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Relationship of Different Species of *Heterodera* with Taxonomic Grouping of Host Plants

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Abstract: ***Studies on the affiliation of 62 species of Heterodera to taxonomic groups of host plantsrevealed that thirty heteroderids parasitized only monocotyledons and out of these 17 were monophagous. Thirteen species showed monophagy in dicotyledons. Heteroderid groups (clades) revealed that Avenae and Sacchari groups intimately affiliated with monocots and perhaps co-evolved with them. Sacchari group do not feed on dicots. Schachtii group co-evolved with dicots. Humuli group was associated with plants of wide taxonomic range. Cyperi group parasitized plants largely from monocots and species from Goettingiana group feed on plants of both dicots and monocots. The species affiliation with monocots was not restricted at family level but continued upto subfamily and tribe levels.Strong relationships in dicots was noticed with Fabaceae, Brassicaceae and Chenopodiaceae. Races of some species of Heterodera showed close association with certain genera.***

Keywords: *Heterodera*, host plants, taxonomic affiliation, monocotyledons, dicotyledons, lignosae, herbaceae, co-evolution, monophagous, polyphagous, calyciferae, corolliferae, glumiflorae.

1. Introduction

The genus *Heterodera* contains at least 80 species (Subbotin *et.al.*, 2010) which inflict moderate to severe yield reduction in agricultural crops. In certain species their occurrence is limited to endemic areas, whereas in others they are globally distributed. Host plants of these species differ greatly but the nature of damage is quite similar. The juvenile (J2) invades the host roots, by penetrating in cortex, endodermis or vascular parenchyma. Feeding in root cell results in the formation syncytium.Syncytia contain many plastids, mitochondria, ribosomes, increased rough endoplasmic reticulum and enlarged lobed nuclei (Nemaplex, 2013). Syncytia undergo repeated S- phase endoreduplication without meiosis. Once J2 established at feeding sites, the juveniles feed and develop as endoparasites and remain there. After full development males leave the roots, while females remain in the roots to feed and develop. They are biotrophic pathogens and considered as cell grazers(Nemaplex, 2013). In general, plant growth parameters are adversely affected resulting in poor yield.

Thorsteinson (1960) propounded that host preference in phytophagous insects to host plants follows certain taxonomic groups. Rathore and Lal (1998) observed the same while studying the host range of pod borer, *Maruca vitrata*, which is restricted to plants belonging to Leguminous group only. Further, Rathore and Tiwari (2014) reported that whitefly, *Bemisia tabaci*, preferred plants of certain groups and in some cases evolutionary lineages were evident. Recent studies of Rathore and Ali (2014) on relationships of root-knot nematode, *Meloidogyne incognita*, to its host species explicitly revealed that it prefers dicotyledonous plants and six phylogenetic lineages were observed. Viewing the vast number of species of *Heterodera*, varied host range and similar feeding habits prompted to study the relationships of nematode species vis-à-vis to host preference.

2. Materials and Methods

Plant classification of Hutchinson (1973) was adopted to studythe relationship of heteroderids to their host species. He divided Angiosperms in two subphylum, dicotyledons and monocotyledons. Dicotyledons were divided into lignosae division (fundamentally woody plants) and herbaceaedivision (fundamentally herbaceous plants). Monocotyledons were divided into three divisions viz., Calyciferae (calyx bearer-with distinct calyx and corolla), Corolliferae (calyx and corolla are more or less similar) and Glumiflorae (perianth is much reduced or represented by lodicules). Plants reported as hosts of various species of *Heterodera* were aligned with families and orders following the system of Hutchinson (1973). Groups or clades of various species of *Heterodera* formed on the basis of morphometric (Mulvey, 1979, Mulvey and Golden,1983,Handoo, 2002) and molecular studies (Rivoal *et. al*., 1993, Subbotin *et. al.*, 2000, 2001, Subboti *et. al*.(n.d.), Ma *et. al.*, 2008, Skantar *et. al.*, 2012) were also utilized for discussion. Phylogenetic relationship was discussed in general as well as with races of some species of *Heterodera.*

3. Results and Discussion

Information available on host preference of 62 species of *Heterodera* revealed that monocots were parasitized by thirty species of host plants (Table 1). Out of these, 17 species viz., *H. aucklandica, H. iri, H. pratensis, H. spinicauda* (Avenae group); *H. cyperi, H. delvii, H. elachista, H. fengi, H. hainanensis, H. koreana, H. oryzicola, H. raskii, H. sinensis* (Cyperi group); *H. Canadensis, H. cardiolata, H. longicolla* (Goettingiana group) and *H. pakistanensis*were parasitizing single plant species and can be categorized as monophagous (Table 2). On the other hand, species like *H. arenaria, H. hordecalis, H. latipons, H. mani* (Avenae group); *H. leucilyma, H. sorghi* (Sacchari group); *H. zeae* (Humuli group); *H.*

graminophila (Goettingiana group), and *H. bifenestra* and *H. gambiensis* confirmed their feeding on various genera of a single family, i.e., Poaceae and were classified as oligophagous parasite. Furthermore, *H. goldeni* of Sacchari group and *H. graminis* of Cyperi group parasitized plants of more than one family within the monocots, hence designated as polyphagous (Table 2).

Information presented in Table 2 and 3 elucidate that all the species of *Heterodera* which were found exclusive feeder on monocots were parasitizing plants from glumiflorae division only. According to Hutchinson (1973), 3 families viz., Juncaceae (Juncales), Cyperaceae (Cyperales) and Poaceae (Graminales) belong to glumiflorae division of monocots. Study revealed that 91.9% hosts parasitized were from the family Poaceae and 5.4 and 2.7% from Cyperaceae and Juncaceae, respectively. This taxonomic affinity was not restricted at family level only but continued upto subfamily levels as 62.2% host plants parasitized in Pooideae and 22.9% from Panicoideae. Strong taxonomic association was also visible at the tribe's level. Out of 15 tribes (Table 2), Hordeeae, Paniceae, Festuceae, and Andropogoneae had 16.4, 13.4, 11.9, and 10.4% host species, respectively, at their credit. Other tribes like Aveneae/Oryzeae also shared a good number of host species of *Heterodera.*

In case of polyphagous species both monocots and dicots were definitely represented by the family Poaceae except in *H. trifolii* where family Liliaceae (corolliferae) and *H. schachtii*, in addition of Poaceae, were reported from Amaryllidaceae (corolliferae) and Bromeliaceae (calyciferae)(Table 2).

Among dicots strong preference of 17 species of *Heterodera* was observed to Fabaceae; 11 to Chenopodiaceae; 10 to Brassicaceae and 9 to Caryophyllaceae and so on (Table 3). Plant species from some of the taxonomic groups were more parasitized than others further indicating greater affiliation. For example, *H. cruciferae* parasitized 86% plant species from family Brassicaceae; *H. glycines* 86.1% from Fabaceae; *H. trifolii* 40.9% from Fabaceae + 20.9% Caryophyllaceae; *H. schachtii* 32.7% from Brassicaceae + 14.9% Chenopodiaceae + 11.7% Fabaceae and *H. betae* 34% Fabaceae + 22.7 Brassicaceae (Table 3).

Krall and Krall (1978) and Stone (1979) opined that different heteroderid groups co-evolved with their hosts. Studies of phylogeneticrelationships within cyst-forming nematodes based on analysis of sequences from ITS regions of rDNA by Subbotin *et. al.* (2001) supported the above view and mentioned that different heteroderid groups co-evolved with single or closely related families of plants.Our results tend to support their findings as Avenae and Sacchari groups perhaps co-evolved with monocots.Ma *et. al.* (2008) also reported closeness of aforesaid two groups. Nevertheless, Sacchari group never parasitized dicots. Similarly, Schachtii group infested fewer plants in monocots. Subbotin *et. al.* (2001) reported that *H. cajani* parasitizes agricultural crops from Fabaceae. In our study this species besides Fabaceae infests plants of Pedaliaceae (Bignoniales). Their findings further revealed that *H. cajani* shares a common ancestor with *H. schachtii*. Therefore, Schachtii group primarily co-evolved with host plants from Fabaceae and secondarily colonized Chenopodiaceae.However,Radice *et. al.* (1988) considered *H. schachtii* and *H. glycines* as sibling species and their study on mDNA suggested that two specie diverged from common ancestor 7.3-14.8 million years ago. Successful hybridization between the two species has also been reported(Potter and Fox, 1965; Miller, 1976). Present study showed that all the species of *Heterodera* from Schachtii group showed strong affinity with Fabaceae but not necessarily with Chenopodiaceae. For example, *H. cajani, H. ciceri, H. davertii* do not feed on Chenopodiaceae (Table 3). Similarly, other species in Schachtii group parasitize host plants of several other families more than Chenopodiaceae. *H. schachtii* parasitized higher number of plants from Brassicaceae than Fabaceae and Chenopodiaceae and representatives of 27 families are also in the list of this nematode which encompasses highly diverse group of plants (Table 3).

In the present study 5 *Heterodera* species fall in Humuli group, out of these *H. fici, H. humuli* and *H. ripae* parasitize plants from Moraceae and Urticaceae families of order Urticales in dicotyledons-lignosae, while *H. zeae* feeds on Poaceae (Graminales) in monocotyledons and *H. littoralis* feeds on Chenopodiaceae (Chenopodiales) in dicotyledons-herbaceae. Subbotin*et. al.* (2001) put *H. salixophila* with Humuli group and was confirmed by Ma *et.al.* (2008). The nematode parasitizes 2 species from Salicaceae (Salicales). This group appeared to be homogenous with Urticales. Hutchinson (1973) described evolutionary lineage of plant families like Rosales—Hamamelidales—Fagales—Urticales, whereas the other lineage was Rosales—Salicales. On evolutionary scale,position of Rosales is 6^{th}, Salicales 12^{th}, Urticales 19^{th}, Chenopodiales 64^{th} and Graminales 111^{th}. Therefore, co-evolution of plant species with Humuli group + *H. salixophila* from plant taxonomic view is highly variable and full of contradiction(Table 3).

Cyperi group includes 11 species of *Heterodera*, out of these 10 exclusively feed on monocots and *H. mothi* both on monocots and dicots. However, all tend to feed on Poaceae, Cyperaceae and Juncaceae belonging to division glumiflorae of monocots. Present findings are in accordance of Subbotin*et. al.* (2001) who found *H.cyperi* and *H. oryzicola* of this group infest grass like plants.

Goettingiana group is considered oldest to the origin of genus (Subbotin *et. al.*, 2001) and consists of the species which parasitize both monocots and dicots. In this group, three species are monophagous in monocots, three in dicot-herbaceae and one in dicot-lignosae (Table 1, 3). Species *H. goettingiana, H. circeae, H.oryzae* and *H. cruciferae* were noted as polyphagous and parasitized several plants in different families. However, *H.goettingiana* and *H. circeae* showed high preference to Fabaceae;*H. oryzae* to Poaceae and *H. cruciferae* to Brassicaceae (Table 3).

As far as affiliation with taxonomic groups is concerned, it will be more relevant to search co-evolution pattern on individual species basis rather than on group (clade) basis. Monophagy is a specialization from a general feeder and in the present study 46.5% species of *Heterodera* were found monophagous, 19.4%oligophagous and rest as polyphagous.

Tendency to develop monophagy in particular with Poaceae and in general with monocots is a co-evolutionary phenomenon. The order Graminales is a climax group and perhaps developed parallel with Cyperaceae through Juncaceous stock from Liliales (Hutchinson, 1973). According to APG II system, monocots is no more a taxonomic rank instead a clade. In this clade the Poales or Graminales appearscomparatively of recent origin. Molecular study also confirmed the monophyly of the monocots. Greater preference of Heteroderids towards monocot perhaps could be because parasite preference (monophagy) and host plants are of newer origin. Development of monophagy on dicots could be at a slower pace than monocots due to their paraphyletic evolution.

Races of some heteroderids documented by Nemaplex (2014) are given in Table 4. Races of *H. avenae*are common on all the hosts except *Hordeum vulgare* which had additional races 1, 2, Dutch and Pathotype A. Five *Triticum* specieswere parasitized by Algeria and Syria races only. *Secale cereale* got infestation from three different races viz., Seville, Teruel and Toledo. No host plants other than from Poaceae and not all the plants in Poaceae were parasitized indicating strong affiliation to certain genera of Poaceae. *H. filipjevi* had one race specific to *Avena*, *Hordeum and Triticum* species. *H.glycines* embraced several races which parasitized *Glycine max* and shared Race 2, Race 3 and Race 5 *with Phaseolus vulgaris*.*P.vulgaris*had two additional races HG Type 0 and Race 14. *H.latipons* had only Syria race which parasitized all the host plants. The foregoing description again depicts taxonomic affiliation of races with their host plants as *H. avenae* races were associated only with Poaceae followed by *H. filipjevi* and *H. latipons*. Similarly, *H. glycines* races were parasitizing dicotyledons only.

It is generally believed that climatic conditions affect the host preference due to its influence on plant and parasite growth and development. Climatic conditions may influence the degree of damage or escape but not the affinity to the host. For example, *H. avenae*, a polyphagous heteroderid, known as major production constraint of cereals in Europe (Rivoal and Cook 1993), Australia (Brown 1984), India (Khan *et. al.* 1990), North America (Miller 1986) and in several countries of North Africa and West Asia (Al-Yahya *et. al.* 1998). In spite of its wide distribution, tolerating varied climates and exposure to various habitats, *H. avenae* never left monocots and 75% host plants are from Poaceae (Graminales)and climate of various eco-zones could not alter its preference to the preferred group or taxonomic groupings and this supports the view of Thorsteinson (1960). Heteroderids have immense power of host discrimination and adaptation and host species are gifted with infinite potential to sustain and overcome the injury.

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Table 1: Relationships between taxonomic groups of host plants with different species of *Heterodera* along with their groups/clades

***Heterodera* species**	**Groups/Clades***
Monocotyledons-Glumiflorae	
H. arenaria, H. aucklandica, H. iri, H. hordecalis, H. latipons, H. mani, H. pratensis, H. spinicauda	Avenae
H. goldeni, H. leucilyma, H. sacchari, H. sorghi	Sacchari
H. zeae	Humuli
H. cyperi, H. delvii, H. elachista, H. graminis, H. hainanensis, H. fengi, H. koreana, H. oryzicola, H. raskii, H. sinensis	Cyperi
H. Canadensis, H. cardiolata, H. graminophila, H. longicolla	Goettingiana
H. bifenestra, H. gambiensis, H. pakistanensis	Not Confirmed
Dicotyledons-Lignosae	
H. fici, H. humuli, H. ripae	Humuli
H. cajani, H. ciceri, H. davertii	Schachtii
H. goettingiana, H. urticae	Goettingiana
H. cacti, H. salixophila, H. swarupi	Not Confirmed
Dicotyledons-Herbaceae	
H. bergeniae, H. carote, H. scutellariae	Goettingiana
H. littoralis	Humuli
H. achilleae, H. rumicis, H. tarcomanica	Not Confirmed
Dicotyledons-Lignosae Herbaceae	
H. circeae	Goettingiana
H. galeopsidis, H. lespedezae, H. medicaginis	Schachtii
Monocotyledons+Lignosae +Herbaceae	
H. avenae	Avenae
H. betae, H. glycines, H. mediterraneae, H. schachtii, H. trifolii	Schachtii
H. oryzae	Goettingiana
Monocotyledons+Herbaceae	
H. cruciferae	Goettingiana
H. mothi	Cyperi
Monocotyledons+Lignosae	
H. filipjevi	Avenae

*Based on morphometric and molecular studies

Table 2: Distribution of host plants of *Heterodera* species in different families and subfamilies of monocotyledons

Heterodera species	Host species	Family	Sub-family	Tribe	Sub-tribe	Order	Group
H. arenaria	*Ammorphila arenaria*	Poaceae	x	x	x	Graminales	Avenae
	Calamagrostis epigejos	Poaceae	Pooideae	Agrosteae	x	Graminales	Avenae
	Elymus athericus	Poaceae	Pooideae	Hordeeae	Elyminae	Graminales	Avenae
	Elymus farctus	Poaceae	Pooideae	Hordeeae	Elyminae	Graminales	Avenae

	Festuca rubra	Poaceae	Pooideae	Festuceae	Festucinae	Graminales	Avenae
H. aucklandica	*Microlaena stipoides*	Poaceae	Pooideae	Phalarideae	x	Graminales	Avenae
H. iri	*Agrostis tenuis*	Poaceae	Pooideae	Agrosteae	x	Graminales	Avenae
H. hordecalis	*Avena sativa*	Poaceae	Pooideae	Avenae	x	Graminales	Avenae
	Avena sterilis	Poaceae	Pooideae	Avenae	x	Graminales	Avenae
	Bromus arvensis	Poaceae	Pooideae	Festuceae	Festucinae	Graminales	Avenae
	Festuca pratensis	Poaceae	Pooideae	Festuceae	Festucinae	Graminales	Avenae
	Hordeum vulgare	Poaceae	Pooideae	Hordeeae	Elyminae	Graminales	Avenae
	Lolium multiflorum	Poaceae	Pooideae	Festuceae	Loliinae	Graminales	Avenae
	Lolium perenne	Poaceae	Pooideae	Festuceae	Loliinae	Graminales	Avenae
	Secale cereale	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	Avenae
	Triticum aestivum	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	Avenae
H. latipons	*Avena sativa*	Poaceae	Pooideae	Avenae	x	Graminales	Avenae
	Avena sterilis	Poaceae	Pooideae	Avenae	x	Graminales	Avenae
	Hordeum vulgare	Poaceae	Pooideae	Hordeeae	Elyminae	Graminales	Avenae
	Secale cereale	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	Avenae
	Triticum sp.(6 species)	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	Avenae
H. mani	*Dactylis glomerata*	Poaceae	Pooideae	Festuceae	Festucinae	Graminales	Avenae
	Festuca pratensis	Poaceae	Pooideae	Festuceae	Festucinae	Graminales	Avenae
	Lolium perenne	Poaceae	Pooideae	Festuceae	Loliinae	Graminales	Avenae
H. pratensis	*Grass hosts*	Poaceae	x	x	x	Graminales	Avenae
H. spinicauda	*Phragmites australis*	Poaceae	Pooideae	Arundineae	x	Graminales	Avenae
H. goldeni	*Juncus acutus*	Juncaceae	x	x	x	Juncales	Sacchari
	Oryza sativa	Poaceae	Pooideae	Oryzeae	Oryzinae	Graminales	Sacchari
	Panicum coloratum	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Sacchari
	Phragmites australis	Poaceae	Pooideae	Arundineae	x	Graminales	Sacchari
	Sorghum bicolor	Poaceae	Panicoideae	Andropogoneae	Andropogoneae	Graminales	Sacchari
	Zea mays	Poaceae	Panicoideae	Maydeae	x	Graminales	Sacchari
H. leucilyma	*Cynodon dactylon*	Poaceae	Pooideae	Chlorideae	x	Graminales	Sacchari
	Stenotaphrum secundatum	Poaceae	x	x	x	Graminales	Sacchari
H. sacchari	*Axonopus compressus*	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Sacchari
	Brachiaria brizantha	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Sacchari
	Cynodon dactylon	Poaceae	Pooideae	Chlorideae	x	Graminales	Sacchari
	Echinochloa colona	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Sacchari
	Eleusine indica	Poaceae	Pooideae	Eragrosteae	x	Graminales	Sacchari
	Mariscus umbellatus	Cyperaceae	x	Cypereae	x	Cyperales	Sacchari
	Oryza sativa	Poaceae	Pooideae	Oryzeae	Oryzinae	Graminales	Sacchari
	Paspalum conjugatum	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Sacchari
	Saccharum officinalis	Poaceae	Panicoideae	Andropogoneae	Saccharinae	Graminales	Sacchari
	Saccharum officinarum	Poaceae	Panicoideae	Andropogoneae	Saccharinae	Graminales	Sacchari
	Saccharum spontaneum	Poaceae	Panicoideae	Andropogoneae	Saccharinae	Graminales	Sacchari
H. sorghi	*Sorghum* sp.	Poaceae	Panicoideae	Andropogoneae	Andropogoneae	Graminales	Sacchari
	Zea mays	Poaceae	Panicoideae	Maydeae	x	Graminales	Sacchari
H. zeae	*39 species*	Poaceae	**			Graminales	Humuli
H. cyperi	*Cyperus esculentus*	Cyperaceae	x	Cypereae	x	Cyperales	Cyperi
H. delvii	*Eleusine coracana*	Poaceae	Pooideae	Eragrosteae		Graminales	Cyperi
H. elachista	*Oryza sativa*	Poaceae	Pooideae	Oryzeae	Oryzinae	Graminales	Cyperi
H. graminis	*Cynodon dactylon*	Poaceae	Pooideae	Chlorideae	x	Graminales	Cyperi
	Juncus acutus	Juncaceae	x	x	x	Juncales	Cyperi
	Pennisetum clandestinum	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Cyperi
	Panicum coloratum	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Cyperi
	Phragmites australis	Poaceae	Pooideae	Arundineae	x	Graminales	Cyperi
H. hainanensis	*Phyllostachys pubescens*	Poaceae	Pooideae	Bambuseae	Arundinariinae	Graminales	Cyperi
H. fengi	*Phyllostachys pubescens*	Poaceae	Pooideae	Bambuseae	Arundinariinae	Graminales	Cyperi
H. koreana	*Phyllostachys pubescens*	Poaceae	Pooideae	Bambuseae	Arundinariinae	Graminales	Cyperi
H. oryzicola	*Oryza sativa*	Poaceae	Pooideae	Oryzeae	Oryzinae	Graminales	Cyperi
H. raskii	*Cyperus bulbosus*	Cyperaceae	x	Cypereae	x	Cyperales	Cyperi
H. sinensis	*Cogon grass*	Poaceae	x	x	x	Graminales	Cyperi
H. canadensis	*Eleocharis acicularis*	Cyperaceae	x	Scirpeae		Cyperales	Goettingiana
H. cardiolata	*Cynodon dactylon*	Poaceae	Pooideae	Chlorideae	x	Graminales	Goettingiana
H. graminophila	*Echinochloa colona*	Poaceae	Panicoideae	Paniceae	Panicinae	Graminales	Goettingiana
	Oryza sativa	Poaceae	Pooideae	Oryzeae	Oryzinae	Graminales	Goettingiana
	Sorghum halepense	Poaceae	Panicoideae	Andropogoneae	Andropogoneae	Graminales	Goettingiana
H. longicolla	*Buchloe dactyloides*	Poaceae	x	x	x	Graminales	Goettingiana
H. bifenestra	*Avena sativa*	Poaceae	Pooideae	Avenae	x	Graminales	*
	Avena sterilis	Poaceae	Pooideae	Avenae	x	Graminales	*

	Hordeum vulgare	Poaceae	Pooideae	Hordeeae	Elyminae	Graminales	*
	Triticum aestivum	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	*
H. gambiensis	*Sorghum* sp.	Poaceae	Panicoideae	Andropogoneae	Andropogoneae	Graminales	*
	Pennisetum typhoideum	Poaceae	Pooideae	Paniceae	Panicinae	Graminales	*
H. pakistanensis	*Triticum aestivum*	Poaceae	Pooideae	Hordeeae	Triticinae	Graminales	*

Table 3: Distribution of host plants of Heterodera species in families of dicotyledons and in combination with monocots(Contd.)

No.	Heterodera species	No. of Genera	No. of Species	Host Family	Order	Group-Phylum	Group
1	*H. fici*	1	5	Moraceae (5)	Urticales	Dicotyledons-Lignosae	Humuli
2	*H. humuli*	4	5	Moraceae (3)	Urticales	Dicotyledons-Lignosae	Humuli
				Urticaceae (2)	Urticales	Dicotyledons-Lignosae	Humuli
3	*H. ripae*	1	1	Urticaceae (1)	Urticales	Dicotyledons-Lignosae	Humuli
4	*H.cajani*	11	23	Fabaceae (21)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Pedaliaceae (2)	Bignoniales	Dicotyledons-Lignosae	Schachtii
5	*H. ciceri*	9	20	Fabaceae (20)	Leguminales	Dicotyledons-Lignosae	Schachtii
6	*H.davertii*	14	21	Fabaceae (21)	Leguminales	Dicotyledons-Lignosae	Schachtii
7	*H. goettingiana*	10	35	Fabaceae (34)	Leguminales	Dicotyledons-Lignosae	Goettingiana
				Rubiaceae (1)	Rubiales	Dicotyledons-Lignosae	Goettingiana
8	*H. urticae*	1	2	Urticaceae (2)	Urticales	Dicotyledons-Lignosae	Goettingiana
9	*H. cacti*	1	2	Cactaceae (2)	Cactales	Dicotyledons-Lignosae	*
10	*H. salixophila*	1	2	Salicaceae (2)	Salicales	Dicotyledons-Lignosae	*
11	*H. swarupi*	1	1	Fabaceae (1)	Leguminales	Dicotyledons-Lignosae	*
12	*H. bergeniae*	1	1	Saxifragaceae (1)	Saxifragales	Dicotyledons-Herbaceae	Goettingiana
13	*H. carote*	1	3	Apiaceae (3)	Umbellales	Dicotyledons-Herbaceae	Goettingiana
14	*H. scutellariae*	1	1	Lamiaceae (1)	Lamiales	Dicotyledons-Herbaceae	Goettingiana
15	*H. littoralis*	1	1	Chenopodiaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	Humuli
16	*H. achilleae*	1	1	Asteraceae (1)	Asterales	Dicotyledons-Herbaceae	*
17	*H. rumicis*	1	2	Polygonaceae (2)	Polygonales	Dicotyledons-Herbaceae	*
18	*H. tarcomanica*	2	2	Chenopodiaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	*
				Polygonaceae (1)	Polygonales	Dicotyledons-Herbaceae	*
19	*H. circeae*	16	21	Fabaceae (11)	Leguminales	Dicotyledons-Lignosae	Goettingiana
				Brassicaceae (2)	Brassicales	Dicotyledons-Herbaceae	Goettingiana
				Caryophyllaceae (3)	Caryophyllales	Dicotyledons-Herbaceae	Goettingiana
				Chenopodiaceae (2)	Chenopodiales	Dicotyledons-Herbaceae	Goettingiana
				Lamiaceae (1)	Lamiales	Dicotyledons-Herbaceae	Goettingiana
				Polygonaceae (1)	Polygonales	Dicotyledons-Herbaceae	Goettingiana
				Scrophulariaceae (1)	Personales	Dicotyledons-Herbaceae	Goettingiana
20	*H. galeopsidis*	14	30	Fabaceae (5)	Leguminales	Dicotyledons- Lignosae	Schachtii
				Caryophyllaceae (6)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (2)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (7)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (6)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Scrophulariaceae (4)	Personales	Dicotyledons-Herbaceae	Schachtii
21	*H. lespedezae*	6	9	Fabaceae (6)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Caryophyllaceae (1)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (1)	Polygonales	Dicotyledons-Herbaceae	Schachtii
22	*H.medicaginis*	16	21	Fabaceae (11)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Brassicaceae (2)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Caryophyllaceae (3)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (2)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (1)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (1)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Scrophulariaceae (1)	Personales	Dicotyledons-Herbaceae	Schachtii
23	*H. avenae*	56	112	Fabaceae (11)	Leguminales	Dicotyledons-Lignosae	Avenae
				Amaranthaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	Avenae
				Apiaceae (6)	Umbellales	Dicotyledons-Herbaceae	Avenae
				Asteraceae (1)	Asterales	Dicotyledons-Herbaceae	Avenae
				Brassicaceae (4)	Brassicales	Dicotyledons-Herbaceae	Avenae
				Chenopodiaceae (3)	Chenopodiales	Dicotyledons-Herbaceae	Avenae
				Primulaceae (1)	Primulales	Dicotyledons-Herbaceae	Avenae
				Solanaceae (1)	Solanales	Dicotyledons-Herbaceae	Avenae
				Cyperaceae (1)	Cyperales	Monocotyledons-Glumiflorae	Avenae
				Poaceae (83)	Graminales	Monocotyledons-Glumiflorae	Avenae

24	*H. betae*	23	44	Fabaceae (15)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Apiaceae (1)	Umbellales	Dicotyledons-Herbaceae	Schachtii
				Brassicaceae (10)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Caryophyllaceae (3)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae ((4)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (2)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (2)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Rosaceae (1)	Rosales	Dicotyledons-Lignosae	Schachtii
				Scrophulariaceae (3)	Personales	Dicotyledons-Herbaceae	Schachtii
				Solanaceae (2)	Solanales	Dicotyledons-Herbaceae	Schachtii
				Poaceae (1)	Graminales	Monocotyledons-Glumiflorae	Schachtii
25	*H. glycines*	56	166	Cucurbitaceae (2)	Cucurbitales	Dicotyledons-Lignosae	Schachtii
				Fabaceae (143)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Malvaceae (1)	Malvales	Dicotyledons-Lignosae	Schachtii
				Passifloraceae (1)	Passiflorales	Dicotyledons-Lignosae	Schachtii
				Pedaliaceae (1)	Bignoniales	Dicotyledons-Lignosae	Schachtii
				Brassicaceae (1)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Caryophyllaceae (1)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (2)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (1)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (2)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Scrophulariaceae (1)	Personales	Dicotyledons-Herbaceae	Schachtii
				Solanaceae (4)	Solanales	Dicotyledons-Herbaceae	Schachtii
				Poaceae (6)	Graminales	Monocotyledons-Glumiflorae	Schachtii
26	*H. mediterraneae*	16	20	Anacardiaceae (3)	Sapindales	Dicotyledons-Lignosae	Schachtii
				Apocynaceae (1)	Apocynales	Dicotyledons-Lignosae	Schachtii
				Fabaceae (2)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Juglandaceae (1)	Juglandales	Dicotyledons-Lignosae	Schachtii
				Moraceae (1)	Urticales	Dicotyledons-Lignosae	Schachtii
				Oleaceae (1)	Loganiales	Dicotyledons-Lignosae	Schachtii
				Rosaceae (4)	Rosales	Dicotyledons-Lignosae	Schachtii
				Apiaceae (1)	Umbellales	Dicotyledons-Herbaceae	Schachtii
				Brassicaceae (1)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Solanaceae (3)	Solanales	Dicotyledons-Herbaceae	Schachtii
				Poaceae (2)	Graminales	Monocotyledons-Glumiflorae	Schachtii
27	*H. schachtii*	30	281	Euphorbiaceae (1)	Euphorbiales	Dicotyledons-Lignosae	Schachtii
				Fabaceae (33)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Rubiaceae (1)	Rubiales	Dicotyledons-Lignosae	Schachtii
				Violaceae (1)	Violales	Dicotyledons-Lignosae	Schachtii
				Vitaceae (1)	Rhamnales	Dicotyledons-Lignosae	Schachtii
				Urticaceae (2)	Urticales	Dicotyledons-Lignosae	Schachtii
				Aizoaceae (1)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Apiaceae (3)	Umbellales	Dicotyledons-Herbaceae	Schachtii
				Amaranthaceae (10)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Asteraceae (11)	Asterales	Dicotyledons-Herbaceae	Schachtii
				Boraginaceae (3)	Boraginales	Dicotyledons-Herbaceae	Schachtii
				Brassicaceae (92)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Caryophyllaceae (19)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (42)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Geraniaceae (1)	Graminales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (6)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Onagraceae (1)	Onagrales	Dicotyledons-Herbaceae	Schachtii
				Papaveraceae (2)	Rhoeadales	Dicotyledons-Herbaceae	Schachtii
				Phytolaccaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Plantaginaceae (2)	Plantaginales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (22)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Protulacaceae (2)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Ranunculaceae (2)	Ranales	Dicotyledons-Herbaceae	Schachtii
				Resedaceae (3)	Resedales	Dicotyledons-Herbaceae	Schachtii
				Scrophulariaceae (3)	Personales	Dicotyledons-Herbaceae	Schachtii
				Solanaceae (6)	Solanales	Dicotyledons-Herbaceae	Schachtii
				Tropaeolaceae (2)	Graminales	Dicotyledons-Herbaceae	Schachtii
				Amaryllidaceae (1)	Amaryllidales	Monocotyledons-Corolliferae	Schachtii
				Bromeliaceae (1)	Bromeliales	Monocotyledons-Calyciferae	Schachtii
				Poaceae (6)	Leguminales	Monocotyledons-Glumiflorae	Schachtii

28	*H. trifolii*	46	110	Cucurbitaceae (3)	Cucurbitales	Dicotyledons-Lignosae	Schachtii
				Fabaceae (45)	Leguminales	Dicotyledons-Lignosae	Schachtii
				Brassicaceae (10)	Brassicales	Dicotyledons-Herbaceae	Schachtii
				Caryophyllaceae (23)	Caryophyllales	Dicotyledons-Herbaceae	Schachtii
				Chenopodiaceae (9)	Chenopodiales	Dicotyledons-Herbaceae	Schachtii
				Geraniaceae (1)	Personales	Dicotyledons-Herbaceae	Schachtii
				Lamiaceae (3)	Lamiales	Dicotyledons-Herbaceae	Schachtii
				Polygonaceae (9)	Polygonales	Dicotyledons-Herbaceae	Schachtii
				Scrophulariaceae (2)	Personales	Dicotyledons-Herbaceae	Schachtii
				Solanaceae (4)	Solanales	Dicotyledons-Herbaceae	Schachtii
				Liliaceae (1)	Liliales	Monocotyledons-Corolliferae	Schachtii
29	*H. oryzae*	17	19	Malvaceae (1)	Malvales	Dicotyledons-Lignosae	Goettingiana
				Fabaceae (5)	Leguminales	Dicotyledons-Lignosae	Goettingiana
				Brassicaceae (1)	Brassicales	Dicotyledons-Herbaceae	Goettingiana
				Solanaceae (3)	Solanales	Dicotyledons-Herbaceae	Goettingiana
				Cyperaceae (1)	Cyperales	Monocotyledons-Glumiflorae	Goettingiana
				Musaceae (1)	Zingiberales	Monocotyledons-Calyciferae	Goettingiana
				Poaceae (7)	Leguminales	Monocotyledons-Glumiflorae	Goettingiana
30	*H. cruciferae*	34	59	Asteraceae (1)	Asterales	Dicotyledons-Herbaceae	Goettingiana
				Brassicaceae (51)	Brassicales	Dicotyledons-Herbaceae	Goettingiana
				Chenopodiaceae (1)	Chenopodiales	Dicotyledons-Herbaceae	Goettingiana
				Lamiaceae (4)	Lamiales	Dicotyledons-Herbaceae	Goettingiana
				Poaceae (2)	Graminales	Monocotyledons-Glumiflorae	Goettingiana
31	*H. mothi*	4	4	Solanaceae (1)	Solanales	Dicotyledons-Herbaceae	Cyperi
				Amaryllidaceae (1)	Amaryllidales	Monocotyledons-Corolliferae	Cyperi
				Cyperaceae (1)	Cyperales	Monocotyledons-Glumiflorae	Cyperi

Table 4: Host -race relationship of Heterodera species

Heterodera species	Host species	Race designation
H. avenae	*Avena sativa*	Algeria, Ha 11 (Group 1), Ha 12 (Group 2), Ha 13 (Group 3), Ha
		31 (Group 1), Ha 41 (Group 1), Ha 51 (Group 1), Ha 61 (Group)
		Ha 12, Ha 13, Ha 21? Saudi, Ha 22, Ha 23, Ha 31, H
		Teruel, and Toledo
	Avena sterilis	All races reported in A. Sativaexept Ha 31 (Group 1), Ha 21
	Hordeum vulgare	All races reported in A. Sativa plus 1, 2, Dutch and Pathotype
	Hordeum pallidum	Ha 31 (Group 1), Ha 12, Ha 21, Ha 31, Ha 51, Ha 61 and Ha 71
	Triticum aestivum	All races reported as A. Sativa except Ha 31 (Group 1) Ha 51
	Triticum durum	Ha 13 (Group 3), 22 Group 2), Ha 41 (Group 1), ha 71 (Group)
		ha41, Ha 71 and Ha 81
	Triticum longissimum	Algeria and Syria
	Triticum tauschii	Algeria and Syria
	Triticum umbellatum	Algeria and Syria
	Triticum variabile	Algeria and Syria
	Triticum ventricosum	Algeria and Syria
	Secale cereal	Seville, Teruel and Toledo
H. filipjevi	*Avena sativa*	India
	Hordeum vulgare	India
	Triticum aestivum	India
	Triticum longissimum	India
	Triticum tauschii	India
	Triticum umbellatum	India
	Triticum variabile	India
	Triticum ventricosum	India
H. glycines	*Glycine max*	1, 2, 2a, 2b, 3,4,5,6,9, Race 1, Race 2, race 3, Race 4, Race 5
	Phaseolus vulgaris	HG Type 0, Race 2, Race 3, Race, race 5, race 14
H. latipons	*Avena sativa*	Syria
	Avena sterilis	Syria
	Hordeum vulgare	Syria
	Triticum aestivum	Syria
	Triticum tauschii	Syria
	Triticum umbellatum	Syria
	Triticum variabile	Syria
	Triticum ventricosum	Syria