitudinally oriented primordium show similarity with each other in their developmental patterns. The diorchic males show more or less similar development sequences throughout the class Adenophorea. Any specific phylogenetic relationship among different groups could not be derived, primarily due to the fact that till date only a few species have been studied in detail. Further, our knowledge of the gonad development in adenophorean nematodes is rather fragmentary.

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