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**DIFFERENT APPROACHES TO AND RECENT DEVELOPMENTS  
IN THE SYSTEMATICS AND CO-EVOLUTION  
OF THE FAMILY HETERODERIDAE (NEMATODA:TYLENCHIDA)  
WITH HOST PLANTS**

Rapid development of the systematics of plant parasitic nematodes of the family *Heteroderidae* (Filipjev et Sch. Stekhoven, 1941) Skarbilo-vich, 1947 (heteroderids, cyst and cystoid nematodes) has obviously been greatly stimulated by the presence of several major pathogens of agricultural crops in this group. Among them, the yellow and pale potato cyst nematodes (*Globodera rostochiensis*, *G. pallida*) are regarded as quarantine pests of potato and tomato on all continents. The cereal cyst nematode (*Biddera avenae*) is widespread in many countries as a harmful pest of wheat, barley and oats. In the USA, Japan, as well as in the Far East of the USSR, the soybean cyst nematode (*Heterodera glycines*) presents a serious problem to farmers. The sugar beet (*H. schachtii*) and cabbage cyst nematodes (*H. cruciferae*) have been known for more than a century in Europe and are also spreading elsewhere. Local problems arise because crops are attacked by the carrot cyst nematode (*H. carotae*), pea cyst nematode (*H. goettingiana*), clover cyst nematode (*H. trifolii*), lucerne cyst nematode (*H. medicaginis*), sugar cane cyst nematode (*H. sacchari*), rice cyst nematode (*H. oryzae*), corn cyst nematode (*H. zaeae*), tobacco cyst nematode (*Globodera tabacum*), and several others. The ficus and cactus cyst nematodes (*Heterodera fici*, *Cactodera cacti*) may present a problem in growing ornamentals. Other cyst and cystoid nematode species are parasitizing roots of many plants, however, the economic significance of most of them is not yet well recognized.

The number of hitherto known heteroderid species approximates a hundred. Descriptions of species and even genera new to science are currently being published each year. Not all species described are commonly recognized as valid, and some of them need redescription. Several species are so closely related that their morphological features are overlapping. The range of the cyst and cystoid nematode family has remained a matter of many discussions. Contrasting approaches to classification and general instability of systematics contribute to difficulties in the identification of species (Baldwin, 1989).

Our objective is to give a brief review of several approaches to the heteroderid taxonomy. A comprehensive historical review of taxonomic changes in the group has been presented by Siddiqi (1986). Further, we shall try to explain our hypothesis on co-evolution of cyst nematodes with their host plants (Кралль, Кралль, 1970; 1978; 1979; Кралль, 1989; Krall, 1987; Krall, Krall, 1983) and to compare the results of our studies with the cladistic analysis of the phylogeny of this group presented by Wouts (1985).

First steps to classify cyst and cystoid nematodes have been made using their morphological characteristics only. These investigations were started using light microscopy, but in the last two decades scanning electron microscopy has greatly enlarged the possibilities of morphology



also in studying cyst nematodes. No review of numerous morphological and taxonomic papers will be given here.

Behrens (1975) and Mulvey and Stone (1976) have divided the complex group of the genus *Heterodera* into three separate genera: *Heterodera*, *Globodera* and *Punctodera*. The heteroderid family has been greatly enlarged by Wouts and Sher (Wouts, 1973a, b, c; Wouts and Sher, 1971). They have presented the first detailed revision of heteroderids. Since then the family includes also species lacking the cyst stage.

Numerous authors have contributed to the taxonomy of the group and different approaches to the matter have appeared. Thus, information on the heteroderid karyotype has been used to explain relations of sibling species in which polyploidy occurs. Triantaphyllou (1970) has established three lines of parthenogenetic evolution in the genus *Heterodera*. Unfortunately, the basic chromosome number ( $n=9$  in most cases) in the heteroderid family is extremely similar and thus the karyotype may not serve as a basis for establishing a phylogenetic classification of this group as a whole.

Numerous investigations have been published on chemotaxonomy of heteroderids. The study of specific proteins might contribute to better understanding of the relationships between species and pathotypes of potato cyst nematodes and several others.

The principles of ecological morphology used by Paramonov (Парамонов, 1967) in studying phylogenetic relationships in higher taxonomic groups of plant nematodes and especially in the order *Tylenchida*, are considered generally valid also in the case of cyst and cystoid nematodes. However, a high degree of specialization accompanied by the acquisition of convergent morphological adaptations for inhabiting root tissues, and general simplification of the morphology in females due to parasitism limit the possibilities of establishing phylogenetic relations using Paramonov's approach only. Thus, in adult females, the reduction of most organs except the reproductive ones greatly restricts the phylogenetic significance of the morphological approach. Because of all that, Tchizhov and Berezina (Чижов, Березина, 1988) succeeded in differentiating several heteroderid genera, studying the morphology of the female genital tract. Thus, the genus *Bidera* proposed by Krall and Krall (1978) mainly on the grounds of the phylogenetic conclusions was accepted by them on the basis of the morphological features of the preuterine gland which proved to be clearly different in *Bidera* from those of the closely related genus *Heterodera* sensu strictu.

Computer-assisted phylogenetic analysis of heteroderids was started by Baldwin (1989) using operational taxonomic units (OTUs) that roughly correspond to the genera. Besides the morphology of adults and juveniles, the most promising characters for computer-assisted identification of the *Heteroderinae* subfamily are thought to be the locality, host and habitat of the species as well as host response to the invasion determined by the hand section of the attacked roots. The cyst and cystoid nematodes induce in the roots either a single uninucleate giant cell (*Meloidodera*, *Hylonema*, *Sarisodera*, *Rhizonema*, *Bellodera*) or multinucleate syncytium (*Atalodera*, *Sherodera*, *Thecavermiculatus*, *Heterodera*, *Bidera*, *Cactodera*, *Globodera*, *Punctodera*, *Afenestrata*) which may be diminutive in the genus *Verutus*. This response seems to be determined by the nematode rather than the host (Baldwin, 1989; Luc, 1989). The including of several readily obtainable geographical, ecological and pathomorphological data undoubtedly leads to easier identification of species than the use of morphological features only. However, such an approach to the phylogenetic analysis of heteroderids suggested by Baldwin and Schouest (Baldwin, 1989) has not yet become available to us.



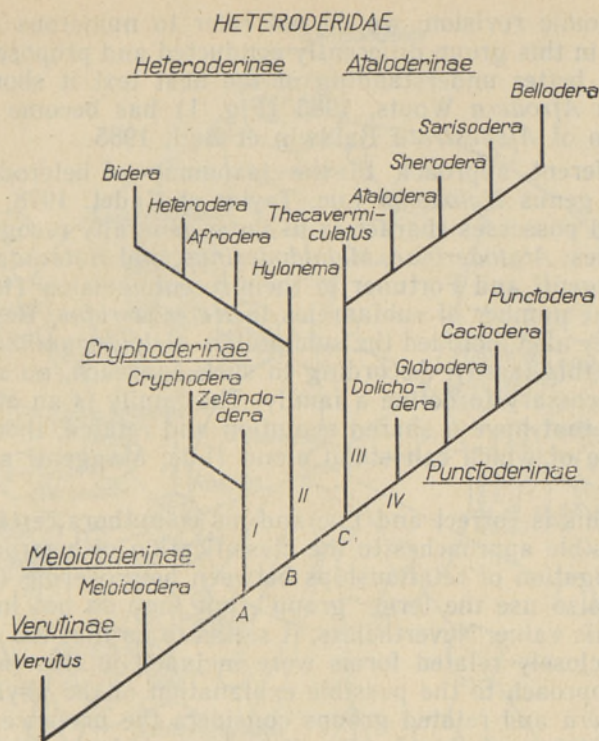


Fig. 1. Phylogenetic tree of the subfamilies and genera of the family *Heteroderidae* (after Wouts, 1985).

Ferris (1985) has used the cladistic approach in her studies on phylogeny of heteroderid nematodes. Using eight morphological characters, Ferris presented a cladogram, where *Meloidodera* was considered the most primitive genus and *Punctodera* the most developed within the ten genera investigated. We cannot agree with Ferris in considering the group of "*Heterodera avenae*" the most primitive one among cyst-forming species of heteroderids. All species of the "*avenae*" group (*Bidera* spp.) belong without any exception to the parasites of grasses, i. e. a highly specialized plant order, and they are thought to be highly specialized, too (see below). Baldwin has more recently (1986) critically revised this approach and reviewed the phylogeny of heteroderids.

In his phylogenetic classification of the family *Heteroderidae*, Wouts (1985) constructed a cladogram of the family with six branches, each of them corresponding to a subfamily (*Verutinae*, *Meloidoderinae*, *Cryphoderinae*, *Heteroderinae*, *Ataloderinae*, *Punctoderinae*) which included 17 valid genera (Fig. 1). Some authors, Krall and Krall (Кралль, Кралль, 1978) among them, have treated the subfamilies of heteroderids at the family level. At present we consider this premature and reject it. Further investigations are needed to specify the status of the species at subfamily or family levels. In this paper, the subfamilies presented by Wouts are accepted, however. According to Wouts, the heteroderid family is considered in a wide sense and so it includes cyst-forming genera as well as many closely related groups which, however, lack the cyst stage.

Since the revision by Wouts, three new genera have been proposed: *Camelodera* Krall, Schagalina et Ivanova, 1988 (*Ataloderinae*), *Brevicephalodera* Kaushal et Swarup, 1988, and *Ekphymatodera* Baldwin, Bernard et Mundo-Ocampo, 1989 (*Heteroderinae*). As the object of this paper



is not a taxonomic revision, we do not refer to numerous replacements and synonyms in this group differently conducted and proposed by various authors. For a better understanding of the next text it should be noted that the genus *Afrodera* Wouts, 1985 (Fig. 1) has become an objective junior synonym of *Afenestrata* Baldwin et Bell, 1985.

A very different approach to the taxonomy of heteroderids is also available. The genus *Hylonema* Luc, Taylor et Cadet, 1978, is extremely remarkable and possesses characters of three generally recognized heteroderid subfamilies: *Ataloderinae*, *Meloidoderinae*, and *Heteroderinae*. Therefore, Luc, Maggenti and Fortuner in their recent revision (1988) drastically reduced the number of subfamilies in *Heteroderidae*. Besides *Heteroderinae* s. l. they also included the subfamilies *Meloidogyninae* and *Nacoboderinae* into this family. According to such approach, no single unique character is necessary to define a family. The family is an assemblage of related genera that have a shared evolution and related, though differing characters none of which can stand alone (Luc, Maggenti and Fortuner, 1988).

No doubt, this is correct and Luc and his co-authors certainly indicate one of the possible approaches to the classification of heteroderid genera. In their investigation of relationships between heteroderine (s. l.) genera, these authors also use the term "group", but they do not intend to give it any taxonomic value. Nevertheless, it seems to us that too different and obviously not closely related forms were included in this family.

Our own approach to the possible explanation of the phylogeny of the genus *Heterodera* and related groups considers the presence of evolution in the feeding types of this family. It is beyond doubt that the trophic adaptation of cyst nematodes has occurred to enable them to survive in specific conditions prevailing in the roots of their host plants. Since cyst nematodes are a group of highly specialized parasites, their relationships with the host plants must be balanced very exactly physiologically (trophic relations) as well as genetically. Every disturbance of the well-balanced host-parasite system during the evolutionary development of higher plants might consequently lead to the manifestation of adaptive radiation in cyst nematodes.

It seems very unlikely that the presently existing groups of cyst nematodes which are characterized by wide ranges of host plants could have evolved from highly specialized ancestors. Regarding specialization as a restriction to adaptation potentiality one must consider that preconditions for further evolution of highly specialized cyst nematodes are apparently far more limited than those of the less specialized groups.

Krall and Krall (Кралль, Кралль, 1978) have demonstrated that the comparative ecological approach must be considered of prime importance in the studies of the evolution of cyst nematodes. Thus, they have proposed a hypothesis of co-evolution of heteroderids with their host plants. This hypothesis has been checked and developed by Stone (1979, 1985). In the present paper more detailed information is presented on trophic specialization of cyst nematodes. We have used for our analyses the concepts on the phylogeny of flowering plants as given by Grossgeim (Гроссгейм, 1945) and Takhtadzhyan (Тахтаджян, 1970).

Grossgeim states that the evolution of flowering plants belonging to *Angiospermae* can be viewed in three stages of development (Fig. 2). In their earlier papers, Krall and Krall have demonstrated that species of cyst nematodes parasitizing on angiosperms which are at lower stages of their phylogenetic development are characterized by a wider host plant range, i. e. by a lower degree of trophic specialization than those species which parasitize on plants at higher stages of their phylogenetic development and which are characterized by a more limited host plant range.







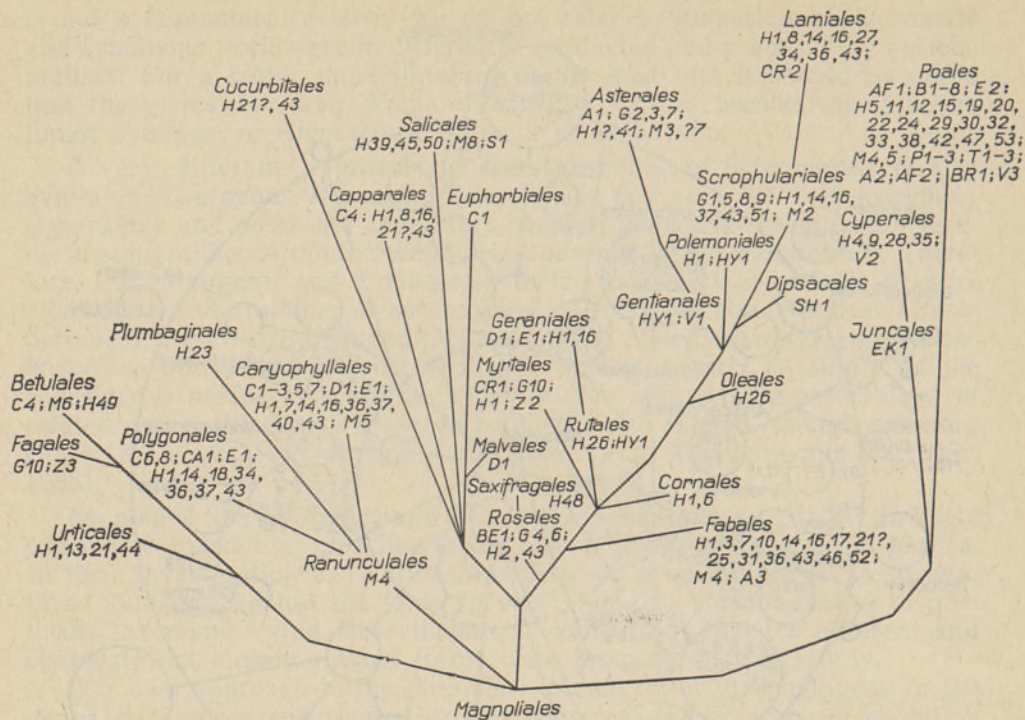


Fig. 3. Host specificity of the species of *Heteroderidae* with respect to plant groups in accordance with phylogenetic relations of the orders of angiosperms as outlined by Takhtadzhyan (1970). After Krall, 1989 (emend.).

We have checked our statements using the phylogenetic tree of the orders of angiosperms as given by Takhtadzhyan (Fig. 3). In this scheme, more primitive plant groups are situated at the bottom, and the tops of various phylogenetic branches are also (as in the outer concentric rings by Grossgeim) presented by specialized plant orders. Except for the terminology in the designation of plant orders which is somewhat different, no principal discrepancies exist in both schemes (Figs. 2 and 3). Stone (1979), using the evolutionary system of flowering plants presented by Cronquist, has come to the same conclusions regarding trophic specialization of heteroderids.

Consequently, the data of all analyses clearly indicate that cyst nematodes in general have co-evolved with their host plants. Thus, a direct correlation has been established between the character of the host ranges, i. e. the homo- or heteroxenity, and their position in the natural systems of the angiosperms carefully studied by botanists. According to this statement, the phylogenetic relationships of host plants must similarly reflect also the phylogeny of cyst nematodes parasitizing on them.

We assume that the phylogenetic classification of heteroderids based on the cladistic method of analysis recently presented by Wouts (1985) may be regarded as the most promising morphological approach to explain relationships within this group (Fig. 1). We shall make an attempt to comment upon this classification with respect to our hypothesis of co-evolution of cyst-forming heteroderids with their host plants.

According to Wouts, the hypothetical heteroderid ancestor (as supposed also by Paramonov and several others) developed from a nematode that resembled some forms in the family *Hoplolaimidae*. The genus *Verutus* is considered the most primitive form within heteroderids (Fig. 1). The genus *Meloidodera* developed by a reduction in vulval size. Later, Wouts



(1985) suggested four evolutionary lines in the phylogenetic tree of heteroderids: 1) a posterior shift of the vulva and the formation of vulval lips gave rise to the genera *Zelandodera* and *Cryphodera*; 2) changes in the lip configuration of the second-stage juvenile gave rise to the genera *Hylonema*, *Afenestrata*, *Heterodera* and *Bidera*; 3) changes in the composition of the female cuticle resulted in the genera *Thecavermiculatus*, *Atalodera*, *Sherodera*, *Sarisodera* and *Bellodera*; and 4) a reduction on vulval slit size led to the development of the genera *Dolichodera*, *Globodera*, *Cactodera* and *Punctodera*.

In the phylogenetic lines of *Heteroderinae* as well as *Punctoderinae* good fitness of the morphological evolution with the regularities in the host specificity with respect to plant groups in accordance with their phylogenetic relations has been established in the systems by Wouts and ourselves. The genus *Hylonema* possessing characters of several subfamilies may be placed only tentatively in the heteroderine branch (Fig. 1, II) of the phylogenetic tree, however. It will apparently continue to be a subject of discussions. But we fully agree with Wouts that the process of cyst forming might convergently occur in the evolution of several not closely related groups. As to the same heteroderine branch we also fully agree with the placement of the genus *Bidera* at the top of it. This genus has been exclusively specialized in parasitism on grasses (*Glumiflorae* in Fig. 2, and *Poales* in Fig. 3). Further, we are of the opinion that the genus *Ehippiodera* synonymized with *Bidera* by Wouts is clearly distinctive from it and should therefore be re-established as a group, phylogenetically derived from a common ancestor with *Bidera*. The morphological adaptations of *Ehippiodera* are remarkable. This group apparently has evolved in the extremely dry climate of Asian deserts. The validity of the genus *Ehippiodera* (but not *Bidera*) has also been supported by Siddiqi (1986). As indicated by Schagalina and Krall (Шаралина, Кралль, 1981), after the exclusion of *Ehippiodera*, the genus *Bidera* remained much more homogeneous.

The phylogenetic branches of *Ataloderinae* and *Punctoderinae* (Fig. 1, III, IV) are thought to have evolved from a common ancestor (Fig. 1, C). The development of an extra basal layer, the so-called *D*-layer in the cuticle of the females is characteristic of these branches. This layer is always absent in the lower groups of heteroderids. In the ataloderine line of evolution the thickening of the female cuticle also takes place, but the cuticle always remains elastic and no cyst stage occurs. Krall, Schagalina and Ivanova (Кралль et al., 1988) have observed this phenomenon in the genus *Camelodera* described by these authors from the Kara-Kum desert in Soviet Central Asia. This genus should be placed close to *Bellodera* at the top of the ataloderine branch (Fig. 1, III). Simultaneously, the finding of the genus *Camelodera* is the first record of the subfamily *Ataloderinae* outside America, indicating that the ancestors of the subfamily could have been distributed also in the Old World.

As a discrepancy with Wouts, however, the genus *Thecavermiculatus* (Fig. 1, III) parasitizing on grasses may not be considered the most primitive one in ataloderines from the viewpoint of co-evolutionary relationships. It is impossible to understand that a genus which has obviously been evolved with a group of the most specialized hosts gave rise to forms that attack plants on a lower, viz. second or complicated stage of the phylogenetic development. On the other hand, we fully agree with placing exclusively grass-attacking *Bidera* (*Heteroderinae*) as well as *Punctodera* (*Punctoderinae*) at the tops of the respective branches of the phylogenetic tree (Fig. 1, II, IV). As we can see (Figs. 2 and 3), sixteen species of the genus *Heterodera* and several representatives of some other genera also attack grasses. All these species are highly specialized as



well and no case of their parasitizing on any other plant group has been recorded so far.

In the phylogenetic branch of *Punctoderinae* (Fig. 1, IV), the genus *Dolichodera* has been thought to be the most primitive one. Unfortunately, the host plants of this nematode group are unknown and so we cannot check this postulate from our viewpoint. We do not agree with Wouts in deriving *Cactodera* from *Globodera*. The former genus has been proposed by Krall and Krall in 1978 considering the lemon-shaped body of females and some other features. We suppose that the lemon-shaped body in heteroderids should be regarded as more primitive than the spherical body shape in females like in *Globodera*. Thus the loss of vulval cone in the evolution is regarded by us as a secondary feature. No doubt, both genera mentioned above are closely related.

As expected, the most primitive phylogenetic lines of heteroderids and especially the subfamilies *Meloidoderinae* and *Cryphoderinae* express a great variability in their host-parasite relations. Two species of lower heteroderids, viz. *Meloidodera floridensis* and *Zelandodera podocarpi* are parasitizing on gymnosperms which are not attacked by any species belonging to the higher groups of this family. We cannot explain the single exception from this rule — the parasitism of *Rhizonema* (*Sarisdodera*) *sequoiae* of the subfamily *Ataloderinae* on gymnosperms, either. It may be caused by secondary passage of rhizonemas from angiosperms to gymnosperms or may be a result of the paucity of our knowledge on many genera of heteroderids. We suppose that such unexpected findings as the establishment of an ataloderine genus (*Camelodera*) in Asia clearly demonstrate that more relict forms of some rare groups of heteroderids might be established further. In Figs. 2 and 3 data are presented on host specificity of various heteroderid species with respect to plant groups in accordance with phylogenetic relations of the orders of angiosperms as outlined by Grossgeim and Takhtadzhyan, respectively. The designations for plant orders are partially different on the schemes presented by these botanists. The main differences are presented here as follows, whereas the designations given by Takhtadzhyan are in parentheses:

*Centrospermae* and *Cactales* (*Caryophyllales*), *Fagales* (*Fagales* and *Betulales*), *Glumiflorae* (*Poales*), *Tubiflorae* (*Scrophulariales* and *Polemoniales*), *Contortae* (*Gentianales*), *Ligustrales* (*Oleales*), *Tricoccae* (*Euphorbiales*), *Umbelliflorae* (*Cornales*), *Rubiales* (*Dipsacales*), *Anacardiales* (*Rutales*), *Leguminosales* (*Fabales*), *Rhoedales* (*Capparales*), *Campanulales* (*Asterales*), *Ranales* (*Ranunculales*).

In this paper only general trends in the phylogenetic development of the heteroderid nematodes could be presented. No doubt, more detailed analysis of various genera using several approaches would lead to a better understanding of the evolutionary process within this economically important nematode family.

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#### A list of species of the family *Heteroderidae* with abbreviations in Figs. 2 and 3

Subfamily *Verutinae* Esser, 1981. Genus *Verutus* Esser, 1981 (V):  
V 1 — *V. volvoingentis* Esser, 1981; V 2 — *V. californius* Baldwin, Bernard et Mundo-Ocampo, 1989; V 3 — *V. mesoangustus* Minagawa, 1986.



Subfamily *Meloidoderinae* Golden, 1971. Genus *Meloidodera* Chitwood, Hannon et Esser, 1956 (M): M 1 — *M. floridensis* Chitwood, Hannon et Esser, 1956\*; M 2 — *M. armeniaca* Pogosyan, 1960; M 3 — *M. belli* Wouts, 1973; M 4 — *M. charis* Hopper, 1960; M 5 — *M. eurutyla* Bernard, 1981; M 6 — *M. sikhotealiniensis* Eroshenko, 1978; M 7 — *M. tadshikistanica* Kirjanova et Ivanova, 1966; M 8 — *M. tianschanica* Ivanova et Krall, 1985.

Subfamily *Cryphoderinae* Coomans, 1978. Genus *Cryphodera* Colbran, 1966 (CR): CR 1 — *C. eucalypti* Colbran, 1966; CR 2 — *C. kalesari* Bajaj, Walia, Dabur et Bhatti, 1989. Genus *Zelandodera* Wouts, 1973 (Z): Z 1 — *Z. podocarpus* Wouts, 1973\*; Z 2 — *Z. coxi* Wouts, 1973; Z 3 — *Z. nothopagi* Wouts, 1973.

Subfamily *Heteroderinae* Filipjev et Sch. Stekhoven, 1941. Genus *Hylonema* Luc, Taylor et Cadet, 1978 (HY): HY 1 — *H. ivoriensis* Luc, Taylor et Cadet, 1978. Genus *Ekphymatodera* Baldwin, Bernard et Mundo-Ocampo, 1989 (EK): EK 1 — *E. thomasoni* Baldwin, Bernard et Mundo-Ocampo, 1989. Genus *Afenestrata* Baldwin et Bell, 1985 (AF): AF 1 — *A. africana* (Luc, Germani et Netscher, 1973) Baldwin et Bell, 1985; AF 2 — *A. sacchari* Kaushal et Swarup, 1988. Genus *Brevicephalodera* Kaushal et Swarup, 1988 (BR): BR 1 — *B. bamboosi* Kaushal et Swarup, 1988. Genus *Heterodera* Schmidt, 1871 (H): H 1 — *H. schachtii* Schmidt, 1871; H 2 — *H. amygdali* Kirjanova et Ivanova, 1975; H 3 — *H. cajani* Koshy, 1967; H 4 — *H. canadensis* Mulvey, 1979; H 5 — *H. cardiolata* Kirjanova et Ivanova, 1969; H 6 — *H. carotae* Jones, 1950; H 7 — *H. ciceri* Vovlas, Greco et di Vito, 1985; H 8 — *H. cruciferae* Franklin, 1945; H 9 — *H. cyperi* Golden, Rau et Cobb, 1962; H 10 — *H. daverii* Wouts et Sturhan, 1978; H 11 — *H. delvii* Jairajpuri, Khan, Setty et Govindu, 1979; H 12 — *H. elachista* Oshima, 1974; H 13 — *H. fici* Kirjanova, 1954; H 14 — *H. galeopsidis* Goffart, 1936; H 15 — *H. gambiensis* Merny et Netscher, 1976; H 16 — *H. glycines* Ichinohe, 1952; H 17 — *H. goettigiana* Liebscher, 1892; H 18 — *H. graduni* Kirjanova, 1971; H 19 — *H. graminis* Stynes, 1971; H 20 — *H. graminophila* Golden et Birchfield, 1972; H 21 — *H. humuli* Filipjev, 1934; H 22 — *H. leuceilyma* Di Edwardo et Perry, 1964; H 23 — *H. limonii* Cooper, 1955; H 24 — *H. longicolla* Golden et Dickerson, 1973; H 25 — *H. medicaginis* Kirjanova, 1971; H 26 — *H. mediterranea* Vovlas, Inserra et Stone, 1981; H 27 — *H. menthae* Kirjanova et Narbaev, 1977; H 28 — *H. moths* Khan et Husain, 1965; H 29 — *H. oryzae* Luc et Berdon Brizuela, 1961; H 30 — *H. oryzicola* Rao et Jayaprakash, 1978; H 31 — *H. oxiana* Kirjanova, 1962; H 32 — *H. pakistanensis* Maqbool et Shahina, 1986; H 33 — *H. phragmitidis* Kazachenko, 1986; H 34 — *H. polygoni* Cooper, 1955; H 35 — *H. raskii* Basnet et Jayaprakash, 1984; H 36 — *H. rosii* Duggan et Brennan, 1966; H 37 — *H. rumicis* Pogosyan, 1961; H 38 — *H. sacchari* Luc et Merny, 1963; H 39 — *H. salixophila* Kirjanova, 1969; H 40 — *H. schleranthii* Kaktina, 1957; H 41 — *H. sonchophila* Kirjanova, Krall et Krall, 1976; H 42 — *H. sorghi* Jain, Sethi, Swarup et Srivastava, 1982; H 43 — *H. trifolii* Goffart, 1932; H 44 — *H. urticae* Cooper, 1955; H 45 — *H. uzbekistanica* Narbaev, 1980; H 46 — *H. vigni* Edward et Misra, 1968; H 47 — *H. zae* Koshy, Swarup et Sethi, 1971; H 48 — *H. bergeniae* Maqbool et Shahina, 1988; H 49 — *H. kirjanovae* Narbaev, 1988; H 50 — *H. turangae* Narbaev, 1988; H 51 — *H. plantaginis* Narbaev et Sidikov, 1987; H 52 — *H. lespedezae* Golden et Cobb, 1963; H 53 — *H. cynodontis* Shahina et Maqbool, 1989. Genus *Bidera* Krall et Krall, 1978 (B): B 1 — *B. avenae* (Wollenweber, 1924) Krall et Krall, 1978; B 2 — *B. arenaria* (Cooper, 1955) Krall et Krall, 1978; B 3 — *B. bifenestra* (Cooper, 1955) Krall et Krall, 1978; B 4 — *B. filipjevi* Madzhidov, 1981; B 5 — *B. hordecalis* (Andersson, 1975) Krall et Krall, 1978; B 6 — *B. iri* (Mathews, 1971)



Krall et Krall, 1978; *B 7* — *B. mani* (Mathews, 1971) Krall et Krall, 1978; *B 8* — *B. ustynovi* (Kirjanova, 1969) Krall et Krall, 1978. Genus *Ephippiodera* Schagalina et Krall, 1981 (*E*): *E 1* — *E. turcomanica* (Kirjanova et Schagalina, 1965) Schagalina et Krall, 1981; *E 2* — *E. latipons* (Franklin, 1969) Schagalina et Krall, 1981.

Subfamily *Ataloderinae* Wouts, 1973. Genus *Thecavermiculatus* Robbins, 1978 (*T*): *T 1* — *T. gracilancea* Robbins, 1978; *T 2* — *T. carolynae* Robbins, 1978; *T 3* — *T. crassicrustata* Bernard, 1981. Genus *Atalodera* Wouts et Sher, 1971 (*A*): *A 1* — *A. ucri* Wouts et Sher, 1971; *A 2* — *A. festucae* Baldwin, Bernard et Mundo-Ocampo, 1989; *A 3* — *A. trilineata* Baldwin, Bernard et Mundo-Ocampo, 1989. Genus *Sherodera* Wouts, 1973 (*SH*): *SH 1* — *S. loniceriae* Wouts, 1973. Genus *Sarisodera* Wouts et Sher, 1971 (*S*): *S 1* — *S. hydrophila* Wouts et Sher, 1971; *S 2* — *S. sequoiae* (Cid del Prado Vera, Lownsbery, Magenti, 1983) Wouts, 1985\*. Genus *Bellodera* Wouts, 1985 (*BE*): *BE 1* — *B. utahensis* (Baldwin, Mundo-Ocampo et Othman, 1983) Wouts, 1985. Genus *Camelodera* Krall, Schagalina et Ivanova, 1988 (*CA*): *CA 1* — *C. eremophila* Krall, Schagalina et Ivanova, 1988.

Subfamily *Punctoderinae* Krall et Krall, 1978. Genus *Dolichodera* Mulvey et Ebsary, 1978 (*D*): *D 1* — *D. andinus* (Golden, France, Jatala et Astogaza, 1983) Wouts, 1985. Genus *Globodera* (Skarbilovich, 1959) Behrens, 1975 (*G*): *G 1* — *G. rostochiensis* (Wollenweber, 1923) Behrens, 1975; *G 2* — *G. achilleae* (Golden et Klindic, 1973) Behrens, 1975; *G 3* — *G. artemisiae* (Eroshenko et Kazachenko, 1972) Behrens, 1975; *G 4* — *G. chaubattia* (Gupta et Edward, 1973) Wouts, 1984; *G 5* — *G. leptonepia* (Cobb et Taylor, 1953) Behrens, 1975; *G 6* — *G. mali* (Kirjanova et Borisenko, 1975) Behrens, 1975; *G 7* — *G. millefolii* (Kirjanova et Krall, 1965) Behrens, 1975; *G 8* — *G. pallida* (Stone, 1973) Behrens, 1975; *G 9* — *G. tabacum* (Lownsbery et Lownsbery, 1954) Behrens, 1975; *G 10* — *G. zelandica* Wouts, 1984. Genus *Cactodera* Krall et Krall, 1978 (*C*): *C 1* — *C. cacti* (Filipjev et Sch. Stekhoven, 1941) Krall et Krall, 1978; *C 2* — *C. acnidae* (Schuster et Brezina, 1979) Wouts, 1985; *C 3* — *C. amaranthi* (Stoyanov, 1972) Krall et Krall, 1978; *C 4* — *C. betulae* (Hirschmann et Riggs, 1969) Krall et Krall, 1978; *C 5* — *C. eremica* Baldwin et Bell, 1985; *C 6* — *C. estonica* (Kirjanova et Krall, 1963) Krall et Krall, 1978; *C 7* — *C. thornei* (Golden et Raski, 1977) Wouts, 1985; *C 8* — *C. weissii* (Steiner, 1942) Krall et Krall, 1978. Genus *Punctodera* Mulvey et Stone, 1976 (*P*): *P 1* — *P. punctata* (Thorne, 1928) Mulvey et Stone, 1976; *P 2* — *P. chaltoensis* Stone, Sosa Moss et Mulvey, 1976; *P 3* — *P. matadorenris* Mulvey et Stone, 1976.

Note. Only species with established host plants have been included in this list. *Meloidodera floridensis* (*M 1*), *Zelandodera podocarpi* (*Z 1*) and *Sarisodera sequoiae* (*S 2*) are marked with an asterisk (\*) because they are parasitizing on gymnosperms and thus could not be shown in Figs. 2 and 3 which demonstrate trophic relations and supposed co-evolution of nematodes with angiosperms only.

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ERINEVAD LÄHENEMISVIISID JA UEMAD SEISUKOHAD  
SUGUKONNA *HETERODERIDAE* (*NEMATODA:TYLENCHIDA*) SÜSTEMAATIKA  
NING PEREMEESTAIMEDEGA KOEVOLUTSIOONI UURIMISEL

On antud lühikärgelise taimedel parasiteerivate nematoodide sugukonna *Heteroderidae* süstemaatika arenemisest viimasel aastakümnel. Põhjalikumalt on käsitletud heteroderiidide koevolutsiooni peremeestaimedega ning kriitiliselt analüüsitud tulemusi, mis on saadud nematoodide fülogeneesi selgitamisel erinevate meetoditega.

Эйно КРАЛЛЬ

РАЗЛИЧНЫЕ ПОДХОДЫ И НОВЕЙШИЕ ДОСТИЖЕНИЯ В ОБЛАСТИ  
ИЗУЧЕНИЯ СИСТЕМАТИКИ И СОПРЯЖЕННОЙ ЭВОЛЮЦИИ СЕМЕЙСТВА  
*HETERODERIDAE* (*NEMATODA:TYLENCHIDA*)  
С РАСТЕНИЯМИ-ХОЗЯЕВАМИ

Приведен краткий обзор развития систематики семейства фитопаразитических нематод *Heteroderidae* за последнее десятилетие. Более подробно рассматриваются вопросы сопряженной эволюции гетеродерид с их растениями-хозяевами и критическому анализу подвергаются результаты исследований, полученные при выяснении филогении нематод с применением различных методов.