STRUCTURAL CHARACTERISTICS OF THE FEMALE REPRODUCTIVE SYSTEM IN SOME SEDENTARY NEMATODE SPECIES OF THE ORDER TYLENCHIDA

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Zoologicheskii Zhurnal, 1986, 65(12): 1788-1798

The cellular structure of the female genital system has been studied in the following representatives of the tylenchids: Tylenchulus semipenetrans, Sphaeronema alni, Meloidoderita kirjanovae, Rotylenchulus reniformis, Meloidodera alni, two species of the genus Meloidogyne and four species of the subfamily Heteroderinae. It is demonstrated, that during increasing of specialization level the genital system of female has been undergone some natural changes leading to increasing the egg productivity. These changes are expressed in an increase of general size of the gonad and its sections, in a clearer morphological differentiation of some parts of the oviduct and in activization of their functions (or in changes of a function), as well as in development of original adaptations increasing the gonad productivity.

The study of the characteristics of the cellular structure of the genital system of parasitic nematodes of the order Tylenchida has not only important taxonomic significance, but it is necessary for understanding the phylogenetic relations between different groups of plant parasitic nematodes. The comparison of the data in the morphology of genital system and the functional characteristics of some parts of the gonads can give important information for understanding some possible ways of evolution of parasitic nematodes. The female sexual tube of tylenchids are easier to study and most various in structure. In 1962, A.A. Paramonov pointed out, that "the organization of the female gonads correlates evidently with ecological (trophic) and taxonomic characteristics of corresponding groups of nematodes."

A number of articles devoted exclusively to the structure of female sexual tube of free-living and plant-parasitic nematodes have been published in the last two decades in foreign and home literature (Yuen, 1965; Coomans, 1965; Geraert, 1973; Hirschmann, Triantaphyllou, 1967, Geraert et al. 1980; Geraert, 1981; Chizhov, 1981, 1984, and others). At present, the structure of female gonads of some dozen species of parasitic nematodes from different taxonomic groups has been studied more or less in detail.

As a result, it has been shown that the structural characteristics of female gonads supplement significantly other morphological criteria and allow to identify nematodes in supra-specific as well as in specific level. The cellular structure of some part of the sexual tube, its functional significance and variability as well as the degree of significance of one or another part of female gonads in taxonomy of different groups of nematodes have been determined.

However, at present day the united system of terminology of the parts of female gonads has not been established, and some investigators (Paramonov, 1962; Geraert, 1973) designate the same parts of sexual tube differently. In the present paper we will confine to the system proposed by Paramonov (1962) with some additions.

The female sexual tube of tylenchids consists of two main parts: the ovary and the oviduct, each of these parts being also functionally and morphologically differentiated into sections. The ovary consists of three sections: germinal zone, growth zone, and maturation zone of oocytes, but the separation between these zones in the ovary is more or less conditionally, insofar as the distinct morphological boundaries between these parts cannot been seen.

The structure of the oviduct is more varied and distinct boundaries exist between its different functional parts. The sexual tube narrows bluntly at once behind the ovary and forms a post-ovary sphincter, the ostium postovarialis (oviduct). This sphincter is followed by a well morphologically differentiated part, the spermatheca. However, all tylenchids do not have a separated spermatheca. The spermatheca is followed by the columned uterus or glandula praeuteralis. In a few cases, an ostium praeuteralis can be observed between spermatheca and columned uterus but this structure is not morphologically differentiated in most tylenchids. The structure of the columned uterus in tylenchids is variable and is strictly correlated with the taxonomic characteristics of corresponding groups of plant-parasitic nematodes.

Paramonov (1962) distinguished two types of structure of the columned uterus depending on arrangements of cell rows: regularly columned uterus if the cells are arranged in clearly marked columns; irregularly columned uterus if the cells are not regularly arranged in rows and cell rows cannot clearly be observed.

Wu (1967) proposed a name – crustaformeria – for the ovary structure taking part in the formation of one of the egg shells. Insofar as the important taxonomic characteristics in the structure of the columned uterus is the number of its cell rows, then the following types of columned uteri can be distinguished. The columned uteri with cells arranged in three rows, that look like columns were named tricolumella (Hirschmann & Triantaphyllou, 1968). The columned uteri with cells arranged in four rows were named quadricolumella (Wu, 1958; Mulvey, 1958).

The interesting peculiarity of the structure of the columned uterus in some high specialized species of nematodes from the families Anguinidae, Meloidoderitidae and Heteroderidae is that, this structure has two morphologically and functionally differentiated parts. The first part of such columned uteri, next to the spermatheca, is a crustaformeria in functional respect, that is it forms one of the egg shells; this part is as a rule characterized by having cells of a different form and arranged in a greater numbers of cell rows. This section of the columned uterus has often more than four rows of cells, and although these cells do not form true rows, we propose to name it polycolumella. The second part of the columned uterus borders on the uterus and its function is to promote a faster maturation of the egg shell. As a rule, its cells are arranged in three rows. A smooth passage exists between these two parts of the columned uterus.

Some more important functional peculiarity of the columned uterus in these forms is that, the egg is moving constantly and slowly inside this structure. Such a columned uterus is a combined structure that we propose to name glandula combinata. This structure has been described in detail earlier by one of the authors of this article (Chizhov, 1984). The columned uterus joins the uterus through a narrow sphincter (according to Paramonov, 1962, it is the oviduct) (Wu, 1958, 1967; Hirschmann, 1962; Geraert & Kheiri, 1970).

Uterus, or uterial sac – This structure consists of muscular cells that is functionally responsible for egg extrusion from the female body in some species, or is a small cavity before vulva having not distinct cell differentiation in other species. Other forms of uteri can be rarely observed.

The present paper is based on female gonads extracted from 11 species of nematodes of specific pathogenic effect. The objective of this work was to research the structural characteristics of female gonads of nematodes that are most interesting for taxonomic purposes, as well as to observe the evolution of the genital system and some of its parts depending on the level of species specialization.

The sexual tubes were extracted from live nematodes placed in a water or physiological solution. Polychrome blue was used as a nuclear dye. It was impossible to extract the whole genital system in some species, particularly the uterus and some structures connected with the uterus. In such cases, the genital system was pictured as whatever shapes we could observe through the cuticle of live nematodes. The measurements of cells in different sections of oviduct were made only in gonads extracted in a physiological solution.

Pratylenchus, Merlinius, Rotylenchus (Fig.1, a1, a2, a3). In spite of the fact that *Pratylenchus* has a monodelphic genital system while *Merlinius* and *Rotylenchus* have a didelphic system with gonads arranged longitudinally and opposed, these systems have approximately the same type of structure. Ovary is oligopropagatory, relatively short and separated from the spermatheca by a postovary sphincter that appears as a short narrowing. The postovary sphincter consists of cells arranged into two rows with 4 cells per row. This structure is typical for tylenchids (Geraert, 1981); besides that, the first two cells can become part of the ovary and the two last cells can become part of the spermatheca. Cells included in the postovary sphincter are very small, therefore this structure is not always morphologically differentiated and can be observed as a short contraction of the sexual tube. The spermatheca is round or oval, sometimes looking like as a lateral lobe. It contains 12-16 cells (in number of visible nuclei), or a smaller number of cells in some species. The columned uterus is a tricolumella (4-5 cells in a row) of the same size (Table). Sometimes the cells close to uterus have a smaller size. The columned uterus is joined to the uterus through a small cell group forming a narrowing of the sexual tube (oviduct). The uterus has not distinct cell differentiation.

Tylenchulus semipenetrans (Fig.1, b). The genital system is monodelphic. Eggs are laid in an egg-sac. The gonad extracted from live nematodes into water form an angle, first cells of the columned uterus being located in its apex. Two sides of the angle are formed by the basis of the ovary and the columned uterus. The last oocyte in the maturation zone does not reach down to the ovary basis and leaves the free part of the ovary being equal to approximately haft of its own length. The postovary sphincter is short and consists of small dark cells arranged typically for tylenchids – into two rows, with four cells per row (Table). The spermatheca is not morphologically differentiated. The columned uterus looks like an irregular tricolumella, with three rows of 6-7 cells per row, if the gonad was extracted from body. However, it was impossible to extract the whole gonad from the female body, and drawing of the columned uterus in the figure was made by observing the arrangement of the first 7-10 cells extracted through a cut at the basis of the neck of a female. It is quite possible that the columned uterus forms a regular tricolumella inside the female body. The structure of uterus and the adjacent part of the columned uterus is not also entirely clear. The vagina consists of four cells narrowing into a vulva.

Sphaeronema alni. (Fig. 1, c). The genital system is monodelphic. The eggs are laid in an egg-sac. The gonads extracted from live nematodes into water form an angle, the first cells of the columned uterus being located at its apex. The two sides of the angle are formed by the ovary and the columned uterus. The ovary is polypropagatory, flexed two or three times. The last oocyte does not reach to the basis of the ovary for approximately half of its length. The postovary sphincter appears as a short contraction consisting of small, slightly elongated, and well visible cells. The cell arrangement of the postovary sphincter is typical for tylenchids: two rows with 4 cells in a row. The spermatheca is not morphologically differentiated, but the first cells of the columned uterus are distinguished by lighter cytoplasm. Inside live female the columned uterus is observed as a regular quadricolumella. When this structure is extracted in

water, the cells are arranged in 3-5 rows of cells. The larger numbers of rows can be observed in the center of the columned uterus. One row contains from 11 to 15 cells (Table). The columned uterus is joined to the uterus through a short contraction. The uterus is very large and has a cavity. According to the arrangement of the nuclei, it seems that the uterus contains two rows of muscular cells with 5-6 cells per row, including the cells that form the vagina. Only one egg at a time can be found in the uterus.

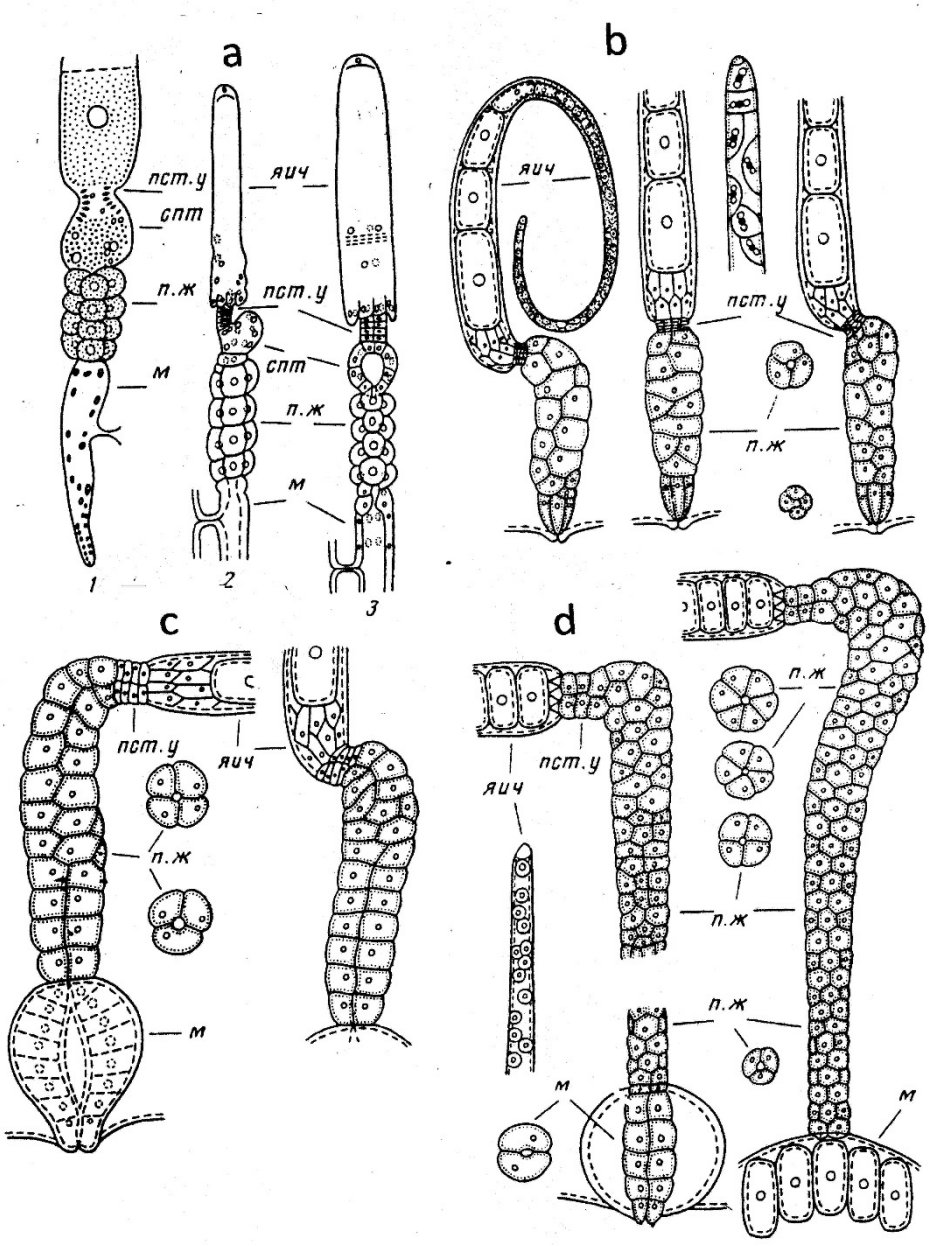

Fig. 1. Female genital system: a1 – *Pratylenchus* (according to Roman & Hirschmann, 1969); a2 – *Merlinius*; a3 - *Rotylenchus* (according to Geraert, 1981); b – *Tylenchulus semipenetrans*; c – *Sphaeronema alni*; d - *Meloidoderita kirjanovae*

Legend:

яич	**Ovary**	спт	**Spermatheca**
пст.у	Post-ovary sphincter	п. ж	Columned uterus
м	Uterus		

Meloidoderita kirjanovae (Fig.1, d). The genital system is monodelphic. The first eggs are laid in an egg-sac, the last ones in the uterus cavity. Gonads extracted from live nematodes into water form a right angle, the anterior enlarged part of the columned uterus being at its apex. The two sides of the angle are formed by the ovary with postovary sphincter and the columned uterus. The ovary is polypropagatory and flexed several times. The ovary of this type is characterized by diametral arrangement of oocytes relative to the ovary axis. The postovary sphincter is well developed and consists of large oval cells (in all 7- 9 cells arranged into two-three rows, the last cells often becoming part of the anterior part of the columned uterus). The spermatheca is not morphologically differentiated, but the gonad is most enlarged in this place. The columned uterus is combined, the anterior part (crustaformeria) 1ooking like an irregular polycolumella (cells arranged into 4-6 rows, in average about 25 cells per row), while the posterior part forms a tricolumella with up to 20 cells per row (Table). These two parts are separated by a smooth passage. The structure of the uterus in that species is original: a group of muscular cells that may be arranged in two rows with 4-5 cells per row is surrounded by a thin film cover. In young females, the uterus functions normally and the eggs are laid in an egg-sac; in older females, the muscular cells stop functioning and break up, and the eggs are laid in the uterus cavity. The uterus enlarges and gradually occupies a larger part of the female body. In dead nematodes, the uterus shell takes a light brown color and turns into an original "cyst".

Rotylenchulus reniformis (Fig.2, a). The genital system is didelphic with gonads longitudinally opposed. The eggs are laid in an egg sac. Gonads extracted in water are straight. The ovary is polypropagatory, flexed two or three times, the last oocyte does not reach to the basis of the ovary for approximately half of its length, therefore the basis of ovary is observed as transparent. The postovary sphincter is well developed and morphologically distinctly differentiated, with round cells in two rows of 4 cells per row. The spermatheca is also morphologically well separated. It contains from 9 to 15 round cells arranged into 3 rows with 3-5 cells per row; the number of cells in the spermatheca being variable in different individuals. The columned uterus is a regular tricolumella. It contains larger cells with dark cytoplasm. The cells of the columned uterus placed close to the uterus are smaller than anterior cells. One row contains 4-6 cells (Table). The columned uterus joins the uterus through the short narrowing of the gonad, consisting of 6 cells arranged into 3 rows. The muscular uterus consists of two rows of projected cells, with 4 cells per row. Such cell arrangement of the uterus can be seen through the cuticle in live nematodes. When this uterus is extracted in water a different structure is seen: the number of cell rows remains the same, but the form is changed and the size is larger: 25-35 x 45-65 μm in water.

Meloidodera alni. (Fig.2, b). The genital system is didelphic with a bilateral arrangement of the gonads. The eggs are laid in a body cavity. The gonad extracted from live nematodes into water forms a right angle, the spermatheca being located at its apex. The two sides of the angle are formed by the ovary and the columned uterus. The ovary is polypropagatory and flexed several times. The last oocyte does not reach to the basis of the ovary for a distance of half of its length. The postovary sphincter is well developed, with large cells; the cell arrangement is typical for tylenchids. The last two cells of the postovary sphincter become usually part of the spermatheca. The spermatheca is distinctly differentiated. It consists of two rows of much elongated cells, often filled with spermatozoids. A short narrowing (with 3 cells) of gonad forms a preuteral sphincter between the spermatheca and the columned uterus. The columned uterus is a regular tricolumella, with 7- 9 cells per row (Table). The uterus is membranous, the eggs are placed in it transversely to the gonad axis.

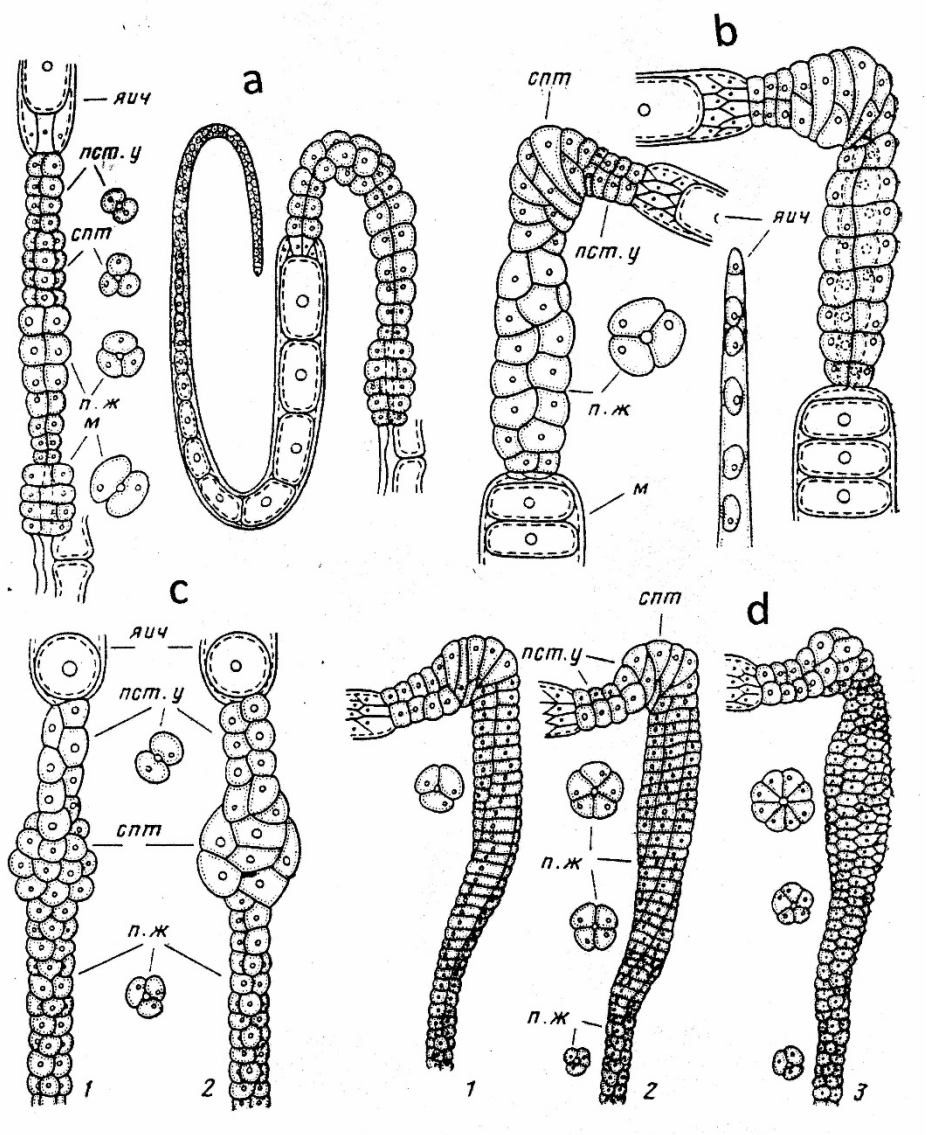

Fig. 2. Female genital system: a – *Rotylenchulus reniformis*; b – *Meloidodera alni*; c – *Meloidogyne incognita*; c2 – *M. hapla*; d1 – *Bidera avenae*; d2 – *Heterodera schachtii*; d3 – *Globodera rostochiensis*

Legend:

яич	**Ovary**	спт	**Spermatheca**
пст.у	Post-ovary sphincter	п. ж	Columned uterus
м	Uterus		

Genus *Meloidogyne* (Fig.2, c). Genital system didelphic with bilateral arrangement of gonads. The eggs are laid in an egg-sac. The gonad extracted in water is straight. The ovary is polypropagatory, twisted in spiral inside the female body. The postovary sphincter is well developed. It contains oval cells arranged into two rows, the last pair of cells sometimes becoming part of the spermatheca. The spermatheca is always morphologically differentiated. Two types of spermatheca can be distinguished: the spermatheca of species with obligate parthenogenesis (M. incognita) and that of females with facultative parthenogenesis (M. hapla) (Chizhov, 1981). In the first case, the spermatheca consists of a greater number of smaller

projected cells and it functions exclusively as a crustaformeria (i.e., it participates in the egg shell formation). In the second case, the spermatheca has larger cells, but fewer cell number and sometimes these cells are slightly projected in different sides, or sometimes the spermatheca has almost ball-like form and functions as a sperm-receiver, but the function of the egg shell formation cannot be excluded. The columned uterus is as a regular tricolumella, but always very long (Table). The two sexual tubes have a common uterus.

Table. Some numerical and linear characteristics of the female genital system of tylenchids (p: number of rows, k: number of cells per row).

Genus	Nbr of gonads	Postovary sphincter		Spermatheca		Columned uterus	
		p x k	size (µm)	p x k	size (µm)	p x k	size (µm)
Pratylenchus	1	2 x 4				3 x 4-5	9-12 x 13-16
Tylenchulus	1	2 x 4	6-10			3 x 6-7	15-20 x 25-35
Sphaeronema	1	2 x 4	5-10 x 20-25			3-5 x 11-15	15-35 x 20-50
Meloidoderita	1	2-3 x 3-4	15-20 x 20-25			4-6 x 20-30	20-35 x 35-50*
Merlinius	2	2 x 4	4-6	4x2	8-12	3 x 4-5	10-16
Helicotylenchus	2	2 x 4				3 x 4-5	7-12 x 11-18
Rotylenchulus	2	2 x 4	15-25	3 x 3-5	18-24	3 x 4-6	20-25 x 30-40
Meloidodera	2	2 x 3-4	10-15 x 20-25	2-3 x 4-6	10-25 x 35-55	3 x 7-9	15-30 x 25-60
Bidera	2	2 x 4	30-50	2-3 x 4-6	10-25 x 50-80	3 x 30-40	10-25 x 50-90*
Heterodera	2	2 x 4	25-45	2-3 x 4-6	10-25 x 50-80	3-5 x 30-35	10-35 x 35-80*
Cactodera	2	2 x 4	20-30	3-4 x 4	20-50	5-7 x 20-35	10-25 x 20-40*
Globodera	2	2 x 4	20-35	4-5 x 3-4	20-50	5-8 x 25-35	10-25 x 20-40*
M. hapla	2	2 x 3-4	35-55	4-5 x 3-4	20-35 x 30-55	3 x 60-80	35-50
M. incognita	2	2 x 3-4	35-55	5-6 x 3-4	25-35	3 x 60-80	35-50

* Crustaformeria only

Subfamily Heteroderinae (Fig.2, d). The genital system is didelphic with gonads bilaterally arranged. The eggs are laid in both an egg-sac and a body cavity, or only in a body cavity, depending on the species. The gonad extracted in water usually forms an acute angle, the spermatheca being located at its apex. The two sides of the angle are formed by the ovary plus postovary sphincter and the columned uterus. The ovary is polypropagatory and twisted in spiral inside the female body. The postovary sphincter is well developed with two rows of large round cells in 4 cells per row. The spermatheca is distinctly morphologically differentiated in the parthenogenetic species *Heterodera trifolii*. In species of the genera *Bidera* and *Heterodera,* it consists of much elongated cells arranged into two-three rows. In *Cactodera cacti* and species of the genus *Globodera*, the cells of the spermatheca are oval-shaped and arranged into 4-5 rows; in all the spermatheca contains 10-16 cells.

The columned uterus is composed of two parts. In species of the genus *Bidera*, the anterior part of this structure (crustaformeria) looks like as a regular tricolumella and consists of cells rectangular in shape, with 30-40 cells per row. In species of the genus *Heterodera*, it is a regular

quadricolumella with cells that perhaps are arranged into five rows and with the same cell number in a row. In *C. cacti* and species of the genus *Globodera,* the anterior part looks like an irregular polycolumella (5-8 rows of oval cells with 25-35 cells per row). In heteroderids, the posterior part of the columned uterus is always a regular tricolumella. In species depositing some of the eggs in an egg-sac, this part of the columned uterus is very long – up to 80 round cells in a single row; if the eggs are deposited only in the body cavity, this part is significantly shorter (Table). There is a smooth passage between these two parts of the combined columned uterus. In species depositing some of the eggs in an egg-sac, every gonad has a uterus; but if the eggs are laid only in the body cavity, the uterus is not observed.

The analysis of the data on the structure of genital system of females in the sedentary species of the order Tylenchida revealed some common characters in gonad evolution in these species of plant-parasitic nematodes. The general enlargement of the sexual tubes and their part as well as a more distinctly morphological differentiation of some parts of gonad and intensification of its function can be observed during the increase of specialization level and egg productivity of gonads.

Ovary. The main trend in the development of this part of gonads is an increase of the general size (length) and in the number of transversal rows of oogonia and oocytes in the germinal zone and the growth zone. The ovary is always flexed several times inside the female body of the sedentary tylenchid species investigated in the present paper. Such ovary is practically never observed in vermiform nematodes (with the exception of species of the subfamily Anguininae). The interesting peculiarity of the ovary structure of some species is the transversal arrangement of oocytes relative to the ovary axis and the presence of some free space between the ovary basis and the last mature oocyte. However, the adaptative significance of these characteristics is not clear. The structure of the oviduct and its parts is correlated with the development level of the ovary.

Postovary sphincter. As a rule, in vermiform species, the postovary sphincter appears like a short contraction of gonad; a cellular structure is not observed in all species. It seems that the main function of this structure is to lock the ovary and that it is physiologically passive towards the eggs. In our opinion *T. semipenetrans* being the species closest to vermiform nematodes has the structure of the postovary sphincter typical for these nematodes. In other sedentary nematodes, the postovary sphincter is always well developed and differentiated into an independent morphological structure, evidently with an increased functional significance. The postovary sphincter continues to play a part as a structure locking the ovary and, perhaps, it also has an additional function. It can be concluded on the basis of the type of cell arrangement and size as well as the coloring of cells by polychrome blue, its cells have the same color intensity as cells of the columned uterus. All the tylenchids are characterized by the cell arrangement of the postovary sphincter in two rows with four cells per row (Geraert, 1981). However, the size and functional significance of this part of the oviduct increases during the rise of the specialization of species and the egg productivity.

Spermatheca. In many vermiform species, the spermatheca is more or less morphologically differentiated, but in some species this structure is absent. Most parthenogenetic sedentary species do not have a morphologically differentiated spermatheca, as in *T. semipenetrans*, *S. alni* and *M. kirjanovae* where it is replaced by a crook in the gonad. However, parthenogenetic species of the genus *Meloidogyne* are characterized by a well-developed spermatheca, which in some species has lost its initial function as a sperm-receiver and now functions as a crustaformeria forming one of egg shells. Thus, a change of function in this part of the gonad

occurs in these species. In species with obligate sexual process, such as *M. alni* and species of the subfamily Heteroderinae, the spermatheca functions as a sperm-receiver and is morphologically well differentiated. As a rule, its cells are distinguished by their shape and a lighter cytoplasm from the cell of the columned uterus. Thus, in the species described in present paper, can be observed a well-developed and morphologically differentiated spermatheca as well as a totally reduced spermatheca. The initial function of the spermatheca changes and it turns into a crustaformeria.

Columned uterus. Two main trends can be observed in the development of the columned uterus during the increase of the level of species specialization. The first trend is an increase of the general number of cells as well as the number of cells per row; the second trend is the increase of cell rows of the columned uterus. An enlargement of the cell size also takes place (Table). As a rule, the vermiform species have a regular tricolumella with 3-5 cells per row, so the columned uteri of *T. semipenetrans* and *R. reniformis* have the same structure of but the number per row is increased up to 6-7. In *M. alni*, the columned uterus is also a tricolumella, but the cell number per row is increased up to 9. The columned uterus of S. alni looks like a quadricolumella, but the cell number per row is increased up to 15. However, the columned uterus of these species looks like as a united morphological structure having a length not more than an egg length. In this structure, two processes take place simultaneously - the formation of egg shell and its maturation (fixing). Similar processes occur in vermiform nematodes. That is why the time during which the eggs remain static in the columned uterus is rather long (sometimes several days), which significantly decreases the general egg productivity of female and prolongs the duration of ontogenesis.

In more evolutionary advanced forms, another type of columned uterus is observed, the combined columned uterus. In *M. kirjanovae* the anterior part of this structure (crustaformeria) consists of 4-6 rows with 20-30 cells per row. It changes smoothly into a tricolumella at a distance of approximately half of its length. The columned uterus of heteroderids has the same structure. It is also a combined columned uterus, with an anterior part of 3 to 8 rows, depending on species, and with up to 40 cells. The posterior part of the columned uterus in all heteroderids looks like a regular tricolumella of different length. During evolution and the rise of specialization level, these nematodes have developed an important adaptation for the increase of egg productivity, which is expressed in the division of the columned uterus into two morphologically and functionally different parts. The anterior part (crustaformeria) forms the egg shell, while the posterior part, connected with the anterior part by a smooth passage, promotes the quick maturation of this shell (fixing). This explains one important functional peculiarity of this structure: eggs are constantly moving in it. All these adaptations work together to significantly reduce the time spent by an egg in the female gonad (only several hours) and to increase the general egg productivity.

In nematodes of genus *Meloidogyne*, the columned uterus looks like a regular tricolumella, but the cell number per row is up to 80. As said above, the spermatheca carries out a function of crustaformeria, and the columned uterus promotes a quick maturation of the egg shell. Therefore, an analogous adaptation has developed in these species, but in another part of the ovary (spermatheca), t significantly increasing egg productivity. Thus, during the increase of the level of species specialization, the genital system of females of sedentary nematodes undergoes some natural changes that reflects the phylogenesis of these species and directly or indirectly increase egg productivity.

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