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SYNOPSIS OF THE GENUS *MELOIDOGYNE* GOELDI, 1887[1]

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ABSTRACT

Hewlett, T.E., and A.C. Tarjan. 1983. Synopsis of the genus *Meloidogyne* Goeldi, 1887. Nematropica 13:79-102.

Morphometrics and ratios of each nominal species were compared and evaluated. Primary diagnostic characters used were: the basic shape of the perineal pattern, juvenile body length and "c" ratio, and stylet lengths of females, males, and juveniles. Secondary diagnostic characters were: position of excretory pore and existence of vulval protuberance on females, number of male lateral incisures, spicule length, and position of the hemizonid in juveniles. Accordingly, the value of the perineal pattern as the major diagnostic character is deemphasized because of variability within populations and lack of sufficient objectivity in descriptions. A key to species and species groups is proposed. A statistical cluster analysis was performed to further determine relationships between species. Diagnostic characters used were: juvenile body length and "c" ratio; stylet lengths of females, males, and juveniles; spicule length and number of lateral incisures on males. *Meloidogyne acrita, M. bauruensis, M. chitwoodi, M. elegans, M. incognita wartelli, M. inornata, M. kirjanovae, M. litoralis, M. lordelloi, M. lucknowica,* and *M. thamesi* are discussed in detail. *Meloidogyne vialae* is placed in *species inquirendae.*
Additional key words: root-knot nematode, systematics, numerical taxonomy.

RESUMEN

Hewlett, T.E., and A.C. Tarjan. 1983. Sinopsis del genero *Meloidogyne Goeldhi,* 1887. Nematrópica 13:79-102.

Las dimensiones externas y las proporciones para cada especie nominal fueron comparadas y evaluadas. Los carácteres diagnósticos primarios usados fueron: la forma básica de la región perineal, longitud del cuerpo y la proporción "c" de las formas juveniles y la longitud del estilete de las hembras, machos y juveniles. Los carácteres diagnósticos secundarios fueron: posición del poro excretor y la existencia de protuberancias en la vulva de las hembras, el número de incisuras lateralis y longitud de las espículas en los machos y la posición del hemizonido en las formas juveniles. Por consiguiente, el valor de la región perineal como un caracter mayor de diagnosis es desenfatizado dibido a su variabilidad dentro de las poblaciones y la falta de suficiente subjetividad en las descripciones. Se propone una clave para las especies y los grupos de especies. Se realizó un analisis estadístico de grupos para determinar relaciones adicionales entre las especies. Los carácteres diagnósticos usados fueron:

longitud del cuerpo y proporción "c" de las formas juveniles, longitad del estilete de las hembras, machos y juveniles, longitud de las espículas y número de incisuras laterales de los machos. *Meloidogyne acrita, M. bauruensis, M. chitwoodi, M. elegans, M. incognita wartelli, M. inornata, M. kirnajovae, M. litoralis, M. lordelloi M. lucknowica,* and *M. thamesi* son descutidas en detalle. *Meloidogyne vialae* es colocada en la especie *inquirendae.*

Palabras claves adicionales: nematodo nodulador, sistemática, taxonomía número rica.

INTRODUCTION

Chitwood (4) presented the first key to 5 species and one subspecies of *Meloidogyne,* using male, female, and juvenile characteristics. Whitehead (60) constructed two keys, one using juvenile measurements and the other using female perineal pattern characteristics. Esser et al. (19) compiled a compendium of 35 species comparing morphological and morphometric criteria of juveniles, males, and females.

Between the resurrection of the genus by Chitwood (4) and this writing, 52 species and one subspecies of *Meloidogyne* have been described (Table 1). One species, *M. poghossianae* Kirjanova, 1963, was considered *species inquirenda* by Whitehead (60), while *M. vialae* (Lavergne, 1901) Chitwood and Oteifa, 1952, was regarded as "inadequately" described by Chitwood and Oteifa (5), and has been overlooked or avoided by subsequent authors. We therefore regard *M. vialae* as *species inquirenda.* Neither of these species is included in the analyses presented in this paper.

Meloidogyne is one of the most ubiquitous and economically important groups of nematodes affecting agriculture. Species identification can be crucial, yet it is difficult to identify populations of *Meloidogyne* using current techniques, morphological comparisons, and morphometric criteria. Several morphological characters which have been used in descriptions are variable, particularly perineal patterns. Some diagnostic differences are highly subjective and based on the author's interpretation. Some of the descriptions of species being offered are complicated, cite minute differences from nominal species, or may suggest use of complex equipment or elaborate diagnostic techniques for determination, such as electrophoresis (13), scanning electron microscopy (16,17), and cytogenetics (57). Chitwood (7) alluded to these problems when she pointed out that there is not yet "even a gentlemen's agreement as to which characters have value for species delineation." It was the objective of this study to compare the biometrics and morphology and to attempt to clarify relationships among nominal species of *Meloidogyne* using original descriptions and subsequent authoritative works.

Table 1. Nominal Species of *Meloidogyne*

1. *acrita*	Chitwood and Oteifa, 1952
2. *acronea*	Coetzee, 1956
3. *africana*	Whitehead, 1960
4. *ardenensis*	Santos, 1968
5. *arenaria*	(Neal, 1889) Chitwood, 1949
6. *artiella*	Franklin, 1961
7. *bauruensis*	Lordello, 1956
8. *brevicauda*	Loos, 1953
9. *camelliae*	Golden, 1979
10. *carolinensis*	Eisenback, 1982
11. *chitwoodi*	Golden, O'Bannon, Santo, and Finley, 1980
12. *coffeicola*	Lordello and Zamith, 1960
13. *cruciani*	Garcia-Martinez, Taylor, and Smart, 1982
14. *decalineata*	Whitehead, 1968
15. *deconincki*	Elmiligy, 1968
16. *elegans*	da Ponte, 1977
17. *ethiopica*	Whitehead, 1968
18. *exigua*	Goeldi, 1887
19. *grahami*	Golden and Slana, 1978
20. *graminicola*	Golden and Birchfield, 1965
21. *graminis*	(Sledge and Golden, 1964) Whitehead, 1968
22. *hapla*	Chitwood, 1949
23. *incognita*	(Kofoid and White, 1919) Chitwood, 1949
24. *incognita wartelli*	Golden and Birchfield, 1978
25. *indica*	Whitehead, 1968
26. *inornata*	Lordello, 1956
27. *javanica*	(Treub, 1885) Chitwood, 1949
28. *kikuyensis*	De Grisse, 1961
29. *kirjanovae*	Terenteva, 1965
30. *litoralis*	Elmiligy, 1968
31. *lordelloi*	da Ponte, 1969
32. *lucknowica*	Singh, 1969
33. *mali*	Ito, Ohshima, and Ichinohe, 1969
34. *megadora*	Whitehead, 1968
35. *megatyla*	Baldwin and Sasser, 1979
36. *megriensis*	(Poghossian, 1971) Esser, Perry, and Taylor, 1976
37. *microtyla*	Mulvey, Townshend, and Potter, 1975
38. *naasi*	Franklin, 1965
39. *nataliei*	Golden, Rose, and Bird, 1981
40. *oteifae*	Elmiligy, 1968

41. *ottersoni*	(Thorne, 1969) Franklin, 1971
42. *oryzae*	Maas, 1978
43. *ovalis*	Riffle, 1963
44. *platani*	Hirschmann, 1982
45. *poghossianae*	Kirjanova, 1963
46. *propora*	Spaull, 1977
47. *querciana*	Golden, 1979
48. *sewelli*	Mulvey and Anderson, 1980
49. *spartinae*	(Rau and Fassuliotis, 1965) Whitehead, 1968
50. *subarctica*	Bernard, 1981
51. *tadshikistanica*	Kirjanova and Ivanova, 1965
52. *thamesi*	Chitwood in Chitwood, Specht and Havis, 1952
53. *vialae*	(Lavergne, 1901) Chitwood and Oteifa, 1952

METHODS

Our initial evaluation of the 52 species and one subspecies was based on the primary characters of: distinctive shape of perineal patterns (cf. *M. brevicauda, M. camelliae, M. javanica,* and *M. ovalis*), juvenile body length and "c" measurement, and stylet length of females, males, and juveniles. Secondary diagnostic characters were: position of excretory pore and existence and description of vulval protuberance in females, number of lateral incisures and spicule length in males, and position of the hemizonid in juveniles (Table 2).

A statistical complete-linkage cluster analysis (50) based on the segregation of 10 clusters was conducted to further evaluate species relationships. The diagnostic characters used were: juvenile body length and "c" ratio; juvenile, female, and male stylet lengths; and spicule length. Several other important characters were not used because of their frequent omission from species descriptions. Morphometric data for the characters used appeared in all but seven descriptions, i.e. *Meloidogyne bauruensis, M. elegans, M. indica, M. lordelloi, M. naasi, M. ottersoni* and *M. tadshikistanica.* Missing measurements and ratios only for these seven species were obtained by deriving the mean value as calculated from the grouped data for that measurement or ratio from all the other species. When only a value, without range, appeared in the original publication, the necessary range was created by adding and subtracting 0.5 μm to the given value, which was needed to perform the analysis. Admittedly, liberties were taken in supplying missing measurements for seven of the 53 taxa and in creating a range when only a single value appeared in the original description. Yet, such data manipulation was wholly necessary for purposes of exploring species relationships through

Table 2. Diagnostic data on species of the genus *Meloidogyne*. Measurements are from original descriptions unless otherwise specified.

Species	Juveniles					Females				Males		
	Body length in μm	"c" Ratio	Stylet length in μm	Hem./ Exc.P.[a]	Rectal dila.[b]	Stylet length in μm	Exc.P./ stylet[c]	Body axis[d]	Post. prot.[e]	Stylet length in μm	Spicule length in μm	No. of lateral incisures
acrita	345-396	7.0-7.5	10-11	?	?	16	?	?	?	20-24	29-34	?
acronea	440-460	9.2	10	?	?	11-13	14	?	PST	16-18	32-34	?
africana	380-470	7.3-14.3	12-18	?	?	15	16-30	?	PST	19-22	26-35	4-5
ardenensis	372-453	8.6-12.3	9-14	POS	NO	15-19	8-11	?	SLT	17-24	28-38	4-5
arenaria	450-490	6.0-7.5	10	?	?	14-16	?	?	?	20-24	31-34	?
arenaria[f]	398-605	?	14-16[f]	?	?	13-17	?	?	?	20-25	?	?
artiella	334-370	13-16	14-16	ANT	?	12-16	?	?	ABS	17-27	25-30	4-5
bauruensis	345-352	?	11-11.6	?	?	15.0-16.6	?	?	?	20.0-23.2	28-32.2	?
brevicauda	460-590	21-29	14.3-14.5	ANT	?	22.1	20-28	?	?	19.5-20.7	34-42.5	2-4
camelliae	443-576	9.5-12	11.2-12	ANT[j]	NO	17.2-18.1	POS	STR	ABS	20.7-23.7	33-39	4-5
carolinensis	417-516	9.7-13.3	10.9-13.1	ANT	?	14.9-16.9	ANT	?	SLT	17.4-21.9	27-35.3	4
chitwoodi	326-417	7.9-9.6	9-10.3	ANT[j]	NO	11.2-12.5	POS	STR	SLT	18.1-18.5	26-29	4
coffeicola	337-424	9.5-13.9	9.2-10.7	?	?	15.3-17.6	13	?	?	23-26	20-29	2-4
cruciana	419-480	8.6-10.5	9.8-12.1	ANT	YES	11.4-16.2	POS	STR	ABS	19.4-24.1	28.7-38.0	4
decalineata	471-573	10.3-12.2	10.7-13.7	ANT	NO	12-17	20-50	?	BTH	19-20	33-37	10
deconincki	340-400	6.8-9.8	10-11	ANT	NO	16-20	ANT	?	?	22-28	29-37	4-5
elegans	360-390	8.0-9.5	9.8-10.8	?	?	13-16	?	?	?	U N K N O W N		
ethiopica	383-432	8.1-9.8	9.1-10.9	ANT	YES	11-15	15-26	?	ABS	14.4-24.1	28.8-36	4-5
exigua[g]	333-358	7.3-7.8	9.2	?	?	10.7	?	?	?	18.4-19.9	20-26	$\geqq$4
grahami	391-459	7.1-8.8	10.1-11.8	ANT[j]	ST	14.6-16.2	POS	STR	ABS	24.1-25.8	30-36	4
graminicola	415-484	5.5-6.7	11.2-12.3	ANT	?	10.6-11.2	POS	STR	?	16.2-17.4	27.4-29.1	4-8
graminis	420-510	5.7-6.8	11.7-13.4	POS	?	11.7-13.4	EVE	OFF	?	17.9-19.0	28-29.1	4
hapla	331-372	6.8-8.0	10	?	?	12-14	?	?	?	17-18	29-31	?

Table 2. Diagnostic data on species of the genus *Meloidogyne*. Measurements are from original descriptions unless otherwise specified (Continued).

Species	Juveniles					Females				Males		
	Body length in μm	"c" Ratio	Stylet length in μm	Hem./ Exc.P[a]	Rectal dila.[b]	Stylet length in μm	Exc.P./ stylet[c]	Body axis[d]	Post. prot.[e]	Stylet length in μm	Spicule length in μm	No. of lateral incisures
hapla A[f]	357-467	?	14-16[k]	?	?	13-17	?	?	?	17-23	?	?
hapla B[f]	410-517	?	15-17[k]	?	?	15-17	?	?	?	19-23	?	?
incognita	360-393	8.0-9.4	10	?	?	15-16	?	?	?	23-26	34-36	?
incognita[f]	346-463	?	14-16[k]	?	?	15-17	?	?	?	23-25	?	?
incognita wartelli	352-404	7.4-9.0	9.5-10.6	ANT[j]	ST	13.6-15.3	POS	STR	ABS	21.3-23.8	28-36	4
indica	381-448	21.2-31.0	10-14	?	NO	12-16	16-22	?	?	?	?	4
inornata	575-420	11.6-12.7	10-13.3	?	?	15-16.6	17-22	?	?	20-25	26.5-33.0	≧4
javanica	340-400	5.8-6.6	10	?	?	16	?	?	?	20-21	30-31	?
javanica[f]	402-560	?	14-16[k]	?	?	14-18	?	?	?	18-22	?	?
kikuyensis	290-360	10.0-12.3	12-15	ANT	?	13.5-16	9-19	?	ABS	17-20	31-35	3-4
kirjanovae	359-433	6-8	11	?	?	13-15	?	?	?	20-24	27-35	4
litoralis	330-450	9.7-11.8	11-15	?	NO	14-18	7-8	?	?	19-24	29-33	5
lordelloi	340-380	?	10-11	?	?	12.3-15.0	12-22	?	?	U N K N O W N		
lucknowica	410-575	8.9-14.4	11-18	?	?	15-24	?	BTH	BTH	15-25	27-58	4-6
mali	390-450	12-15	12-15	?	NO	13-17	20-29	?	SLT	18-22	28-35	4
megadora	413-458	7.6-11.0	10.7-13.2	ANT[j]	NO	13-17	EVE	?	BTH	18.3-21.9	25.2-36.0	4-6
megatyla	393-457	9.5-13.5	13.8-16.6	ANT[j]	NO	14.0-17.7	?	?	ABS	21.7-25.5	29.3-36.9	4
megriensis	358-467	6-8	13-15	?	?	13-18	POS	?	PST	13-18	23-30	4-6
microtyla	350-400	8.2-8.7	11-12	ANT	ST	13-15	POS	?	ABS	18-20	28-30	4
naasi	418-465	6.2	13-15	POS[j]	NO	11-15	7-11	?	SLT	16-19	25-30	4
nataliei	539-641	19-26	21.9-22.8	POS	NO	21.1-22.4	ANT	STR	PST	28.4-29.2	41.3-44.3	5

Table 2. Diagnostic data on species of the genus *Meloidogyne*. Measurements are from original descriptions unless otherwise specified (Continued).

Species	Juveniles					Females				Males		
	Body length in μm	"c" Ratio	Stylet length in μm	Hem./ Exc.P[a]	Rectal dila.[b]	Stylet length in μm	Exc.P./ stylet[c]	Body axis[d]	Post. prot.[e]	Stylet length in μm	Spicule length in μm	No. of lateral incisures
oteifae	320-400	7.5-9.2	11-13	?	NO	13-14	POS	?	?	19-23	29-37	4-5
ottersoni	430-500	?	13-15	ANT[j]	?	10-12	POS	OFF	BTH	14-16	19-23	4
oryzae	500-615	6.8-8.6	14-15	ANT	YES	14-18	POS	?	SLT	19-20	25-34	4-8
ovalis[h]	350-430	8-9	8.6-11.7[l]	ANT	YES	17-24	10-12	?	?	18-23	31-38	4
platani	395-497	7.1-8.5	11.6-12.6	ANT	YES	15.8-17.3	POS	?	ABS	19.4-24.3	25.1-31.6	4-8
poghossianae	?	?	?	?	?	15	POS	?	PST	?	?	?
propora	335-430	17.3-24.1	16.5-18.5	POS	NO	13.8-19.6	18-22	?	BTH	18.1-23.2	32-35	4-7
querciana	411-451	7-13	10.2-11.6	ANT[j]	NO	17-18.9	POS	STR	ABS	19-19.6	32-32.5	4
sewelli	460-540	6.6-7.9	11-13	?	YES	14-15	POS	?	ABS	18-20	29-30	4
spartinae	612-912	6.7-9.0	14-16.8	POS	?	11-17	POS	?	PST	16.8-21	25.2-40	4
subarctica	349-507	8.2-11.0	13.5-15.4	ANT	NO	12.7-15.7	POS	STR	ABS	17.2-19.7	32.9-36.9	4
tadshikis-tanica	350-435	?	12-15	?	?	14.5-15	POS	?	?	22.4-25	27-36.6	4
thamesi[i]	410-476	7.6-8.6	10.2-12.7	?	ST	15-18	20-33	?	ABS	20.5-28.1	21.6-28.1	?

[a]Hemizonid anterior (ANT) or posterior (POS) to excretory pore.
[b]Rectal dilation present (YES), absent (NO), sometimes (ST)
[c]Excretory pore position in relation to base of stylet: Anterior (ANT), posterior (POS), even (EVE), or number of annules from anterior end
[d]Position of neck in relation to a median plane through the body passing through the vulva: neck lying in the median plane (STR), neck offset (OFF), or both (BTH)
[e]Posterior protuberance present (PST), absent (ABS), slight (SLT), or both (BTH)
[f]Measurements from Eisenback et al., 1981
[g]*M. exigua* measurements from Lordello & Zamith, 1959
[h]*M. ovalis* juvenile stylet length, position of excretory pore, and presence of rectal dilation from Whitehead, 1968
[i]*M. thamesi* measurements from Whitehead, 1968
[j]Position determined from author's drawings
[k]Base of stylet to tip of head
[l]Measurement from Whitehead 1968

cluster analysis. Unfortunately, descriptions of three newer species[2] were received after the analysis was completed and thus do not appear in the dendrogram (Fig. 1). A recent publication by Eisenback, et al. (17) gives new morphometric data for *M. incognita, M. arenaria, M. hapla,* and *M. javanica* which were incorporated into the analysis as separate entities from the species originally described by Chitwood (4). A provisional key illustrating the existing similarities in morphometrics among species and species groups is presented (Table 3).

REVIEW OF SPECIES

Comparison of primary and secondary characters of *Meloidogyne* species was often very difficult, if not impossible, due to similarity of characters and morphometrics. *Meloidogyne thamesi* and *M. chitwoodi* are similar to *M. arenaria* and *M. hapla* respectively. *M. acrita* and *M. incognita wartelli* are difficult to separate from *M. incognita. M. bauruensis and M. lordelloi* are closely related to *M. javanica.* These species should be reevaluated to bring out additional differentiating characters.

The following accounts illustrate the need for additional studies.

M. thamesi Chitwood in Chitwood, Specht, and Havis, 1952

Chitwood (6) first recognized *M. thamesi* as a subspecies of *M. arenaria.* Goodey (30) raised it to species level. The diagnostic characters for *M. thamesi* as stated by Chitwood are: perineal pattern with vertical series of transverse markings, asymmetrical male stylet knobs, male head in semioblique position, dorsal esophageal gland orifice situated 33 μm behind stylet in males and females, larval tail blunt and tending to terminate in bifid or trifid lobes, larval rectum tending to be dilated. He also observed that Spanish peanuts are not a host of *M. thamesi,* unlike *M. arenaria.*

Whitehead (60) studied type populations and topotypes of *M. thamesi.* He did not mention the vertical series of transverse markings in the perineal pattern nor the position of the male head. In describing the male he states "occasionally knobs appearing unequal." He observed the position of the dorsal esophageal gland orifice of males and females to be the same as measurements given for *M. arenaria.* He also described and illustrated juvenile tails without lobation.

Data recently published (17) extend *M. arenaria* juvenile body length range to completely encompass the range of *M. thamesi.* Although there is a difference in spicule length given for the two species (21-28 μm for *M. thamesi;* 31-34 μm for *M. arenaria*), spicule length is a secondary

[2]*Meloidogyne carolinensis, M. cruciani,* and *M. platani*

Table 3. Key to Species of *Meloidogyne* Goeldi, 1887

1.	Perineal pattern shape rectangular, distinctly circular, star-shaped, or with two rope-like striae 2
	Perineal pattern shape not as above 8
2.(1)	Perineal pattern with rounded arch and two separated, rope-like striae ..... *M. nataliei* Golden, Rose, & Bird, 1981
	Perineal pattern not as above 3
3.(2)	Perineal pattern shape circular 4
	Perineal pattern not circular 7
4.(3)	Mean female stylet length greater than 15μm 5
	Mean female stylet length less than 15μm 6
5.(4)	Mean juvenile "c" measurement greater than 15 ..... *M. propora* Spaull, 1977
	Mean juvenile "c" measurement less than 15 ..... *M. ovalis* Riffle, 1963
6.(4)	Mean juvenile length greater than 415μm, ... *M. ottersoni* (Thorne, 1969) Franklin, 1971
	Mean juvenile length less than 415μm, ... *M. oteifae* Elmiligy, 1968
7.(3)	Perineal pattern star-shaped to rectangular, striae rope-like ..... *M. camelliae* Golden, 1979
	Perineal pattern rectangular, never star-shaped, striae not rope-like ..... *M. brevicauda* Loos, 1953
8.(1)	Mean juvenile length greater than 500μm 9
	Mean juvenile length less than 500μm 11
9.(8)	Mean juvenile length greater than 600μm, ... *M. spartinae* (Rau & Fassuliotis, 1965) Whitehead, 1968
	Mean juvenile length less than 600 μm 10
10.(9)	Male with 10 lateral incisures. Mean juvenile "c" measurement 11.2 ..... *M. decalineata* Whitehead, 1968
	Male with 8 or less lateral incisures. Mean juvenile "c" measurement less than 9 ..... *M. oryzae* Maas, Sanders, & Dede, 1978 ..... *M. sewelli* Mulvey & Anderson, 1980
11.(8)	Mean juvenile "c" measurement 13 or higher (*M. lucknowica* 12.2) 12
	Mean juvenile "c" measurement 10.5 or less (*M. carolinensis* 10.9) 14
12.(11)	Mean juvenile length less than 375μm ..... *M. artiella* Franklin, 1961
	Mean juvenile length greater than 375μm 13

13.(12) Mean juvenile "c" measurement greater than 20
..... *M. indica* Whitehead, 1968
Mean juvenile "c" measurement less than 20
..... *M. mali* Ito, Ohshima, & Ichinohe, 1969
..... *M. lucknowica* Singh, 1969

14.(11) Mean juvenile length 410μm or greater 15
Mean juvenile length 400μm or less 29

15.(14) Mean juvenile "c" measurement below 7.0 16
Mean juvenile "c" measurement above 7.5 19

16.(15) Mean male stylet length greater than 20μm
..... *M. arenaria* (Neal, 1889) Chitwood, 1949
M. thamesi Chitwood in Chitwood, Specht, & Havis, 1952
Mean male stylet length less than 20μm 17

17.(16) Position of juvenile hemizonid posterior to excretory pore .. 18
Position of juvenile hemizonid anterior to excretory pore
..... *M. graminicola* Golden, 1965

18.(17) Juvenile stylet length range 13-15μm .. *M. naasi* Franklin, 1965
Juvenile stylet length range 11.7-13.4μm
.... *M. graminis* (Sledge & Golden, 1964) Whitehead, 1968

19.(15) Mean male stylet length 19.6μm or less 20
Mean male stylet length 20μm or more 22

20.(19) Female stylet length 17-19μm ..... *M. querciana* Golden, 1979
Female stylet length 11-14μm 21

21.(20) Female with posterior protuberance, no stippled
zone near anus .....*M. acronea* Coetzee, 1956
Female without posterior protuberance, usually stippled
zone between anus and tail terminus
..... *M. hapla* Chitwood, 1949
M. chitwoodi Golden, O'Bannon, Santo, & Finley, 1980
..... *M. subarctica* Bernard, 1981

22.(19) Mean male stylet length 23-25μm 23
Mean male stylet length 20-22μm 24

23.(22) Juvenile stylet length range 14-17μm, mean male stylet
length 24μm ..... *M. megatyla* Baldwin & Sasser, 1979
Juvenile stylet length range 10-12μm, mean male stylet
length 25μm ..... *M. grahami* Golden & Slana, 1978

24.(22) Excretory pore posterior to base of female stylet 25
Excretory pore anterior or even with base of female stylet .. 28

25.(24) Adult female with posterior protuberance
..... *M. africana* Whitehead, 1960
Adult female without posterior protuberance 26

26.(25) Juvenile stylet length 11.6-12.6μm, female stylet length

15.8-17.3μm ..... *M. platani* Hirschmann, 1982
Juvenile stylet length 9.1-12.1μm, female stylet length 11.0-16.2μm 27

27.(26) Perineal pattern with lateral incisures and punctations around anus .... *M. cruciana* Garcia-Martinez, Taylor, & Smart, 1982
Perineal pattern without lateral incisures or anal punctations ..... *M. ethiopica* Whitehead, 1968

28.(24) Mean juvenile length 417μm, hemizonid posterior to excretory pore ..... *M. ardenensis* Santos, 1968
Mean juvenile length 451μm or greater, hemizonid anterior to excretory pore ..... *M. megadora* Whitehead, 1968
..... *M. carolinensis* Eisenbach, 1982

29.(14) Mean juvenile body length 340μm or greater 30
Mean juvenile body length 320μm
..... *M. kikuyensis* De Grisse, 1961

30.(29) Juvenile stylet length 9μm, female stylet 11μm
..... *M. exigua* Goeldi, 1887
Juvenile stylet length 9μm or greater, female stylet length 13μm or greater 31

*31.(30) Male stylet length 13-18μm long, female with posterior protuberance ..... *M. megriensis* (Poghossian, 1971) Esser, Perry, & Taylor, 1976
Male stylet length 18μm or more, female without posterior protuberance 32

32.(31) Female excretory pore posterior to base of stylet 33
Female excretory pore anterior to base of stylet 35

33.(32) Juvenile stylet mean length 12μm or greater
.....*M. tadshikistanica* Kirjanova & Ivanova, 1965
Juvenile stylet mean length less than 12μm 34

34.(33) Juvenile "c" measurement 5.8-6.6
..... *M. javanica* (Treub, 1885) Chitwood, 1949
.....*M. bauruensis* Lordello, 1956
.....*M. lordelloi* daPonte, 1969
Juvenile "c" measurement 9.5-13.9
.....*M. coffeicola* Lordello & Zamith, 1960

35.(32) Female perineal pattern with distinct punctations present at body terminus above anus
..... *M. deconincki* Elmiligy, 1968
Female perineal pattern without punctations present at body terminus above anus 36

36.(35) Male stylet length range 18-26μm, spicules 28-36μm

..... *M. acrita* Chitwood & Oteifa, 1952
.. *M. incognita* (Kofoid & White, 1919) Chitwood, 1949
.... *M. incognita wartelli* Golden & Birchfield, 1978
..... *M. inornata* Lordello, 1956
..... *M. kirjanovae* Terenteva, 1965
..... *M. litoralis* Elmiligy, 1968
... *M. microtyla* Mulvey, Townshend & Potter, 1975

*M. elegans da Ponte, 1977 keys to this couplet but its description lacks male measurements and female protuberance data. It cannot be further separated in this key.

diagnostic character and hardly adequate as the sole differentiating characteristic between the species. *Meloidogyne thamesi* is morphologically indistinguishable from *M. arenaria* but can be separated due to a physiological difference which exists in host preference between the two species (6). It should be noted that Taylor and Sasser (52) recognize races within species based on physiological differences, e.g. *M. arenaria* and *M. incognita*.

M. incognita wartelli Golden and Birchfield, 1978

The diagnosis by Golden and Birchfield (26) compares *M. incognita wartelli* with *M. incognita incognita* and *M. incognita acrita*. They state that it differs from the other subspecies by: female stylet shape, position of dorsal esophageal gland orifice, position of excretory pore, and the usual absence of labial annulations on the male. They admit, however, ". . . that a subspecies cannot always be identifiable apart from its nominate subspecies in the same species group."

Ranges of the position of the female dorsal esophageal gland orifice for *wartelli* and *incognita* do not overlap, but are separated by only 0.06 μm. The value of this diagnostic characteristic is dubious. Priest and Southards (44) studied juveniles of *M. incognita* and found that the distance from the stylet base to the dorsal esophageal gland orifice was among those measurements having the greatest variation. The range of the position of the excretory pore from the anterior end overlaps the range for *M. incognita* given by Whitehead (60). Little value is placed on the presence or number of male lip annulations due to reports of variability (1,4,17). Also, the male stylet length range for the subspecies overlaps that of the nominate subspecies (*wartelli*, 22-23 μm; *incognita*, 23-25 μm). Morphological differences of *M. incognita wartelli* from the nominate subspecies are so slight that the two could be regarded morphologically indistinguishable, yet distinct differences in host preference do exist (26).

M. acrita Chitwood and Oteifa, 1952

Chitwood (4) first regarded *M. acrita* as a variety of *M. incognita.* Chitwood and Oteifa (5) elevated the variety to subspecies level, which Goodey (30) synonymized to *M. incognita.* Terenteva (55) considered this synonymization as invalid. Esser, Perry, and Taylor (19) elevated the subspecies to specific rank but Golden and Birchfield (26) still considered the taxon as *M. incognita acrita.*

The diagnosis by Chitwood separates the variety from the nominal species by: transverse striae (annulations) in the post-anal region of females tend to be straight instead of arched, and stylet knobs are more offset in both sexes. Terenteva utilized variational statistics based on: perineal pattern, stylet knob shape, and head height of males to demonstrate that the two were discrete subspecies. Esser concurred with Chitwood's analysis and pointed out differences in juvenile alpha and gamma ratios and spicule length. He also stated that Chitwood considered the undilated rectum of *M. incognita acrita* juveniles the principle separating character.

Chitwood (4) admitted that the anatomies of *M. incognita* and *M. incognita acrita* are "very similar." Eisenback et al. (17) presented wider ranges for several body measurements of *M. incognita* causing almost a complete overlapping of morphometric ranges between the two species. The intraspecific variability in dilation of the rectum in juveniles of some species (41,60) may reduce its value as a separating character.

The variability of perineal patterns in *M. incognita* and *M. acrita* has been referred to (1,58); therefore this character is without major diagnostic significance in distinguishing between these two species. We concur with the Triantaphyllou and Sasser's (58) statement that, "since morphological distinction between the subspecies is often uncertain and perineal patterns give little information on the physiological behavior of a certain population, present division of the species into two subspecies seems to serve no practical purpose."

M. bauruensis Lordello, 1956

Lordello (37) first regarded *M. bauruensis* as a subspecies of *M. javanica.* Goodey (30) synonymized *M. javanica bauruensis* to *M. javanica* without comment. Whitehead (60) concurred stating that it was not a clearly distinguishable taxon. Esser et al. (19) raised the subspecies to species status for the following reasons: areolations present in lateral field of males, two male labial annules, larger juvenile gamma measurement, and perineal pattern shape.

Lordello erected *M. javanica bauruensis* as a subspecies using the

following diagnostic characters; eggs unusually wide, neck and stylet of juvenile longer than that of *M. javanica,* head of male with single post-labial annule, lateral lines less evident in perineal pattern and not extending to cervical region, higher arch in perineal pattern composed of wavy to zig-zag striae.

Egg dimensions are of little value (60). The difference in juvenile stylet ranges is of questionable value since Chitwood (4) did not give the range of *M. javanica.* Whitehead (60) measured a population of *M. javanica* in which the juvenile stylet length overlapped the range of *M. bauruensis.* Intraspecific variation of head annulations noted by workers (1,4,17) give reason to reject this as a diagnostic character. The juvenile "c" measurement is not recorded by Lordello and cannot be used for comparisons. The areolations of the lateral field, juvenile neck length, and details in the perineal pattern are not, in our opinion, substantial diagnostic characters. The absence of primary diagnostic differentiating characters and lack of host preference data suggest the conspecificity of *M. bauruensis* with *M. javanica.*

M. lordelloi da Ponte, 1969

Da Ponte (10) stated that *M. lordelloi* is closely related to *M. javanica.* The single differentiating diagnostic character observed was the nature of the annulation of the perineal pattern. In terms of measurement, he noted no difference between *M. lordelloi* and *M. javanica* except for body size of females which is longer for *M. lordelloi.* Da Ponte recognized this character as being weak and subject to variations according to environment and host plant.

We find that all morphometric measurements are similar and no characters other than perineal pattern aberrations separate these species. Da Ponte did not find males and gave no host preference data. The validity of *M. lordelloi* is decidedly suspect.

M. elegans da Ponte, 1977

The diagnosis by da Ponte (11) is based solely upon particulars of the perineal pattern. He states that there are no great differences in morphological characters between *M. elegans* and some other species of the genus.

Our analysis confirms that *M. elegans* is morphometrically similar to several species, e.g. *M. coffeicola, M. deconincki, M. incognita,* and *M. microtyla.* No data on males was presented. Perineal patterns should not constitute the only basis on which to create new species. Additional data should be made available before *M. elegans* can be considered a sound species.

M. litoralis Elmiligy, 1968

Elmiligy (18) compared *M. litoralis* with *M. deconincki* and *M. ardenensis* and gave the following diagnostic characters: perineal pattern with arch, cheeks on boths sides of vulva slit, lateral field marked by zig-zag or irregular line on both sides of pattern, prominent cuticular fold covers the anus and diverges obliquely toward the vulva sides, female with relatively long stylet, dorsal esophageal gland orifice with "posterior position," excretory pore located in "anterior position," males with five lateral lines completely areolated.

Descriptions of the perineal pattern are not considered wholly dependable diagnostic characters. The position of the excretory pore and dorsal esophageal gland opening, as well as all other morphometric measurements, overlap with those of *M. deconincki* and *M. incognita.* The male character of five completely areolated lateral lines comes from observation of only two male specimens. As at least nine other species have this character, it is not considered diagnostic.

Similarities in female and juvenile morphometrics with *M. deconincki* and *M. incognita,* as well as the lack of sound diagnostic differentiating characters, make insecure the consideration of *M. litoralis* as a valid species.

M. lucknowica Singh, 1969

The diagnosis by Singh (48) lists the following distinguishing characters: shape of perineal pattern, extent of lateral incisures anteriorly, prominence or absence of post labial annules, presence of cephalids both in male and female, unequal spicules, and distinctive shape of gubernaculum.

None of the diagnostic characters given by Singh are strong differentiating criteria. Perineal patterns are too variable. The presence of cephalids, intra-spicular measurements, and shape of gubernaculum have not been used as diagnostic characters for other species, hence they form no basis of comparison to other species.

Meloidogyne lucknowica has a spicule length range greater than any species yet described. However, observations and measurements by Singh cast doubt on the legitimacy of this species. He states "Female variable in shape, being oval, rounded or oblong and sometimes elongated. No two specimens look alike. The neck sometimes forming a right angle with the body." Juvenile body length and stylet ranges are much wider than found in other species. The geographic range and populations studied were confined to the roots of *Luffa cylindrica* (sponge gourd) from a kitchen garden.

M. kirjanovae Terenteva, 1965

Terenteva (54) compares *M. kirjanovae* only with *M. arenaria* in her diagnosis, without listing any distinct morphometric or morphologic characters separating *M. kirjanovae* from other species of the genus.

In our analysis we noted that *M. arenaria* is readily separated from *M. kirjanovae* by a larger juvenile body length (450-490 vs. 359-433 μm). *Meloidogyne kirjanovae* is close to several other species morphometrically, including *M. coffeicola, M. incognita, M. javanica,* and *M. tadshikistanica.* The lack of clear diagnostic differentiating characters makes recognition of the species virtually impossible.

M. Chitwoodi Golden, O'Bannon, Santo and Finley, 1980

Golden et al. (27) regarded *M. chitwoodi* closely related to *M. hapla* but differing by: the shape of the perineal pattern surrounding a sunken vulva, presence of vesicles or vesicle-like structures in the anterior part of the median bulb of females, and the juvenile tail being short and blunt with a hyaline tail terminus.

We regard the perineal pattern as a weak diagnostic character, as has been repeatedly pointed out in this paper. The sunken vulva, ostensibly detected only by use of the scanning electron microscope (16), cannot be regarded as unique until other nominal *Meloidogyne* species are similarly studied. The presence of vesicles or vesicular-like structures in the female metacorpus is presented as a diagnostic character but is also stated to be "usually" present. Morphometric comparisons of the two species show some overlapping of juvenile, female, and male measurements. The recent paper by Nyczepir et al. (42) cites differential host tests, perineal pattern, and tail shape and morphology as aids for differentiating *M. chitwoodi* from *M. hapla.*

M. inornata Lordello, 1956

This species was originally considered closely related to *M. incognita* (36).It was stated that *M. inornata* differs by: wider eggs, juvenile head showing only one wide post-labial annule, excretory pore in females located more posteriorly, and male bearing one post-labial annule instead of three. Lordello considered the male head annulations as the most outstanding character for separating *M. inornata* from *M. incognita* and *M. acrita.* Taylor and Sasser (53) differentiate *M. inornata* from *M. incognita* by the position of the excretory pore.

Differences in male head annulation are of little value due to reports (1,4,17) of high variability of this character [recent work differentiating the four common root-knot species not withstanding (17)] and

illustrations of *M. incognita* with one post-labial annule (1,60). The limited value of egg length as a taxonomic character was pointed out by Whitehead (60). Position of the excretory pore is also of doubtful value as the ranges recorded for *M. inornata* overlap with the ranges stated by Whitehead for the syntype population of *M. incognita*. Our studies suggest the characters best differentiating *M. inornata* from *M. incognita* are the juvenile "c" measurement and spicule length.

CLUSTER ANALYSIS

The clusters resulting from this computerized statistical technique (Fig. 1) place the species previously reviewed within the same cluster as the species with which they are related. *Meloidogyne spartinae* and *M. kikuyensis* are placed as single members of clusters. *Meloidogyne spartinae* is the most distant (dividing at second cluster split) and therefore the most unique member of the genus due to its juvenile body length range. *Meloidogyne kikuyensis* is also a unique species due to a combination of a low juvenile body length range and relatively large "c" ratio. It is of interest that *M. acrita* and *M. javanica* have the highest degree of similarity as evidenced by their juxtaposition in Group 1.

Meloidogyne arenaria, M. hapla, M. incognita and *M. javanica* as described by Chitwood (4) were not placed into the same clusters as those same species described by Eisenback et al. (17) due to differences in juvenile morphometrics. The descriptions for *M. javanica* have the greatest dissimilarity of the four species. The two races of *M. hapla* are placed in separate clusters again due to differences in juvenile morphometrics.

DISCUSSION

To date, the female perineal pattern has been a major diagnostic character of the genus (17,22,52,53). Admittedly, some species do have typical patterns which are recognizable (52,54,58), and which are subject to some hereditary control (14,58). The genus is rapidly growing in size and several populations with intermediate or aberrant perineal patterns have been described. The ability to distinguish between species primarily by this characteristic has become increasingly difficult. Intraspecific variation of perineal patterns can occur in females arising from a single egg mass (1,58) and morphological changes in patterns may take place during growth of the female (58). Even the chance wrinkling of a pattern during mounting on a slide may result in an erroneous conclusion. Subjective, inconclusive descriptions of patterns are one of the major problems in using this character and often confuse observers

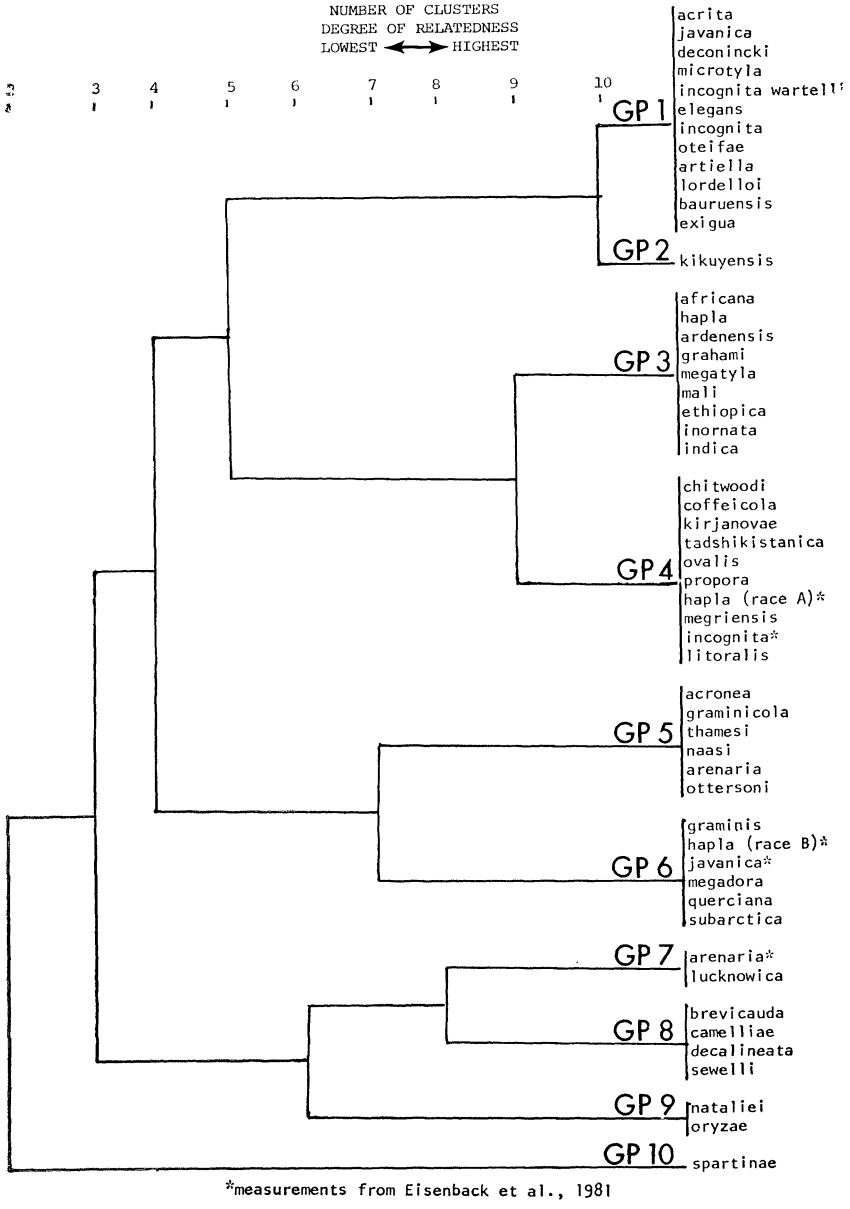

Fig. 1. Phenetic dendrogram based on a 10-cluster analysis of 6 *Meloidogyne* characters.

not familiar with the genus. As descriptions become more detailed, the diagnostic value of perineal patterns decreases.

The use of mean values of the remaining primary characters, i.e. juvenile body length and "c" measurement, and stylet lengths of adults and juveniles, is of benefit but overlapping of ranges and authors' idiosyncrasies in measuring populations allow for errors in subsequent identifications.

The position of the female excretory pore is useful when considered as being positioned anterior or posterior to the base of the stylet. Intraspecific variation is indicated in reports of excretory pore position (35, 26,24) and variable technique in measurement, i.e. number of annules from head, distance from base of stylet, stylet lengths from head, increase the difficulty of using this measurement.

Existence of vulva protuberance must be used with caution since descriptions note its presence as "slight" to "absent" (47,56,60).

Number of male lateral incisures is also used with caution as intraspecific variation occurs and single specimens have varying numbers of striae depending upon the section of body observed.

Position of the juvenile hemizonid is a helpful character. Unfortunately, earlier authors did not record this character and it is of value in only a few cases.

Spicule length ranges and mean values are less useful due to high frequency of overlapping ranges.

The cluster analysis performed concurred with our earlier analysis of certain species by placing them into clusters with closely related species. The value of this analysis is weakened by its use of only six characters and dependence on two male characters, spicule and stylet length, which are not considered to be of value for *Meloidogyne* species identification (17,53). Then too, some species which may appear in close proximity in the dendrogram (e.g. *M. javanica* and *M. acrita*) are separated by morphological characters that are not biometric and cannot be used in cluster analysis. Cluster analysis can become a useful taxonomic tool if methods for species descriptions are standardized and earlier described species are reevaluated.

CONCLUSIONS

New species of *Meloidogyne* will inevitably be published. These new members can only add to the existing confusion caused by subjective descriptions, variable characters, and differing descriptive techniques. The expertise and equipment needed to recognize these species is forming an even wider gap between the applied research scientist and the taxonomist.

Unfortunately, describing a new species is much more rewarding than studying the membership of a genus. The importance of *Meloidogyne* species world-wide is sufficient reason to spend the time and effort to clarify this complex and confusing group. Its evolutionary success as a highly adaptable group of organisms, with many physiological but few morphological differences, remains a challenge to taxonomists.

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