



RELATIONSHIPS OF DIFFERENT SPECIES OF ROOT-KNOT NEMATODES TO THEIR HOST TAXONOMIC GROUPINGS

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ABSTRACT: Host taxonomic affiliations of 68 species of root-knot nematode, *Meloidogyne*, was evaluated. Information revealed that 4 species (*M. californiensis*, *M. ottersoni*, *M. maritime*, *M. thailandica*) in monocotyledons, 10 (*M. arabicida*, *M. brevicauda*, *M. carolinensis*, *M. christiei*, *M. decalineata*, *M. izalcoensis*, *M. litoralis*, *M. lusitanica*, *M. nataliei*, *M. oteifae*) in dicotyledons-lignosae and 3 (*M. graham*, *M. microcephala*, *M. microtyla*) in dicotyledons-herbaceae, and 1 in gymnosperms were monophagous and were associated with their taxonomic groups. Among these 2 species exclusively feed on Poaceae, 5 with coffee (Rubiaceae) and 3 with Solanaceae. Polyphagous species viz., *M. arenaria*, *M. chitwoodi*, *M. hapla*, *M. javanica* and few others co-evolving with Fabaceae, Asteraceae, Solanaceae and Poaceae. Large number of host species from primitive families and gymnosperms make *Meloidogyne* very versatile and prolific feeder. Many other host families do played a role in host range and served as a link in evolutionary lineage and/or collateral and alternate hosts. Races of some root-knot nematode species also tend to affiliate with taxonomic groups. The information will be very useful in planning nematode management strategies with particular reference to cultural practices.

Key words: Angiosperms, Gymnosperms, Dicotyledons, Monocotyledos, Root-knot nematode, *Meloidogyne*, Lignosae, Herbaceae, Calyciferae, Corolliferae, Glumiflorae, Taxonomic affiliation

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INTRODUCTION

Root-knot nematodes are end parasites from the genus *Meloidogyne*. As a result of nematode feeding, large galls or knots are formed in the roots which affects the plant vigour. Infected plants often wilt or show nutritional deficiency, stunting and reduction in crop yield. Approximately 100 species of this nematode has been described [1]. They parasitize crops grown in tropical, subtropical and moderate temperate regions [2]. The great diversity has been observed not only in their host range but also in their mode of reproduction [3]. Species of *Meloidogyne* reported to cause about 5% global crop losses [4], or more than 80 billion Euros/year [5]. Thorsteinson [6] believed that host preference is related to plant taxonomic groups in insects. Rathore and Lal [7] and Rathore and Tiwari [8] found that pod borer, *Maruca vitrata*, and whitefly, *Bemisia tabaci*, respectively select their hosts from certain taxonomic groups and in *B. tabaci* the evolutionary lineage was evident. Recently, Rathore and Ali [9] observed similar trend of host preference in *Meloidogyne incognita* with prominent evolutionary affinities of host taxonomic groups. Rathore and Tiwari [10,11] further observed strong association in 63 species of *Heterodera* and 33 species of *Helicotylenchus*. Since genus *Meloidogyne* is comprised of several important parasitic species which are detrimental to field crops, it was considered pertinent to test this hypothesis in different species of this nematode.

MATERIALS AND METHODS

The present study is comprised of 68 species of *Meloidogyne*. *M. incognita* was excluded from this study as Rathore and Ali [9] has already examined the host preference of this species and reported strong affiliation with host taxonomic groups. The host plants of *Meloidogyne* species were downloaded from internet [12]. They were aligned with the families and orders as per classification of Hutchinson [13]. Hutchinson divided angiosperms into two subphyla- dicotyledons and monocotyledons. Both the subphyla were also divided into divisions. For example, dicotyledons were divided into lignosae (fundamentally woody plants) and herbaceae (fundamentally herbaceous plants). Similarly, monocotyledons were divided into three viz., calyciferae (calyx bearers-with distinct calyx and corolla), corolliferae (calyx and corolla are more or less similar) and glumiflorae (perianth is much more reduced or represented by lodicules). *Meloidogyne* species were designated as mono, oligo and polyphagous by adopting the definitions of Bernays and Chapman [14] where monophagous feeds on plants of a single genus while oligophagous utilizes plants of different genera in a single plant family; polyphagous consumes plants under different plant families. The affiliation to different taxonomic groups was also evaluated on the basis following affiliation indices.

1. Specific Affiliation Index (SAI)= $\frac{HSt + 2}{G + F + O}$

Where, HSt= No. of host plants in a taxonomic group, G= No. of host genera, F= No. of host families and O= No. of host orders

2. General Affiliation Index (GAI) = $\frac{THs + 2}{G + F + O}$

Where, THs= Total number of host plants of a given nematode species, G= No. of host genera, F= No. of host families and O= No. of host orders

The SAI provided information on affiliation of each division of plant taxonomic group whereas, GAI allowed comparison between the species of this nematode. Value 2 was used as a correction factor. Value 1 indicated monophagy, >1 greater association, <1 lower association. Information thus generated on taxonomic group affiliations obtained on different species of *Meloidogyne* was compared with clades identified by genomic studies of Trigano et al [2] and Tomalova et al [15]. Affinity of races of some of the species of *Meloidogyne* to their host taxonomic groups was also described.

RESULTS AND DISCUSSION

A general bird-eye-view of host preference and taxonomic affiliation clearly revealed that dicots were highly preferred over monocots harbouring 80.46% host species (Table 1). However, division herbaceae showed stronger association than lignosae not only by having more host species but these species used fewer families and fewer orders. The SAI was also higher in herbaceae than lignosae. Monocot species were to the tune of 18.74% and among the monocots in general glumiflorae alone shared 12.54% host species. The SAI was 0.701, 0.858 and 1.128 for calyciferae, corolliferae and glumiflorae, respectively. It is amazing that gymnosperms contributed remarkably well in the host preference of some species of *Meloidogyne*.

Species specific picture presented in Table 1 and Fig. 1 was a bit different. The species *M. californiensis*, *M. maritime*, *M. ottersoni* and *M. thailandica* were feeding exclusively on *Scirpas robustus* (Cyperaceae), *Ammophila arenaria* (Poaceae), *Phalaris arundinaceae* (Poaceae) and *Zingiber* sp. (Zingiberaceae), respectively from monocots.

Four species viz., *M. triticoryzae*, *M. graminis*, *M. sasseri* and *M. spartinae*, though polyphagous, but parasitized only host plants from few families in monocots. Aforesaid species are, therefore, only monocot feeders and family Poaceae in glumiflorae division contributed the most. These species can be termed as mono-polyphagous. It appears that all the aforesaid 8 species are co-evolving with monocotyledons.

Similarly in dicotyledons, 10 species showed monophagy in lignosae and 3 in herbaceae. In lignosae *M. arabicida*, *M. decalineata*, and *M. izalcoensis* feed exclusively on *Coffea arabica* and *M. otteifae* on *Coffea canephora* all in family Rubiaceae from order Rubiales. *M. litoralis* feeds only on *Ligustrum* sp. (Oleaceae) and *M. lusitanica* on *Olea europaea* (Oleaceae) from order Loganiales. It is interesting to note that order Rubiales derived from order Loganiales [13]. *Camellia sinensis* (Theaceae) of order Theales hosts *M. brevicauda* and *Vaccinium corymbosum* X *V. lamarcke* (Ericaceae) of order Ericales is parasitized by *M. carolinensis*. Order Ericales is derived from Theales. The taxonomic affinity of last two nematode species is highly interwoven. *M. christiei*, another monophagous species, feeds on *Quercus laevis* (Fagaceae) of order Rhamnales.

In herbaceae division, *M. grahmi* parasitizes *Nicotiana tabacum* (Solanaceae) and *M. microcephala* and *M. microtyla* both feed on *Solanum lycopersicum* (Solanaceae). All the three species, therefore, are feeding on the same family from the order Solanales. Monophagous species from both the divisions of dicotyledons are co-evolving with their respective host groups.

Species *M. ovalis* and *M. partityla* were observed feeding on host species from lignosae group only and 6 species viz., *M. ardenensis*, *M. bauruensis*, *M. coffeicola*, *M. hispanica*, *M. morocciensis* and *M. luci* parasitize both lignosae and herbaceae divisions of dicotyledons only and can be termed as dico-polyphagous.

M. megatyla, a monophagous species infests only *Pinus taeda* (Pinaceae) from order Pinales in gymnosperms.

Thirty-eight species of *Meloidogyne* were observed to be polyphagous by feeding host plants from dicotyledons and monocotyledons of angiosperms (Table 2, Fig. 1). Evaluation of species on the basis of General Association Index (GAI) revealed that all the monophagous species had index value 1. In case of polyphagous species. *M. marylandi*, *M. naasi* and *pini* GAI was 1.063, 1.222 and 1.667, respectively indicating very strong association to their host taxonomic groups, but have a limited host range (Table 2). However, nematode species with higher GAI and wider host range (angiosperms + gymnosperms) were viz., *M. arenaria* (1.194), *M. chitwoodi* (1.266), *M. fallax* (1.136), *M. hapla* (1.630) and *M. javanica* (1.514). Besides being prolific feeders they also showed strong taxonomic affiliation as indicated by SAI values and co-evolving within such taxonomic groups. Trudgill and Blok [16] and Mitkowski and Abawi [1] also mentioned *M. arenaia*, *M. chitwoodi*, *M. graminicola*, *M. hapla*, *M. incognita* and *M. javanica* as extremely polyphagous and economically important species.

Molecular studies on phylogenetics of *Meloidogyne* has not been reported for 68 species reported herein. However, Tigano et al [2] classified 19 test species in 3 groups or clades No host taxonomic relationship was observed for group/clade *per se*. Investigation of Tomalova et al [15] on distribution of map-1 genes in *Meloidogyne* showed that species with this gene reproduce by mitotic parthenogenesis. Therefore, they divided taxa in two clades, i.e., clade clustering species that reproduce by mitotic parthenogenesis and species in other clade reproduce meiotic parthenogenesis/amphimixis. However, it is not known whether parthenogenesis is ancestral or of recent origin [17,18]. These results revealed divergence between mitotic and meiotic species. When the two groups/clades were compared for their host taxonomic affiliation no difference was found between the two. This again highlights the species specific host taxonomic affiliation is of paramount importance.

Table 1. Distribution of host plants of *Meloidogyne* species in different taxonomic groups

Parameters	Dicotyledons		Monocotyledons			Gymnosperms	Total
	Lignosae	Herbaceae	Calyciferae	Corolliferae	Glumiflorae		
Species	1333 (36.73)*	1587 (43.73)	52 (1.43)	173 (4.77)	455 (12.54)	29 (0.80)	3629
Genera	769 (38.07)	782 (38.71)	36 (1.78)	124 (6.14)	295 (14.60)	14 (0.70)	2020
Families	340 (47.03)	253 (34.99)	24 (3.32)	40 (5.53)	55 (7.61)	11 (1.52)	723
Orders	290 (47.31)	203 (33.12)	17 (2.77)	40 (6.52)	55 (8.97)	8 (1.31)	613
SAI	0.954	1.284	0.701	0.858	1.128	0.939	--
*Figures in parantheses are percent values							

Among some of the highly prolific species, *M. arenaria* parasitized on a large number of host species which spread out in angiosperms and gymnosperms and appears to be co-evolving with Fabaceae (Leguminales), Solanaceae (Solanales) and Poaceae (Gramiales) in lignosae, herbaceae and glumiflorae divisions, respectively. Several evolutionary lineages were formed but the most contributing were:

- Rosales-Leguminales-Cunoniales-Araliales, Salicales = contributed 90 host plants
- Ranales-Saxifragales-Solanales-Personales = contributed 119 host plants, and
- Liliales-Graminales = contributed 32 host plants

M. chitwoodi reported to infest 222 host species from both the phyla. In herbaceae, this species feeds on plants of very primitive families like Paeoniaceae and Ranunculaceae (Ranales). The short evolutionary lineage was Ranales-Saxifragales-Solanales and contributed 74 host plants. In monocotyledons Liliales-Graminales parasitized hosts to the tune of 134. Undoubtedly this nematode specie is co-evolving with Poaceae (Graminales) in monoct and secondarily with Solanaceae (Solanales) in dicot.

Nematode species *M. hapla* made a distinguished phylogenetic lineage starting vigoursly from gymnosperms and having 16 plant species (*Juniperus chinensis*, *J.conferta*, *J. horizontalis*, *Metasequoia glyptostroboides*, *Pinus echinata*, *P. elliottii*, *P. palustris*, *P. clausa*, *P. ponderosa* *P. rigida*, *P. serotina*, *P. stobus*, *P. taeda*, *P. virginiana*, *Thuja occidentalis* and *Tsuga canadensis*) belonging to 2 families of order Pinales. It is widely accepted that gymnosperms originated in the late carboniferous period [19] and the ancestors of the angiosperms or flowering plants derived from gymnosperms around 245-202 million years ago [20].

This confirms that evolutionary lineage of *M. hapla* starts from gymnosperms. It parasitizes all the primitive families like Magnoliaceae (Magnoliales) and Lauraceae (Laurales) in lignosae; Paeoniaceae and Ranunculaceae (Ranales) in herbaceae and Commelianaceae (Commelianales) which derived from Alismatales and Butanales in monocotyledons. Families in advanced orders were also parasitized. The top evolutionary lineages were:

- Rosales-Leguminales - contributed 158 host plants in lignosae,
 - Ranales-Saxifragales-Campanales-Asterales = contributed 192 host plants,
 - Ranales-Saxifragales-Solanales-Personales = contributed 191 host plants
 - Ranales-Geraniales-Polemoniales-Lamiales = contributed 116 plant species, all in herbaceae.
- Because of few missing links, evolutionary lineage in lignosae could not be shown as to start from gymnosperms and with other primitive families. It is worthwhile to mention that families Magnoliaceae and Paeoniaceae evolved parallelly. It means lignosae and herbaceae evolved from common angiosperm ancestor which in turn was diversified from gymnosperms. In herbaceae, the most primitive families, Paeoniaceae and Ranunculaceae contributed 40 host plants. The families Fabaceae, Asteraceae, Solanaceae infested 120, 136, and 119 host species, respectively and it is difficult to decide which family is co-evolving primarily with *M. hapla*. The most amazing fact that *M. hapla* parasitize 16 host plants of gymnosperms. Therefore, gymnosperms and host plants from primitive families must be serving as collateral and/or alternate hosts of this nematode species in large numbers in nature. The other important species of root-knot nematode, *M. javanica*, has a host range of 952 plants both from angiosperms and gymnosperms which spread out in 102 families and 70 orders and has a GAI of 1.512. Seven evolutionary lineages were observed in lignosae and 4 in herbaceae. However, the most contributing ones are:
- Rosales-Leguminales = contributed 173 host plants
 - Bixales-Tiliales-Malvales-Euphorbiales-Rhamnales = contributed 66 plants. However, an uncommon evolutionary lineage was observed in this nematode species is: Bixales-Pittosporales-Capparales-Tamaricales, Violales. In herbaceae:
 - Ranales-saxifragales-solanales-Personales = contributed 149 host plants. In monocot:
 - Liliales-Graminales = contributed 105 host species. These host associations indicate co-evolution of *M. javanica* primarily with Fabaceae (158) (Leguminales) and secondarily with Solanaceae (119) (Solanales) and Poaceae (86) (Graminales) families.
- Analysis of contribution of families in host range of *M. arenaria*, *M. chitwoodi*, *M. hapla* and *M. javanica* highlighted that Fabaceae, Asteraceae, Solanaceae and Poaceae played a key role in the co-evolution. Many other families also contributed a lot and appear to serve as a link in co-evolutionary lineage and/or collateral and alternate hosts. Their taxonomic affiliation in no way could be considered less important.

Race-host affiliations

Out of 68 species *Meloidogyne* cited here, 6 species showed variability in the host selection and produced races (Table 3). In *M. arenaria* Race 1, 2 and Thamesi are polyphagous and parasitized the varieties of several host plants in both dicotyledons and monocotyledons. Whereas, Race B and Harmony are host specific in their respective divisions (Table 3). In *M. exigua* virulence of Race 1 and 2 was restricted to dicotyledons only while Race 3 was more virulent and invaded both dicotyledons and monocotyledons. Virulence of A race of *M. hapla* was restricted to dicotyledons only, however, the Race B was more specific and showed affiliation to 2 genera of the same family, thereby indicated oligophagous behaviour. In spite of wide host range of *M. javanica*, the number of hosts parasitized by different races were limited. Race 1 and 3 infested plants in dicots as well as monocots but Race 2 was monophagous in herbaceae. *M. mayaguensis* was obliged with one race, i.e., Race 2 and parasitizing plants from all the divisions. Five races viz. Race 1, 2, 3, 4, and 5 were observed in *M. naasi*. All the races have same host species but the varieties showed different reactions. All the host varieties were from herbaceae and glumiflorae divisions.

Table 3. Races of *Meloidogyne* species associated with their host taxonomic groups

Race	Host taxonomic groups
<i>M. arenaria</i>	
1	Dicot =Lignosae- 40 (7), Herbaceae- 28 (7); Monocot =Calyciferae- 1(1), Corolliferae- 1(1), Glumiflorae- 9(1)
2	Dicot =Lignosae- 21 (7), Herbaceae- 17 (6); Monocot =Corolliferae- 1 (1), Glumiflorae- 8 (1)
Thamesi	Dicot =Lignosae- 26 (11), Herbaceae- 15 (8); Monocot =Corolliferae- 5 (3), Glumiflorae- 3 (1)
B	Dicot =Herbaceae- 1 (1)
Harmony	Dicot =Lignosae- 1 (1)
<i>M. exigua</i>	
1	Dicot =Lignosae- 1 (1), Herbaceae- 2 (1)
2	Dicot =Lignosae- 1 (1), Herbaceae- 2 (1)
3	Dicot =Lignosae- 3 (3), Herbaceae- 4 (1); Monocot =Glumiflorae- 1 (1)
<i>M. hapla</i>	
A	Dicot =Lignosae- 1 (1), Herbaceae- 3 (1)
B	Dicot =Herbaceae- 3 (1)
<i>M. javanica</i>	
1	Dicot =Lignosae- 2 (2), Herbaceae- 3 (1); Monocot =Glumiflorae- 1 (1)
2	Dicot =Herbaceae- 1 (1)
3	Dicot =Lignosae- 2 (2), Herbaceae- 3 (1); Monocot =Glumiflorae- 1 (1)
<i>M. mayaguensis</i>	
2	Dicot =Lignosae- 2 (2), Herbaceae- 2 (2); Monocot =Carolliferae- 1 (1)
<i>M. naasi</i>	
1,2,3,4,5	Dicot =Herbaceae- 4 (4); Monocot - Glumiflorae- 18 (1)
	Values out side the bracket indicate no. of host species and within brackets no. of families

At a glance survey of Table 3 reveals that races too have taxonomic affiliations. For example some races are polyphagous and some are monophagous and attached with one plant species and some are associated with particular plant family. Host species from glumiflorae division of monocotyledons contributed in host race development of most of the *Meloidogyne* species (Table 3) and projected the strong affiliation of monocots. Similarly, the five races of *M. naasi* utilized the same host species for race development.

Comprehensive information thus generated and described has a great potential in planning the root-knot nematode management strategies:

1. Provides information on nature of host specificity of root-knot nematode species to their taxonomic groups and makes aware of their potential host range.
2. Based on host taxonomic affinities appropriate cultural practices can be adopted. For example, coffee plantation is highly susceptible to 5 monophagous species. Introduction of any antagonistic crop could reduce the population and infestation of these species in endemic areas. Species *M. gahami*, *M. microcephala* and *M. microtyla* exclusively feed on solanaceous crops (one on *Nicotiana* and later two on *S. lycopersicum*). Avoidance of sole cultivation of solanaceous crops may help in drastic reduction of nematode infestation. Therefore, introduction of non – host crops in crop rotation may prove beneficial. Mitkowski and Abawi [1] suggested use of non-host crop like corn after vegetables to protect from *M. hapla*. A very useful agronomic recommendation on use of leguminous crops in crop rotations would provide nitrogen to succeeding crops and economize the production. However, if crops from Fabaceae rotated with Poaceae, with every likelihood, will accentuate the infestation of some polyphagous species.
3. Well planned crop rotations with non-hosts or repellent hosts or less susceptible/ resistant varieties may be very useful in managing populations of prolific feeders. *M. incognita* in cotton can usually be managed effectively with crop rotations (Mitkowski and Abawi 2003)s.
4. Polyphagous species of root-knot nematode contain gymnosperms, especially from order Pinales, in their host range. Therefore, cultivation of field crops near forest areas where pines are predominantly grown, avoid such crops which are more vulnerable to these nematode species.
5. Species *M. megatyla* exclusively feeds on gymnosperms. Proper protective measures are recommended before reforestation with gymnosperms in such endemic areas. However, cultivation of other crops will be on safer side if there is no interference from other nematode species.

6. Green manuring always improves the soil structure and fertility. Selection of green manuring crops from non-preferred taxonomic groups will be advisable.
7. Adoption of this information would help in developing appropriate crop rotations, selection or avoidance of crops from taxonomic groups, less or no use of pesticides and will keep you with nature.

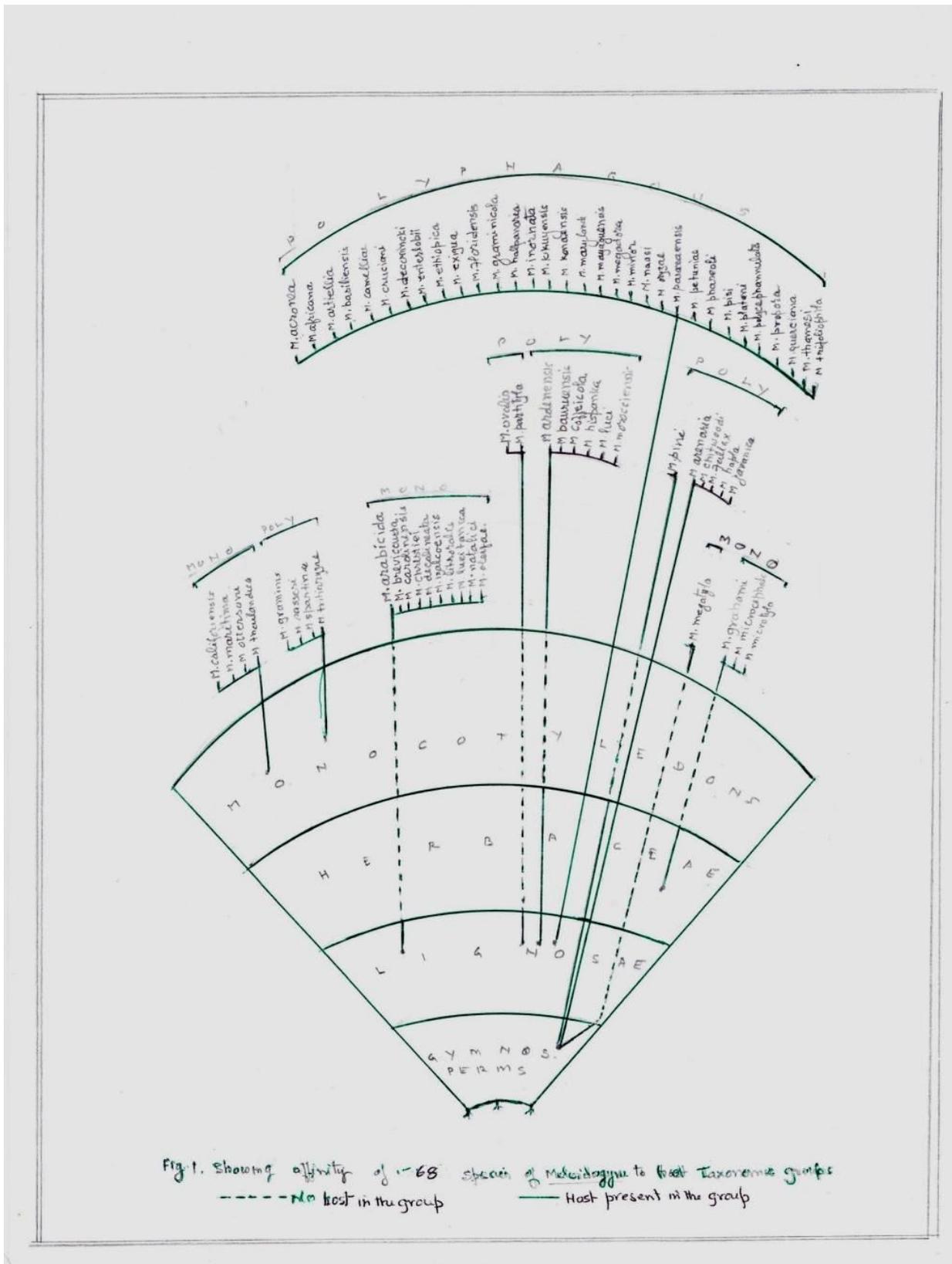


Fig. 1. Showing affinity of 68 species of Meloidogyne to host Taxonomic groups
 - - - - - No host in the group ——— Host present in the group

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