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THE FEMALE REPRODUCTIVE SYSTEM IN NEMATODE SYSTEMATICS

by

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ABSTRACT

Additional information is given on the female genital system in some Tylenchida and Araeolaimida. A comparison between these results and results formerly published on the orders Rhabditida, Dorylaimida and Enoplida revealed the difficulty of homologizing the several gonoduct parts found in these groups. The most important systematic character seems to be the number of cell rows in the oviduct : the orders Dorylaimida and Enoplida have one row, the orders of the Secernentea (Rhabditida, Tylenchida, ...) two rows and at least some Araeolaimida and Chromadorida three rows. The ovarian cap cell has only been found in the Secernentea, not in the Dorylaimida and Enoplida. Information is given on the subdivisions of the ovary, the function of the sphincters, the presence of a spermatheca and other uterus differentiations. Cell-constancy is stressed and the usefulness of the female reproductive system for the systematics and for the evolution is discussed.

INTRODUCTION

The cellular morphology of the female reproductive system in nematodes has already been studied in the Tylenchida (Geraert, 1973, 1974 and 1976), the Dorylaimida and Enoplida (Geraert, Grootaert & Decraemer, 1980) and the Rhabditida (Geraert, Sudhaus & Grootaert, 1980). This article compares the foregoing results and presents some general conclusions; it starts, however, with additional information on the order Tylenchida and with the examination of a representative of the order Araeolaimida.

The methods used, have been described in the articles mentioned above.

OBSERVATIONS

1. *Seinura tenuicaudata* (de Man, 1895) (Figs. 1 B-C)

Tylenchida : Aphelenchina : Aphelenchoididae

The uterus is built up by elongated cells : at the junction with the spermatheca I found about eight cells the nuclei of which lie close to this junction. The spermatheca too consists of elongated cells (six to eight) with their nuclei close to the uterus side; these nuclei were difficult to stain and not more than four were seen in one animal. Internally, the junction carries six sphincter cells. At the other end of the spermatheca four polyhedral cells are found, followed by two oviduct cells.

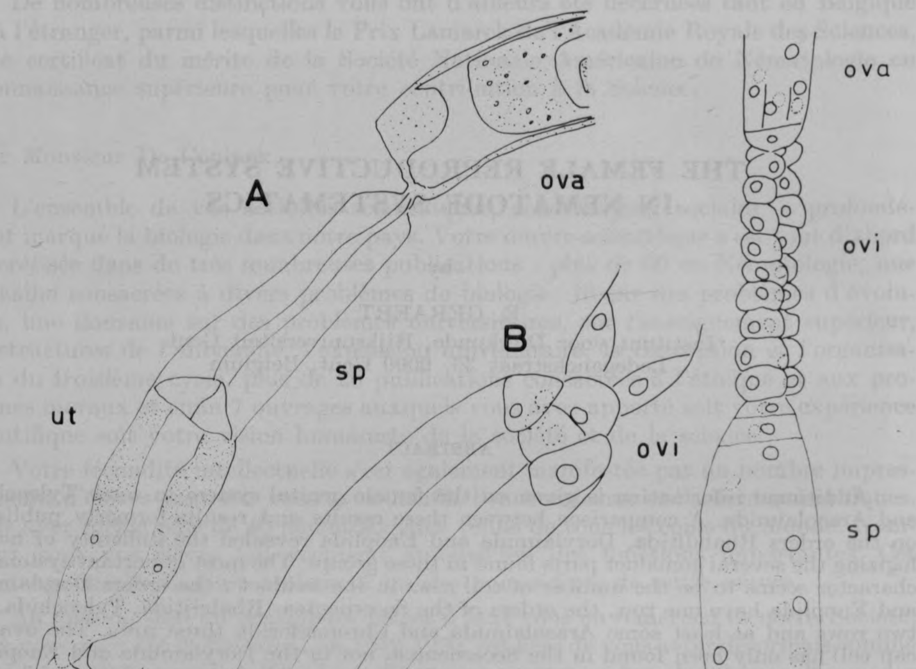

Fig. 1. — The female genital apparatus in Aphelenchina : A : *Laimaphelenchus deconincki* (glycerin preserved animal) ; B, C : *Seinura tenuicaudata*, schematical, B : surface view, C : internal ; D : *Paraphelenchus* sp., schematical.

2. Aphelenchoididae (Fig. 1 A)

Tylenchida : Aphelenchina

Several Aphelenchoididae, studied in glycerin, showed an elongated spermatheca clearly separated from the ovary by a constriction; between the sac-like uterus and the spermatheca an internal mass was visible; *Laimaphelenchus deconincki* El Miligy & Geraert, 1972 is shown as an example (Fig. 1 A).

3. *Paraphelenchus* sp. (Fig. 1 D)

Tylenchida : Aphelenchina : Aphelenchidae

In the uterine sac a large valve protrudes from the uterus; it consists of a left and a right half. Between the cylindrical uterus and the cylindrical spermatheca a constriction is present; at this constriction no special valve was visible. The uterus consists of at least nine cells; the spermatheca cells are arranged as follows : two to four cells at the uterus constriction (these cells are sometimes quite small), then two to three times four cells surrounding the spermatheca lumen, a lumen, that is anteriorly closed by two rows of three cells. The oviduct is formed by a double, slightly spirally coiled row of globose cells; usually nineteen cells were counted but also the smaller number of twelve was found. The ovary cells were visible in only one specimen where six cells formed the transition to the oviduct.

4. *Rotylenchus robustus* (de Man, 1876) Filipjev, 1936 (Fig. 2 A, B)
Merlinius camelliae Kheiri, 1972 (Fig. 2 C)

Tylenchida : Tylenchina : Hoplolaimidae, Dolichodoridae

Because of the similar structure of the female genital tract both species are dealt with together. The uterine sac is formed by a few, flattened cells; at the transition to the uterus some larger cells (not more than four) are found. The uterus consists of no more than twelve cells arranged in three rows when the genital tract is in the body; in extruded genitalia this arrangement is not so clear. When an oocyte is ripening in the ovary the uterus cells become globular; in the centre no lumen is found except, sometimes, with the cells lying towards the vulva.

The spermatheca is formed by twelve cells the spatial arrangement of which is apparently not fixed; the most usual configuration is : two cells at the uterus side, twice four cells making the greater part of the spermathecal wall and two cells at the oviduct side. When the spermatheca is offset as in *M. camelliae* (Fig. 2 C) eight to ten nuclei are found in the offset part. In between uterus and spermatheca two cells of a different nature can be present; their nuclei are not or only slightly visible with the staining technique I used.

The oviduct consists of two rows of four small, flattened cells forming a constriction between spermatheca and ovary; the two cells at the spermatheca side are usually slightly larger with a slightly larger nucleus compared to the remaining three pairs.

At the transition to the oviduct the ovary sometimes contains eight nuclei lying at about the same level; sometimes a slight overlapping of the oviduct by the ovary is found (fig. 2 A). As the ovary cells are usually found in fours (fig. 2 B), I interpret the foregoing results as an overlapping of the first four ovary cells by the second four ovary cells. The total number of nuclei did not exceed sixteen.

5. *Psilenchus hilarulus* de Man, 1921 (Fig. 2 D)

Tylenchida : Tylenchina : Tylenchidae

Uterus consists of about 20 to 30 cells, more or less arranged per 4 except for the transition zones to the uterine sac and the spermatheca where the cells usually lie per 2; these transition zones probably act as valves.

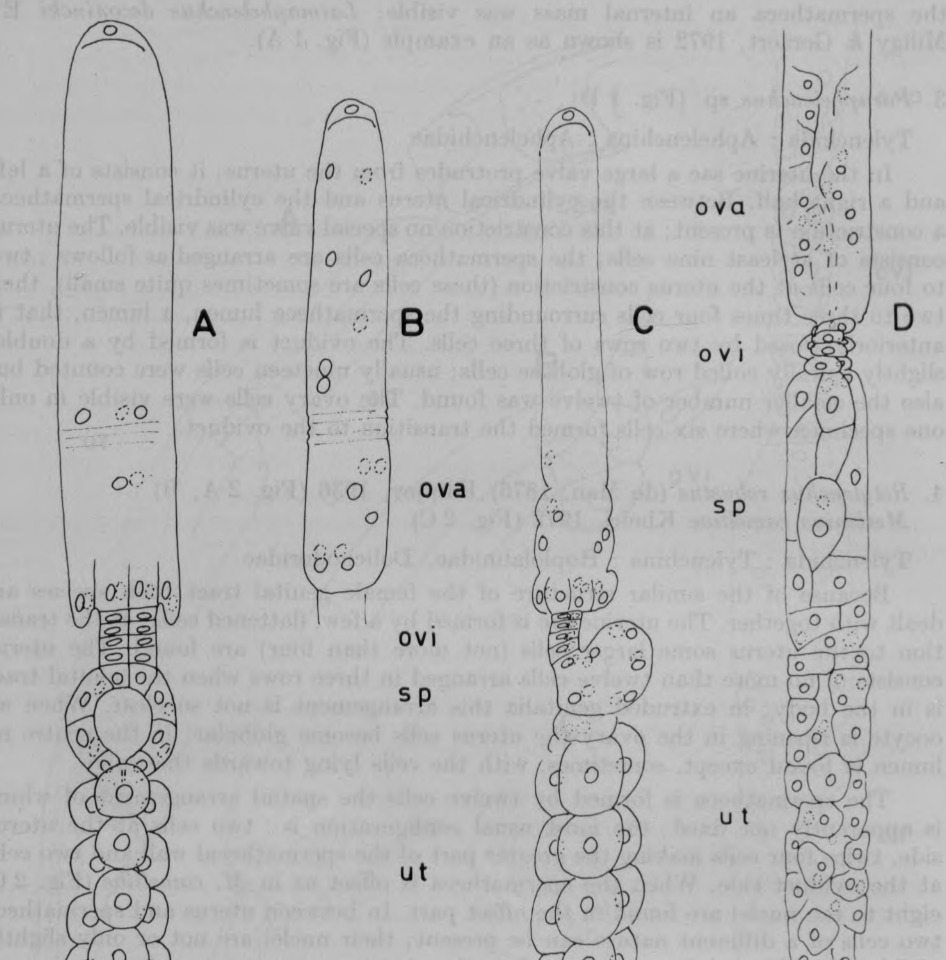

Fig. 2. — The female genital apparatus in Tylenchina, schematical : A, B : *Rotylenchus robustus*, in B only the ovary ; C : *Merlinius camelliae* ; D : *Psilenchus hilarulus*.

The spermatheca is an elongated, not-offset sac of about sixteen cells, more or less arranged per four. The oviduct consists of two rows of four cells. In the ripening zone of the ovary about sixteen nuclei can be counted.

6. *Anaplectus granulosus* (Bastian, 1865) (Fig. 3)

This representative of the order Araeolaimida has been found in soil samples from Belgium and Turkey.

In a few, glycerine preserved specimens it was observed that the uterine sac consists of a limited number of rather large cells. The uterus cells have a finely granulated cytoplasma; their total number is unknown but in a few extruded genital systems I repeatedly found a combination of five to eight cells (Fig. 3 A gives one of the possibilities). The spermatheca consists of two times three cells with large nuclei (only once one set of three large cells was found).

Within the animal the oviduct has the shape of a thin, hyalin tube well separated from the spermatheca; when the genital system is extruded the oviduct is more or less surrounded by the spermatheca cells; in the oviduct two groups of three small nuclei are present but cell walls have not been observed. The oviduct reaches the reversed ovary near the top of the ripening zone.

The ovary is, for half to three quarters of its volume, filled by one ripening oocyte; the rest of the ovary contains about five disc-shaped oocytes and several small oogonia. The wall cells of the ovary are scarcely visible except for two specimens from a Turkish sample where numerous cells with three different nuclei have been observed (after staining I noticed large white, large red and small red nuclei).

DISCUSSION OF THE ORDER TYLENCHIDA

The female reproductive system of *Seinura* can easily be compared to that of *Aphelenchoides* (Geraert, 1973); in *Seinura* fewer cells are found in the spermatheca (four cells at the transition to the oviduct instead of six) and also in the internal uterus-spermatheca valve (six cells instead of eight).

A comparable situation is found for *Paraphelenchus* and *Aphelenchus* (Geraert, 1973); in *Paraphelenchus* I have not found the external uterus-spermatheca valve, typical for *Aphelenchus*; on the other hand the numerous globular cells cannot be differentiated into oviduct cells and fertilization chamber cells as in *Aphelenchus* (Triantaphyllou & Fisher, 1976), although the length of this cell row makes a functional differentiation possible.

The structure of the female genital system described for *Rotylenchus* and *Merlinius* is, with only slight modifications, found in the majority of the Tylenchina (Geraert, 1973); it seems that for these animals the uterus cells are quite constant in number and arrangement (the so-called tricolumella of Hirschmann & Triantaphyllou, 1968); however, sometimes more than twelve cells can be found in this region; the cells of the uterine sac lying at the uterus side can resemble a uterus cell but most probably they act not as uterus cells but as valve cells as De Grisse & Roose (1975) pointed out; neither in glycerine preserved material nor in extruded genitalia can this region be adequately studied. At the transition uterus-spermatheca two cells are often found; I am not sure whether these cells are always present or not, as nuclei have either not or only faintly been stained in this region; when the two nuclei were stained they did not have the nucleolus typical for uterus and spermatheca nuclei; with the electron microscope these cells become easily visible; apart from their valve function a sperm-feeding function can also be presumed (De Grisse & Roose, 1975). The two cells that in *Filenchus* form the empty chamber between oviduct and uterus and in which the spermatheca opens, are possibly of the same nature, although this chamber probably acts as a fertilization chamber.

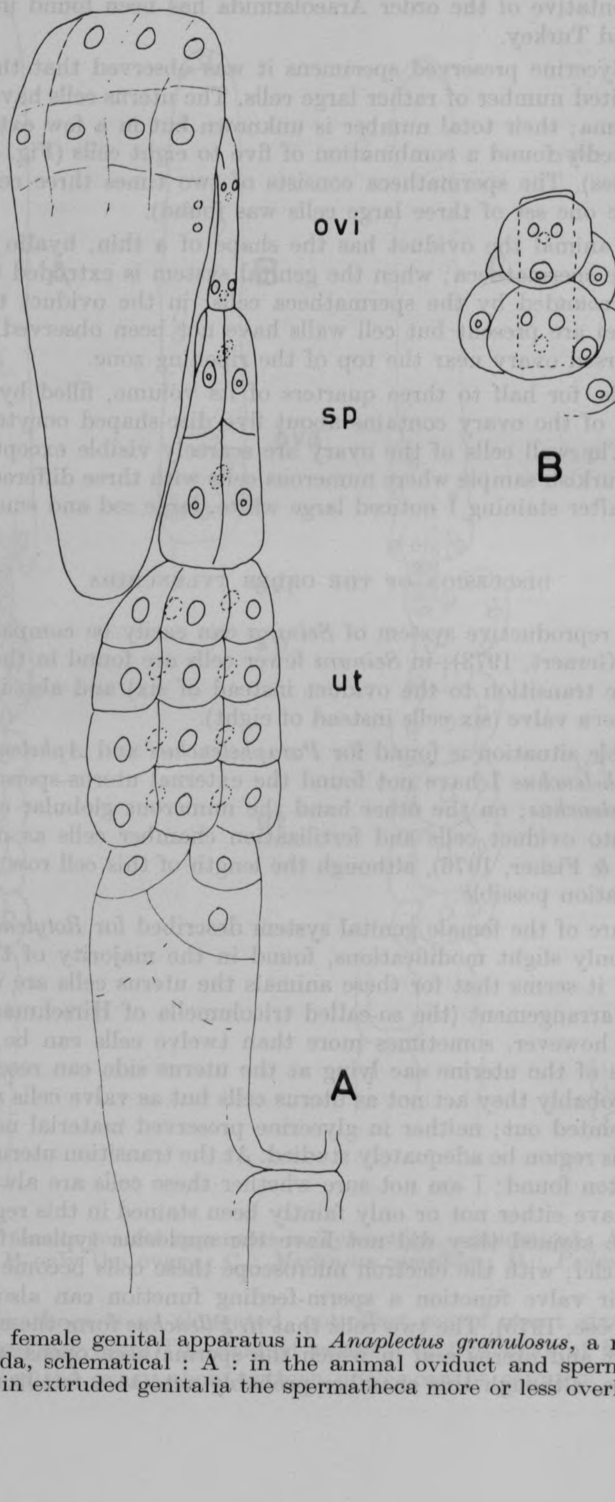

Fig. 3. — The female genital apparatus in *Anaplectus granulosus*, a representative of the Araeolaimida, schematical : A : in the animal oviduct and spermatheca are well separated ; B : in extruded genitalia the spermatheca more or less overlaps the oviduct.

As pointed out earlier (Geraert, 1974), some long-tailed tylenchs (*Thada*, *Cephalenchus*, *Eutylenchus* and *Atylenchus*) show a genital system similar to that of *Ditylenchus*, although on the whole they are probably not that much related to this genus; they have not been included in the table as I am not sure about the numerical data of spermatheca and oviduct.

Tylenchus davainei Bastian, 1865 also has the uterus cells in four rows (quadricolumella of Wu, 1958), on the other hand representatives of *Filenchus* (a.o. *F. thornei* (Andrassy, 1954)) have a tricolumella (Table I).

GENERAL MORPHOLOGY OF THE FEMALE GENITAL SYSTEM

A comparison between the several orders is hampered by the difficulty to homologize the several parts of the female genital system. We can always differentiate an ovary from a gonoduct (ending in a vagina and vulva); between ovary and gonoduct there is a constriction, called oviduct, and on the gonoduct one or more constrictions are present, separating e.g. spermatheca from uterus.

The ovary

In the nematodes studied, the ovary is a hollow, elongated tube one end of which functions as a germinal zone (with formation of oocytes, although in some cases all oocytes were formed during the last ecdysis) and the other end as a ripening zone (the oocytes reach their final size and accumulate yolk). Between both the growth zone is found. In text books however, instead of three zones only germinal and growth zone are mentioned (Chitwood & Chitwood, 1974; De Coninck, 1965; Hirschmann, 1970; Bird, 1971). The subdivision of the former growth zone into a (restricted) growth zone and a ripening zone is not carried out on morphological grounds (although the wall cells can differ) but is based on functional differences. Part of the ovary is not used for storage of the growing oocytes but remains empty until the necessary conditions are fulfilled (temperature, food supply, ...) allowing egg ripening; the frequently found empty ripening zone in Tylenchida was considered by several authors as the oviduct (review in Geraert, 1976).

The rachis, present in some nematodes, unites the oocytes; according to Abi-Rached & Brun (1975) it regulates the differentiation of oocytes. In nematodes without a rachis, this important function is probably taken over by cytoplasmic bridges between the oocytes. Zamboni & Gondosa (1968) showed the presence of these bridges in vertebrates and suggested such a regulatory function. The presence of such cytoplasmic bridges is probably the reason why Hope (1974) did not succeed in separating the oocytes in a freeze-dried ovary of *Deontostoma* (a marine Nematode); on the contrary, the oocytes were broken; Hope's explanation for this attachment was « ... preventing the immature oocytes from slipping out of line and prematurely entering the oviduct ».

The oviduct

On leaving the ovary, a ripe oocyte is squeezed through a tiny canal formed by the oviduct cells. For this reason pression has to be exerted on the egg in the ovary; but in most freeliving nematodes the ripening zone of the ovary has no muscular sheath. Doncaster & Seymour (1977) showed that in a tylench the oocyte is pushed by means of the contraction of the body musculature. The body musculature which consists only of longitudinal muscles gives by the contractions the

TABLE I

Survey of the numerical data in the structure of the female reproductive system in the Tylenchida (r = number of rows ; c = number of cells in a row)

	uterine sac	valve	uterus	valve	spermatheca	fertilization chamber	oviduct	ovary
	r × c	r × c	r × c	r × c	r × c	r × c	r × c	r × c
Aphelenchoides			? + 8 × 1	2 × 4	2 × 8 + 6		2	per 4
Seinura			? + 8 × 1	2 × 3	1 × 8 + 4		2	?
Aphelenchus		2 × 6 — 8	± 18	2 × 5 — 6	19 — 23	2 × 5 — 7	2 × 5 — 9	per 4 ?
Paraphelenchus		same ?	same ?		12 — 22	?	2 × 6 — 10	per 6 ?
Macroposthonia	10	?	16		12	?	2 × 4	per 4 ? max. 21-38
Pratylenchus, *Rotylenchus*, *Helicotylenchus*, *Tylenchorhynchus*, *Merlinius*	min. 8	4 ?	3 × 4	2 ? (always ?)	12		2 × 4	per 4 (min. 16)
Filenchus			3 × 4		12	2 ?	2 × 4	per 4 (min. 16)
Psilenchus			20 — 30 (per 4)	2 × 2	± 16 (per 4)		2 × 4	min. 16
Ditylenchus		2 × 3	4 × 4		4 × 4		2 × 4 — 5	per 6 ? per 8 ?
Anguina millefolii	elongated	2 × 3	4 × 4		4 × 4		2 × 4	
A. moxae	17 — 24	2 × 3	4 × 4		4 × 4		2 × 4	
Deladenus								
mycetophagous	a few large cells		70 (per 4)		25 — 40 (per 6)		2 × 7	per 6 ?
infective			30 — 50 (per 4)		12 (per 4)		2 × 7 — 9	50 — 93
Hexatylus			28 — 32 (per 4)				4 × 2	6 + 39
Meloidogyne			per 3		12 — 16		2 × 3 — 5	per 6, then per 2

typical nematode bendings (Calcoen & Roggen, 1974); these bendings result in body progression (Wallace, 1968); these bendings also assist in egg-transport, egg-laying and transport of gut contents (Seymour & Doncaster, 1973).

Although the evidence that the same muscles serve several purposes is only given for one nematode, we may assume that the explanation holds good for many free-living nematodes.

Constrictions and contractions

All the gonoducts investigated, show, apart from the oviduct, at least one but sometimes two or more sphincters; the gonoduct part at the ovarial side of the sphincter frequently lacks a muscular sheath. As nematodes always move (i.e. show contractions of the somatic muscles), we can assume that pression is continuously exerted on the oocyte; from this we can conclude that sphincters are necessary to prevent a premature advance of the oocyte into the gonoduct.

Complexity of the gonoduct

In the gonoduct fertilization occurs (not in parthenogenetic females) and the egg shell is formed. When the spermatozoids need feeding and/or attachment, one region of the gonoduct is differentiated into a spermatheca. In a few species a region between oviduct and spermatheca is differentiated into a fertilization chamber (Triantaphyllou & Fisher, 1976); at the other side of the spermatheca, some cells could play a role in clearing the region from superfluous sperm and oocyte material (De Grisse & Roose, 1975). The egg-shell is secreted by the egg itself, but in some species the uterus forms an additional uterine layer of varying thickness (Bird, 1971).

As the function(s) of the gonoduct seem(s) rather limited a very simple structure seems logical; the many differentiations found e.g. in some dorylaimids (Coomans, 1965) are rather puzzling.

COMPARATIVE MORPHOLOGY

Ovary

The number of ovaries and their position in relation to the intestine was extensively studied in free-living nematodes by Lorenzen (1978).

The character straight-or-reflexed-genital-system is used to differentiate between ordines except for the ordines belonging to the infraclassis Chromadoria where this feature characterizes the subfamilies (Lorenzen, 1978). In the Chromadoridae the ovary reflexion is said only to occur when in the full grown females the first egg-cell ripens (Lippens, 1976). In the other groups the way in which the reflexion occurs is of taxonomic importance (Fig. 3) : in the order Rhabditida all Rhabditidae and some Panagrolaimidae have the flexion in the ovary (cf. Lorenzen, 1978); in the remaining groups the ovary is straight but reversed (except in the Tylenchida).

In the infra-classis Enoplia the oviduct can be found at the transition germinal zone/growth zone (Enoplida) or in the growth zone (Mononchina) or in the ripening zone of the ovary (Dorylaimina); the available observations suggest that these positions have taxonomic importance (cf. Geraert, Grootaert & Decraemer, 1980).

In the Secernentea the blind end of the ovary (= germinal tip) is formed by a single, hollowed cell the nucleus of which lies at the very tip of the ovary : this cell is usually called the cap cell. In the Enoplia the germinal tip of the ovary is

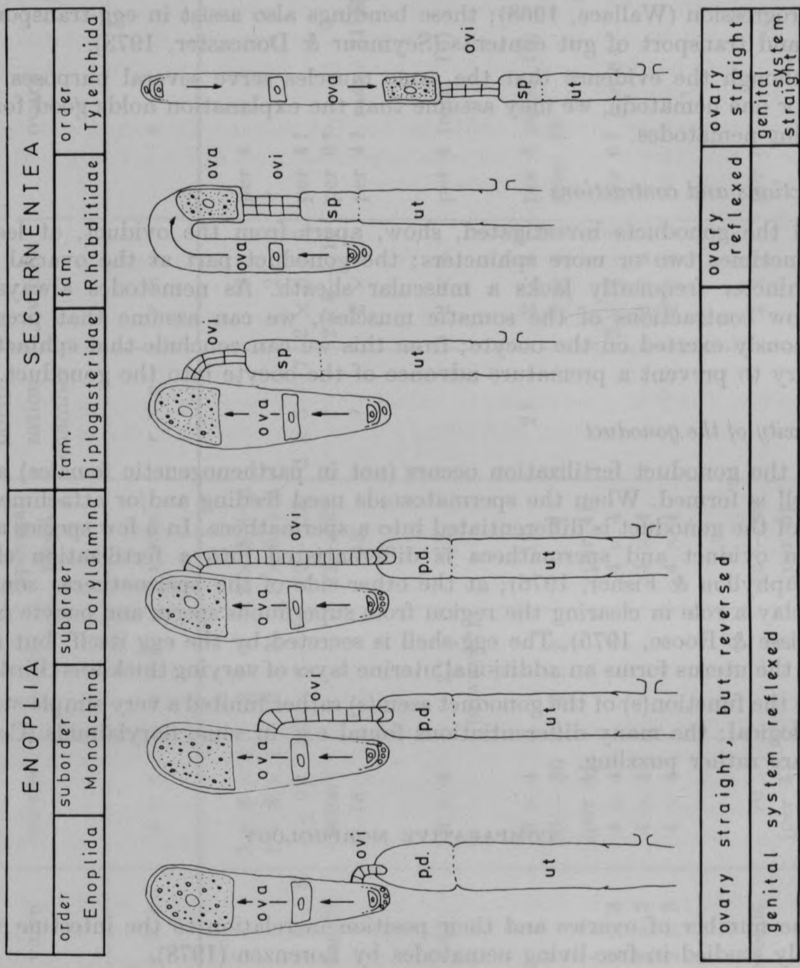

Fig. 4. — Schematical representation of the female reproductive system in Enoplida, Dorylaimida, Rhabditida and Tylenchida. In the ovary (ova) three oocytes are drawn indicating the germinal region, the growth region and the ripening region ; ovi = oviduct; p.d. = pars dilatata ; ut = uterus ; sp = spermatheca.

characterized by numerous nuclei (cells? syncytium?). In the text-books cited above, only the single cap cell is mentioned for the nematodes, indicating that the Secernentea (containing most animal and plant parasites) have attracted more interest than the remaining groups.

Oviduct

It has never been difficult to point out where the ovary ends and the oviduct starts but it has sometimes been impossible to indicate where the oviduct ends (some *Rhabditis* species with a poorly differentiated spermatheca : Geraert, Südhaus & Grootaert, 1980).

The oviduct structure can be reduced to a limited number of systems :

1. the single cell row, characterized by flat, disc-shaped cells, minimum two to three (*Mononchus aquaticus*), maximum 36 (*Mesodorylaimus* sp.). This cell row is remarkable because a lumen is never visible although oocytes quickly pass through it. The single cell row is found in the orders Dorylaimida and Enoplida, constituting the infra-classis Enoplia.

2. the double cell row characterized by the arrangement of the cells in pairs. The minimum number of cells is two (*Demaniella*, *Butlerius*, *Aphelenchoides*?), the maximum 50 (*Rhabditis insectivora*). Usually the cells are found in longitudinal rows slightly spirally twisted around each other. In a few species the paired cells lie not in longitudinal rows : *Hexatylus* (cf. Geraert, 1976), *Rhabditis oxycerca* (Geraert *et al.*, 1980). The double cell row characterizes the species of the orders Rhabditida and Tylenchida, both belonging to the Secernentea.

3. cells per three : this arrangement is found in *Anaplectus*, the only investigated representative of the order Araeolaimida. Lippens (1976) in his study of the genital system of the order Chromadorida (belonging to the same infra-classis Chromadoria) did not find nuclei (nor lumen) in the oviduct but an oviduct gland with three or six nuclei.

From this survey the importance of the oviduct structure for the characterization of the larger groups becomes apparent.

CONCLUSIONS

1. *Cell constancy*

Each nematode species has a typical structure of the female genital apparatus; when there is only a low number of cells (a female genital branch made up by 30 to 100 cells) this number and the spatial arrangement of the cells are rather constant, so that it is clear that cell constancy (= eutely) is also present in the female genital system.

2. *Subdivisions of the ovary*

In the ovary three regions can be indicated : a germinal zone where the oocytes are formed, a growth zone where the oocytes become larger and a ripening zone where (when circumstances permit) the oocytes stack yolk and attain their full grown size.

3. *Differentiations in the gonoduct*

The differentiations in the gonoduct are difficult to homologize among the several nematode orders :

— The cells forming the constriction between the ovary and the rest of the gonoduct are considered to be the oviduct. The oviduct cells are usually neatly differentiated from the cells following them but in some Rhabditidae there is a gradual transition whereas in most Dorylaimida and Enoplida the last oviduct cells are surrounded by other gonoduct cells.

— A spermatheca is a differentiation in the gonoduct that serves only and exclusively for the keeping of the spermatozoa; in groups without such a differentiation, sperm is found throughout the genital tract; in groups with a spermatheca, this differentiation is also developed in parthenogenetic females.

— A fertilization chamber has been shown in a few species but is probably more widespread.

— The uterus is a general term that can be used for the greatest part of the gonoduct; although it only serves for fertilization (if necessary) and eggshell formation, several species show a complex uterus structure.

4. *Sphincters and egg-transport*

Egg-transport has been shown to take place by the kneading action of body-wall muscles. This explains the absence of a muscular sheath around the genital tract in most free-living nematodes. On the other hand the contractions of the somatic musculature, in the first place needed for locomotion are more or less continuous; the several sphincters present in the gonoduct (the oviduct being one of them) are probably needed to prevent premature progress of oocyte or egg in the gonoduct.

5. *Systematical use of the ovary*

In the Secernentea the ovary tip is formed by one cap cell but in the Dorylaimida and Enoplida numerous small nuclei are found. The flexions in the genital system have a well-known systematical importance. Also important is the level of the transition between ovary and oviduct : by this character the Diplogasteroidea can be differentiated from the other Rhabditida, the Dorylaimida from the Enoplida and within the Dorylaimida, the Dorylaimina from the Mononchina.

6. *Systematical use of the oviduct*

The oviduct structure seems to be of fundamental importance; at least three types can be recognized :

— oviduct cells in one row : Dorylaimida, Enoplida

— oviduct cells in two rows : Tylenchida, Rhabditida

— oviduct cells in three rows : Araeolaimida, Chromadorida.

Although a few observations indicate a more complex situation (e.g. Trichodoridae) it is interesting that this division into three groups corresponds with Andrassy's (1976) three subclasses.

At lower systematical levels the oviduct structure can be used to some extent to characterize families, genera and species.

7. *Systematical use of the remaining gonoduct parts*

A spermatheca occurs in the Tylenchida and in most Rhabditida but not in Dorylaimida and Enoplida; in the Chromadorida its presence or absence is a characteristic at family or at subfamily level.

The structure of the spermatheca, of the uterus parts and of the sphincters can to some extent be used; their usefulness depends however on the ordo : in Tylenchida the uterus is characteristic for the family and in Dorylaimida only for the species. A sphincter has a similar structure in related species and can be used to characterize a genus or even a family.

8. *Evolutionary trends*

During evolution a remarkable difference appeared in the way the genital system took part in the differentiation and speciation : in hundreds of species of the order Tylenchida and also of the order Dorylaimida an almost identical reproductive system is found while in the order Rhabditida each species of the families Rhabditidae and Diplogasteridae has a particular system (in the family Cephalobidae belonging to the same order a more uniform system is found).

In Tylenchida and Dorylaimida the structure of the female genital system can be used to elucidate the systematic position of some genera or families; in the families Rhabditidae and Diplogasteridae (order Rhabditida) the structure of the reproductive system can help to gain a better insight into species and genera.

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