

Evolution of modified food cells induced by sedentary nematodes in plant roots

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Summary. The development of modified food cells induced by sedentary nematodes in plant roots are discussed as an example of host-parasite coevolution. The main principles of this evolutionary process are reviewed. Analysis of structures of the modified cells suggests that evolution of these cells is connected with increases of cellular functional activity. Intensification of modified cell function is achieved through multiplication of cell protoplast, proliferation and polymerization of organelles and intensification of contact between cell wall and protoplasm. Increase of functional activity matches the evolution of modified cell development, from nonhypertrophic nurse cells and single giant cell to syncytia and more specialized coenocytes. Increased internal organisation of the modified cells is generally coincident with the level of evolutionary advancement of the nematode. The hypothesis of different levels of evolutionary development of modified cells can be used to help determine systematic and phylogenetic relationships between nematodes. **Key words:** host-parasite coevolution, plant reaction, sedentary nematodes, modified food cell.

Treub (1887) first drew attention to the multinucleate giant cells surrounding the lip region of the root-knot nematodes (Endo, 1971). Since then many investigators have studied the morphology, biochemistry and physiology of plant roots infected by nematodes and the mechanisms involved in nematode feeding on plant cells.

The use of electron and video enhanced contrast microscopy for the analysis of infected roots showed that infective juveniles of sedentary nematodes penetrate the root, become established in the cortex, perforate the cell wall and insert their stylet into cells. Secretions of the dorsal esophageal glands are injected by the nematode stylet into the cytoplasm and significantly change the cell metabolism. Nematodes induce so called modified food cells in the root tissue. The modified cells are specialized pathological cell formation caused by parasitic nematodes in the plant and become the trophic mediator between nematodes and plants. The modified cells are characterized by an enlarged amoeboid nuclei with hypertrophied nucleoli, numerous cytoplasmic organelles: mitochondria, plastids, membranes of endoplasmic

reticulum, dictyosomes. These changes induce high metabolic activity of the protoplast, intensive synthesis and transport of nutrients from the adjacent tissues to the modified cells.

The feeding process of juveniles of sedentary nematodes consists of a series of repeated cycles with distinct phases, during which nematodes introduce the secretions into the cell and form a feeding tube which they use to withdraw the cell contents. Activity of the modified cells depends on the intensity of the nematode feeding. The metabolic activity of the modified cells is much increased during nematode feeding but these cells usually collapse when the nematode ceases to feed.

Detailed investigations using light and electron microscopy showed that sedentary nematodes induce modified cells with different structures. Currently four types of modified cells have been observed: nonhypertrophic nurse cells, a single giant cell, syncytia and coenocytes (Jones, 1981 a,b; Subbotin, 1986). Each nematode species induces its own characteristic modified cell, regardless of tissue and plant (Fig. 1; Table 1).

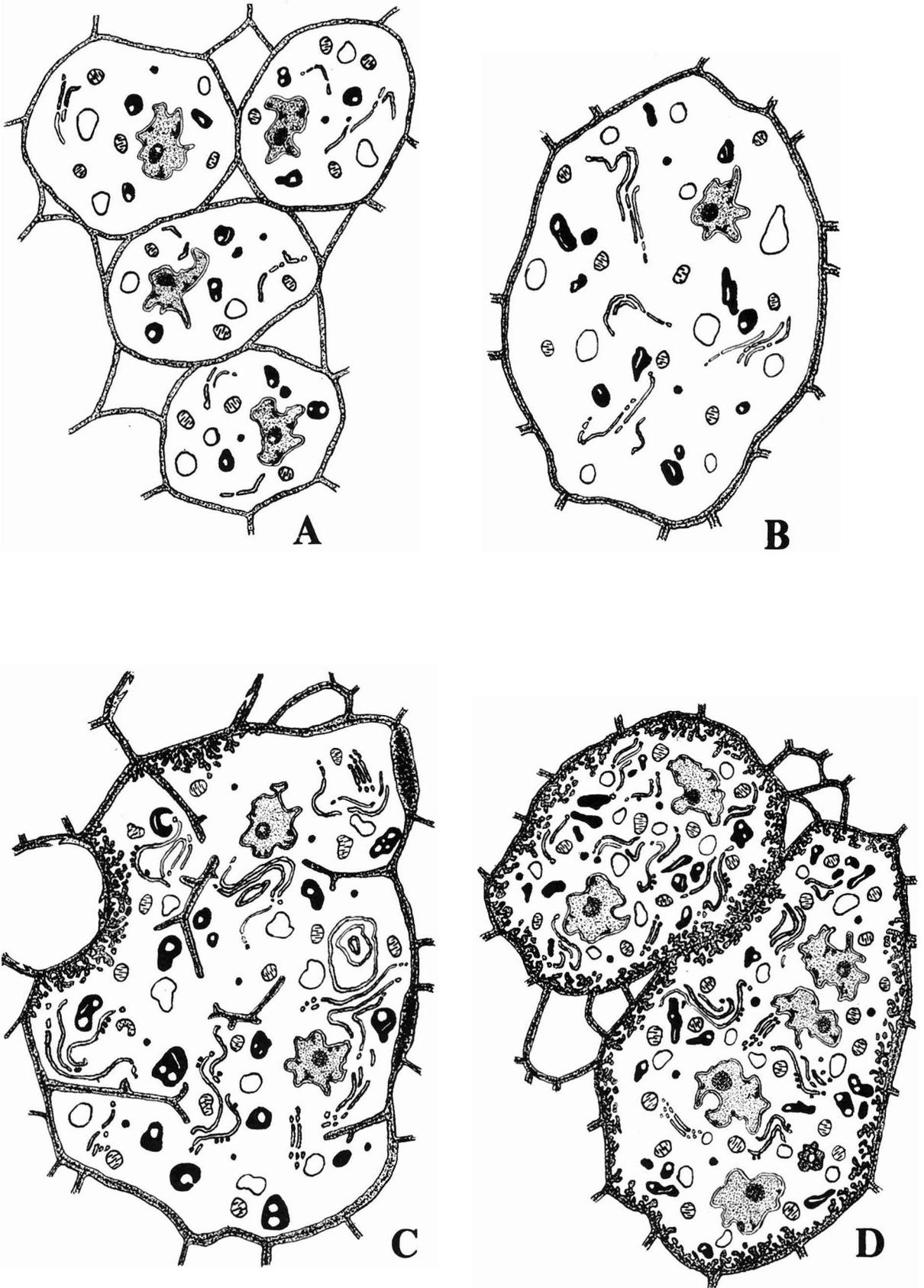


Fig.1. Structure of four types of modified food cells induced by sedentary plant parasitic nematodes. A - nonhypertrophied nurse cells; B - single giant cell; C - syncytia; D - coenocytes.

During the evolution of nematode parasitism these pathological cellular formations have been modified. Analysis of the evolution of modified cells may contribute to our understanding of the development of the relationships between parasitic nematodes and plant hosts.

Mundo-Ocampo & Baldwin (1983 a,b,c, 1984, 1992) and Baldwin (1986) were the first to report on the different level of the evolutionary advance of modified food cells. They used this concept when reviewing the phylogeny of the family Heteroderidae. However, these authors compared only two types of modified cells: a single giant cell and syncytia. They considered that a single giant cell is the more primitive, having originated earlier and preceded the formation of syncytia. We also elaborated on the concept of evolution of modified food cells in several publications (Subbotin, 1986, 1988, 1990b).

We consider modified cells as not only being the plant response to infection but also as a result of long coevolution providing a balanced relationship between the parasite and its host.

According to Paramonov (1967) and Maggenti (1971) the evolution of nematode parasitism in the order Tylenchida occurred from ectoparasitism to semiendoparasitism and subsequently to endoparasitism. This evolutionary pathway reflects increasing interadaptability of the metabolism of both parasite and host and dependence of this relationship by the nematode on its plant host.

The capability for inducing modified cells originated as a definite stage of parasitism. The extended feeding from plant cells can be observed in the group of browsing ectoparasitic nematodes e.g. Tylenchorhynchidae, Paratylenchidae. These nematodes feed from epidermal cells and root hairs. Some nematodes can feed from one cell for several hours. Pathological changes can spread from one to several root cells (Wyss, 1981). The increased ingestion was achieved by the nematode penetrating the root to feed on phloem and xylem parenchyma cells and sieve elements arranged near the solute flow in roots, each of which have a richer cytoplasm content than cortical cells. Feeding from these internal cells

was achieved by the development of a long stylet e.g., *Hemicycliophora*, *Dolichodorus*, or by partial penetration of the nematode's body into the root e.g., Hoplolaimidae. Amongst these nematodes are species, which can influence cell metabolism and significantly extend the period of sedentary feeding in plant roots. For example species of the genera *Helicotylenchus* can feed from single nonhypertrophied cells as sedentary semi-endoparasites, for almost 20 days. In these cells increased cytoplasm, number of mitochondria, plastids and membranes of ER occur. Also nuclei with enlarged nucleoli have been recorded (Jones, 1978 a,b; Vovlas & Inserra, 1985).

The ability to induce the formation of a stable cellular feeding complex was a prerequisite for the transition of ecto- and endoparasitic nematodes from partial to complete sedentary parasitism.

Sedentary plant parasitic nematodes have more complex relationships with plant-hosts. Having induced specific modified cells, which act as trophic mediator between nematode and plant, this group of nematodes became dependent on a limited range of plant hosts. We consider that evolution of the relationships between sedentary nematodes and plant hosts was connected with increased complexity of cell structure and intensification of the functional activity of the modified cells (Subbotin, 1986). According to Severtzov (1939) intensification of cell function may occur in two ways: increase in number of cells and by changes in cell structure. Intensification of the cell function involved the multiplication of the cell protoplast, proliferation and polymerization of organelles and intensification of contact between the cell wall and protoplasm.

Multiplication of the cell protoplast may be achieved: 1. increase of cell number with preservation of their previous size (nonhypertrophied nurse cells), 2. increase in size of only one cell (a single giant cell), 3. simultaneous increase of cell number and size (syncytia and coenocytes) (Fig. 2).

The most primitive sedentary nematodes are the semiendoparasites *Tylenchulus* and *Trophotylenchulus* which feed from clusters of 6-10

Table 1. Changes caused by sedentary plant parasitic nematodes of the order Tylenchida in plant roots.

Genus	Modified cells*	Changes in modified cells			References
		mitosis	hyper-trophy	wall ingrowths	
<i>Tylenchulus</i>	NNC	—	—	—	Cohn, 1965; Himmelhoch et al., 1979; Ambrogioni, 1982; B'Chir, 1988; Subbotin, 1990.
<i>Trophotylenchulus</i>	-"	—	—	—	Cohn & Kaplan, 1983.
<i>Meloidodera</i>	SGC	—	+	—	Ruehle, 1962; Heald, 1984; Mundo-Ocampo & Baldwin, 1983c; Subbotin, 1989.
<i>Rhizonema</i>	--	—	+	—	Cid del Prado Vera & Lownsbey, 1984.
<i>Bellodera</i>	-"	—	+	—	Mundo-Ocampo & Baldwin, 1984.
<i>Sarisodera</i>	-"	—	+	—	Mundo-Ocampo & Baldwin, 1981, 1983 b
<i>Hylonema</i>	-"	—	+	—	Taylor et al., 1978
<i>Rotylenchulus</i> (<i>macrodoratus</i>)	-"	—	+	—	Cohn, 1976; Vovlas & Inserra, 1976; Cohn & Mordechai, 1977; Inserra & Vovlas, 1979, 1980; Vovlas, 1983.
<i>Verutus</i>	S	—	—	?	Mundo-Ocampo & Baldwin, 1983c; Cohn et al., 1983.
<i>Thecavermiculatus</i>	--	—	+	—	Mundo-Ocampo & Baldwin, 1984; Baldwin et al., 1989
<i>Ekphymatodera</i>	--	—	+	—	Baldwin et al., 1989; Mundo-Ocampo & Baldwin, 1992.
<i>Atalodera</i>	--	—	+	—	Mundo-Ocampo & Baldwin, 1981, 1983a.
<i>Afenestrata</i>	-"	—	+	—	Baldwin & Bell, 1985.
<i>Sphaeronema</i>	-"	—	+	—	Vovlas & Inserra, 1986; Subbotin, 1989
<i>Meloidoderita</i>	-"	—	+	—	Andrews & Krusberg, 1981; Cohn & Mordechai, 1982; Subbotin, 1986.
<i>Nacobbus</i>	--	—	+	—	Schuster et al., 1965; Jones & Payne, 1977a, b.
<i>Rotylenchulus</i> (<i>reniformis, borealis, parvus, macrosoma</i>)	--	—	+	—	Birchfield, 1962; Cohn, 1973, 1976; Rebois et al., 1975; Jones & Dropkin, 1975; Vovlas et al., 1985.
<i>Heterodera</i>	--	—	+	+	Endo, 1971 and others.
<i>Bidera</i>	-"	—	+	+	Jones & Fushtey, 1966; Grymaszewska & Golinowskin, 1987; Subbotin et al., 1989, 1991.
<i>Cactodera</i>	--	—	+	+	Baldwin & Bell, 1985.
<i>Punctodera</i>	-"	—	+	+	Suarez et al., 1985; (our unpublished results).
<i>Globodera</i>	--	—	+	+	Endo, 1971; Jones & Northcote, 1972; Melillo et al., 1990 and others.
<i>Meloidogyne</i>	C	+	+	+	Christie, 1936; Dropkin & Nelson, 1960; Bird, 1974; Paulson & Webster, 1972 and others.

*NNC - nonhypertrophied nurse cells; SGC - single giant cell; S - syncytia; C - coenocytes.

+ - present, — - absent.

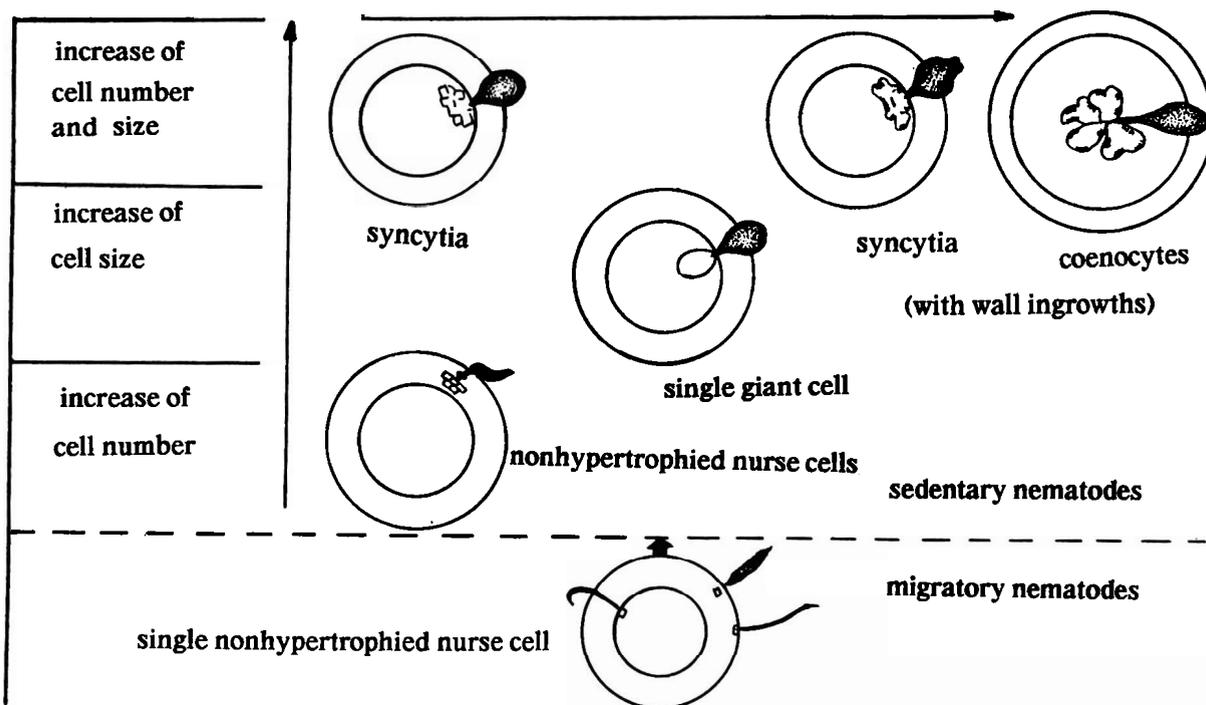


Fig. 2. Scheme of evolutionary levels of modified food cells induced by plant parasitic nematodes.

nonhypertrophic cells, which resemble neighboring normal cells in size. However, the parasitized cells contain nuclei and increased amounts of cytoplasm with numerous organelles. Although nematodes feed from each cell in progression, the cluster of nurse cells functions as a single unit.

Increased protoplasm is achieved by enlargement of one modified cell - formation of a single giant cell. A single giant cell is usually one-nuclear, greatly hypertrophied cell filled with cytoplasm containing numerous organelles. This type of modified cell is induced by nematodes of the family Heteroderidae and by *Rotylenchulus macrodoratus* (Rotylenchulidae). During the evolution of sedentary nematodes these cells originated earlier and preceded syncytial formation. The propinquity of the mechanism inducing a single giant cell and syncytia is believed to be confirmed by the fact that syncytia begin to be formed from one hypertrophied cell. In addition *Rotylenchulus* species induce both a single giant cell and syncytia.

Sedentary nematodes in the families Sphaeronematidae, Rotylenchulidae, Nacobbidae and Heteroderidae have a relatively minor influence on the regulatory processes in plant cells, inducing only wall dissolution and formation of syncytia. Syncytia are a multicellular, multinucleate formation produced by partial cell wall dissolution and fusion of the protoplast of neighboring cells. In syncytia formation the cells fuse and enlarge in size. Small syncytia are produced by primitive species in the genera *Verutus*, *Ekhymatodera* and *Sphaeronema* (Cohn et al., 1984; Vovlas & Inserra, 1986; Baldwin et al., 1989; Subbotin, 1989). *Verutus* species induce syncytia consisting of nonenlarged cells and fusion of the protoplasts occurs only in the final stages of feeding (Cohn et al., 1984). Large syncytia are induced by *Heterodera* and *Globodera* - genera which are more evolutionary advanced. The ability to induce syncytia has developed independently in different nematode groups, having occurred at least twice in the suborders Criconematina and Tylenchina.

The most complex pathological influence on plant roots is caused by root-knot nematodes. These nematodes induce coenocytes which are hypertrophied multinucleate cells formed by repeated mitosis in the absence of cytokinesis. Coenocytes are complexes of giant cells united by plasmodesmata and function as a single unit. Intensive transport of nutrients in these cells occurs from xylem and phloem elements as well as from surrounding hyperplastic cells.

Increases in the functions of modified cells are related to increases in the number and polymerization of organelles. Results of a stereometric analysis of cell imprints (Avtandilov et al., 1984) made by us showed, that coenocytes induced by root-knot nematodes have significantly larger numbers of mitochondria and plastids than syncytia induced by cyst nematodes in different plants (Table 2). For example, in soybean roots infected by root-knot and cyst nematodes the relative square of mitochondria and plastids are greater in coenocytes than in syncytia (2.8 and 3.5 times respectively; Subbotin, 1990b). This index reflects the activity of mitochondria and plastids as well as the general functional condition of cells. Nuclei of coenocytes are polyploid and significantly more

active (Endo, 1987). Our investigations showed that the relative square of nuclei was greater (x3.6) in coenocytes, than in syncytia. Also, the system of endoplasmic reticulum was more developed in coenocytes. This quantitative difference in the ultrastructure of these cells suggests a significantly greater intensification of functions of these modified cells as compared with syncytia (Subbotin, 1990b).

Increased contact of the cell wall with protoplasm is connected with the formation of protuberances or wall ingrowths and labyrinth. The increased plasmalemma area, resulting from the formation of wall ingrowths, significantly enhances the functional activity of modified cells and facilitates increased uptake of the nutrients through the apoplast to the symplast of the modified cell. For example, in coenocytes the plasmalemma surrounds the wall ingrowths which can result in a local amplification of cell membrane area by 10-15 times (Jones & Dropkin, 1976).

Wall ingrowths are typical for plant transfer cells, which can form in plant cells due to the influence of ecological factors inducing changes in the plant water regime and redistribution of solutes in the conductive system (Pate & Gunning, 1972). The formation of

Table 2. Relative square of compartment of the modified cells induced by cyst and root-knot nematodes in plant roots.

Plant-host	Modified cell	Nematode	Stage	Relative square (%)		
				Mitochondria	Plastids	Vacuoles
<i>Glycines max</i>	Syncytia	<i>Heterodera glycines</i>	female	2.7 ± 0.2	2.5 ± 0.3	0.7 ± 0.2
	Coenocytes	<i>Meloidogyne javanica</i>	- -	7.7 ± 0.4	8.8 ± 0.7	4.2 ± 0.5
	Parenchymal cells	Control		0.7 ± 0.1	0.5 ± 0.1	85.3 ± 1.0
<i>Poa annua</i>	Syncytia	<i>Punctodera punctata</i>	L4	2.5 ± 0.2	2.7 ± 0.4	14.2 ± 2.1
	Parenchymal cells	Control		1.3 ± 0.2	0.6 ± 0.3	68.2 ± 3.5
<i>Carex sp.</i>	Coenocytes	<i>Meloidogyne kralli</i>	female	4.1 ± 0.5	5.0 ± 0.4	26.4 ± 3.5
	Parenchymal cells	Control		2.0 ± 0.4	1.4 ± 0.4	68.0 ± 2.4

wall ingrowths in food cells can not be explained as a result only of intensive ingestion of nutrients by the nematode. For example, *Meloidoderita kirjanovae* induces relatively large syncytia without wall ingrowths in roots of *Mentha longifolia* (Subbotin & Chizhov, 1986). Analysis of literature and our own results showed that all species of cyst nematodes induced syncytia with wall ingrowths. We also observed a well developed wall labyrinth in syncytia induced by *Punctodera punctata* in the roots of *Poa annua*. However, in some cases cyst nematodes were not able to induce modified cells containing wall ingrowths. The thickness of the wall labyrinth as well as metabolic activity of modified cells are dependent on the suitability of the plant as a host. In resistant plants or cultivars ingrowths are not formed (Kim et al., 1986; Melillo et al., 1990; Subbotin et al., 1991).

Modified food cells with wall labyrinths are induced by specialized groups of nematodes. Fully developed wall ingrowths are induced in syncytia and coenocytes by cyst and root-knot nematodes respectively. These nematodes are considered as being the most evolutionary advanced groups of sedentary nematodes. Coenocytes have significantly more developed ingrowths formed along the cell perimeter than syncytial cells.

It is interesting that analysis of the distribution of sieve elements with wall ingrowths among herbaceous mono- and dicotyledons shows, that these systems are typical for evolutionary advanced taxa (Gamalei, 1985).

The pathological influence of nematodes on plant roots can extend from the feeding zone to adjacent cells. In the infected roots the hypertrophy, hyperplasia of cells and formation of abnormal xylem occurs around modified cell. The facility to change the regulatory processes in cells leading to hyperplasia of tissue and gall formation was an important stage of evolution of plant parasitism. Galls provide a pathway for nutrients from other plant organs to be directed to the feeding zone of the nematode. Large galls are induced by nematodes from the genera *Nacobbus* and

Meloidogyne.

Our analysis showed that evolution of modified cells was connected with increases in functional activity. The level of modified cell complication is generally coincident with the level of evolutionary advance of the nematode. Coenocytes should be considered as being the most highly specialized cells among known modified cells.

The constancy of pathological responses induced by sedentary plant parasitic nematodes during parasitism of plants enables the type of modified cells to be considered an important taxonomic characteristic. Luc et al., (1988) used this biological feature in their diagnosis of the genera in the family Heteroderidae. The hypothesis about different levels of evolutionary development of modified cell can be used in the systematics and analysis of the phylogenetic relations between nematodes.

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Субботин С.А. Эволюция модифицированных питающих клеток, индуцированных седентарными нематодами в корнях растений.

Резюме. Обсуждаются принципы эволюции модифицированных питающих клеток, индуцированных седентарными нематодами в корнях растений. Индуцирование модифицированных клеток следует рассматривать не только как реакцию растений на заражение, но и как результат длительной сопряженной эволюции, приведшей к наиболее сбалансированным взаимоотношениям между паразитом и хозяином и наиболее эффективному удовлетворению пищевых потребностей нематоды. Анализ строения модифицированных клеток: негипертрофированных клеток, одиночной гигантской клетки, синцитиев и ценоцитов показал, что эволюция этих клеток была связана с увеличением их функциональной активности. В основе интенсификации работы питающих клеток лежат следующие принципы: увеличение количества протопласта клетки, увеличение количества и полимеризация органелл и интенсификация зоны контакта клеточной стенки и протоплазмы. Уровень усложнения модифицированных клеток в общих чертах соответствует уровню эволюционной продвинутости нематод. Ценоциты следует рассматривать как наиболее специализированные из известных модифицированных клеток. Гипотезу о различных уровнях эволюционного развития модифицированных клеток можно использовать в систематике и анализе филогенетических отношений среди нематод.
