

Review Article

An updated checklist of *Meloidogyne* Göldi, 1887 species, with a diagnostic compendium for second-stage juveniles and males

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Abstract: The cosmopolitan root-knot nematodes of the genus *Meloidogyne* are considered as the most important plant-parasitic nematodes damaging almost all higher plant species. This paper provides an updated checklist of 105 valid species of *Meloidogyne*, along with their synonyms and non-valid members. Furthermore, species are grouped based upon their diagnostic characteristics of second-stage juveniles (tail shape, tail length, stylet length and dorsal gland orifice (DGO) distance from stylet base) and males (number of lateral incisures, stylet length, DGO and spicules length).

Keywords: Identification, *Meloidogyne*, Morphology, root-knot nematodes, species list, taxonomy

Introduction

Root-knot nematodes are included in the genus *Meloidogyne* Göldi, 1887 and constitute a relatively small, but important polyphagous group of highly adapted obligate plant parasites (Karssen *et al.*, 2013). Their taxonomic position at family level has been the subject of discussion for many years, and these nematodes have been confused with cyst nematodes (Heteroderidae Filipjev and Schuurmans Stekhoven, 1941) for a long time, and assigning the same or separate families for cyst and root-knot nematodes was controversial.

Chitwood (1949) revised *Meloidogyne* taxonomy for the first time and developed a key for five species (and one subspecies) at

that time. Subsequent reviews on the genus systematics were carried out during 1976-2002, providing identification keys and diagnostic compendia for its species (Esser *et al.*, 1976; Hewlet and Tarjan, 1983; Jepson, 1987; Eisenback and Triantaphyllou, 1991; Karssen and Hoenselaar, 1999; Karssen, 2002). The list of known species, with additional notes on the most important species, has been published by different nematologists, with the number of valid species reaching 54 in Jepson (1987), 68 in Luc *et al.* (1988), 62 in Eisenback and Triantaphyllou (1991), 80 in Siddiqi (2000), 81 in Karssen (2002), 88 in Andrassy (2007), 97 in Hunt and Handoo (2009) and 98 in Karssen *et al.* (2013).

The present study provides an updated list including 105 valid species with their synonyms, as well as lists of *species inquirendae* and *nominanuda*. Moreover, a grouping of recognized species is presented based on diagnostic characters of second-stage juveniles and males.

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Diagnosis of *Meloidogyne* Göldi, 1887

Family Meloidogynidae (Skarbilovich, 1959)
Wouts, 1973

Subfamily Meloidogyninae Skarbilovich, 1959
= Meloidogynini (Skarbilovich, 1959) Coomans, 1979

= Meloidoderellinae Husain, 1976

= Meloidoderellini (Husain, 1976) Coomans, 1979

Genus *Meloidogyne* Göldi, 1887

= *Caconema* Cobb, 1924

= *Spartonema* Siddiqi, 1986

= *Hypsoperine* (*Spartonema*) Siddiqi, 1986

= *Hypsoperine* Sledge and Golden, 1964

= *Hypsoperine* (*Hypsoperine*) (Sledge and Golden, 1964) Siddiqi, 1986

Female. Sedentary, white to transparent, rounded to pear-shaped with protruding neck. Body length from 350 μm to 3 mm. Cuticle annulated, posteriorly with a characteristic unique pattern around the perineum called the perineal pattern. Anus and vulva terminal, phasmids near the anus, the latter usually covered with cuticular fold. The perineum sometimes slightly elevated. Head not or slightly set off, cephalic framework distinct but delicate. Labial disc not, to slightly raised, fused with median and lateral lips. Two slit-like amphidial openings and ten small labial sensilla present. Stylet delicate, ranging in length from 8-25 μm , cone in most species slightly curved dorsally, shaft straight with three knobs. Dorsal pharyngeal gland orifice (DGO) 2-12 μm behind the knobs. Secretory-excretory pore between lip region and metacarpus level. Metacarpus relatively large, pharyngeal glands variable in size and shape, ventrally overlapping the intestine. Reproductive system didelphic, the gonads long, partly convoluted. Most of the unembryonated eggs deposited in an egg-sac, formed by six large rectal glands and secreted through the anus.

Male. Vermiform, non-sedentary, ranging in length between 600-2500 μm . Cuticle annulated. Lip region composed of a cap and post-labial annulus (annuli). Head cap with rounded labial disc and four fused median

lips. Six inner labial sensilla centered around the stoma and one cephalic sensillum present on each median lip. Large slit-like amphidial openings located between labial disc and lateral lips. The latter reduced or absent in some species. Lip region sometimes set off and/or partly subdivided by transverse incisures. Cephalic framework and straight stylet well developed, the latter ranging in length between 10-33 μm . DGO at 1-13 μm behind the stylet knobs. Metacarpus smaller than that in females. Secretory-excretory pore and hemizonid between metacarpus level and the ventrally-overlapping pharyngeal glands. Hemizonid anterior or sometimes posterior to the pore. Pharyngeal glands nuclei reduced to two. A single long testis usually present, rarely two reduced ones were observed. Lateral field in most species with four, up to 15 incisures in certain species, outer bands often areolated. Tail short, bluntly rounded. Bursa lacking. Phasmids near cloaca. Spicules slender, 18-47 μm long; gubernaculum crescentic, about 10 μm long.

Second-stage juvenile. Vermiform, infective stage. Body length 250-600 μm . Cuticle annulated. Lip region structure as in males, but much smaller and with weakly sclerotized cephalic framework. Straight stylet, about 7-23 μm long. DGO 1-8 μm behind the knobs. Metacarpus not well developed. Hemizonid anterior to, at the same level or posterior to the secretory-excretory pore. Three pharyngeal glands ventrally overlapping the intestine. Rectum often inflated. Tail 13-115 μm long, tapering towards hyaline tail part. Lateral field with four incisures.

Third and fourth-stage juvenile. Sedentary inside root and swollen, lacking stylet, develop within second-stage cuticle.

List of *Meloidogyne* species**Type species**

Meloidogyne exigua (Göldi, 1887) Chitwood, 1949

= *Heterodera exigua* (Göldi, 1887) Marcinowski, 1909

Other species

M. aberrans Tao, Xu, Yuan, Wang, Lin, Zhuo and Liao, 2017

M. acronea Coetzee, 1956

= *Hypsoperine acronea* (Coetzee, 1956) Sledge and Golden, 1964

= *Hypsoperine* (*Hypsoperine*) *acronea* (Coetzee, 1956) Siddiqi, 1986

M. actinidiae Li and Yu, 1991

M. aegracyperi Eisenback, Holland, Schroeder, Thomas, Beacham, Hanson, Paes-Takahashi & Vieira, 2019

M. africana Whitehead, 1960

M. aquatilis Ebsary and Eveleigh, 1983

M. arabicida López and Salazar, 1989

M. ardenensis Santos, 1968

= *M. deconincki* Elmiligy, 1968

= *M. litoralis* Elmiligy, 1968

M. arenaria (Neal, 1889) Chitwood, 1949

= *Anguillula arenaria* Neal, 1889

= *Tylenchus arenarius* (Neal, 1889) Cobb, 1890

= *Heterodera arenaria* (Neal, 1889) Marcinowski, 1909

= *M. arenaria arenaria* (Neal, 1889) Chitwood, 1949

= *M. thamesi* (Chitwood in Chitwood, Specht and Havis, 1952) Goodey, 1963

= *M. arenaria thamesi* Chitwood in Chitwood, Specht and Havis, 1952

= *M. thamesi gyulai* Amin, 1993

= *M. gyulai* Amin, 1993

M. artiellia Franklin, 1961

M. baetica Castillo, Vovlas, Subbotin and Troccoli, 2003

M. brevicauda Loos, 1953

M. californiensis Abdel-Rahman and Maggenti, 1987

M. camelliae Golden, 1979

M. caraganae Shagalina, Ivanova and Krall, 1985

M. carolinensis Eisenback, 1982

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

M. chosenia Eroshenko and Lebedeva, 1992

M. christiei Golden and Kaplan, 1986

M. cirricauda Zhang and Weng, 1991

M. citri Zhang, Gao and Weng, 1991

M. coffeicola Lordello and Zamith, 1960

= *Meloidodera coffeicola* (Lordello and Zamith, 1960) Kirjanova, 1963

M. cruciani Garcia-Martinez, Taylor and Smart, 1982

M. cynariensis Fam-Tkhan-Bihn, 1990

M. daklakensis Trinh, Le, Nguyen, Nguyen, Liébanas and Nguyen, 2018

M. decalineata Whitehead, 1968

M. dimocarpus Lio and Zhang, 2001

M. donghaiensis Zheng, Lin and Zheng, 1990

M. dunensis Palomares-Rius, Vovlas, Troccoli, Liébanas, Landa and Castillo, 2007

M. duytsi Karssen, van Aelst and van der Putten, 1998

M. enterolobii Yang and Eisenback, 1983

= *M. mayaguensis* Rammah and Hirschmann, 1988

M. ethiopica Whitehead, 1968

= *M. brasiliensis* Charchar and Eisenback, 2002

M. fallax Karssen, 1996

M. fanzhiensis Chen, Peng and Zhang, 1990

M. floridensis Handoo, Nyczepir, Esmenjaud, van der Beek, Castagnone-Sereno, Carta, Skantar and Higgins, 2004

M. fujianensis Pan, 1985

= *M. fujianensis* Cangsang, Jing and Shengyuan, 1988

M. graminicola Golden and Birchfield, 1965

M. graminis (Sledge and Golden, 1964) Whitehead, 1968

= *Hypsoperine graminis* Sledge and Golden, 1964

= *Hypsoperine* (*Hypsoperine*) *graminis* (Sledge and Golden, 1964) Siddiqi, 1986

M. hainanensis Liao and Feng, 1995

M. hapla Chitwood, 1949

M. haplanaria Eisenback, Bernard, Starr, Lee and Tomaszewski, 2004

M. hispanica Hirschmann, 1986

M. ichinohei Araki, 1992

M. incognita (Kofoid and White, 1919) Chitwood, 1949

= *Oxyuris incognita* Kofoid and White, 1919

= *Heterodera incognita* (Kofoid and White, 1919) Sandground, 1923

- = *M. incognita incognita* (Kofoed and White, 1919) Chitwood, 1949
 = *M. acrita* Chitwood, 1949
 = *M. incognita acrita* Chitwood, 1949
 = *M. elegans* da Ponte, 1977
 = *M. grahamsi* Golden and Slana, 1978
 = *M. incognita grahamsi* (Golden and Slana, 1978) Jepson, 1987
 = *M. kirjanovae* Terenteva, 1956
 = *M. wartellei* Golden and Birchfield, 1978
 = *M. incognitawartellei* Golden and Birchfield, 1978
 = *M. polycephannulata* Charchar, Eisenback, Vieira, Fonseca-Boiteux and Boiteux, 2009
M. indica Whitehead, 1968
M. inornata Lordello, 1956
 = *M. incognitainornata* Lordello, 1956
M. izalcoensis Carneiro, Almeida, Gomes and Hernández, 2005
M. javanica (Treub, 1885) Chitwood, 1949
 = *Heterodera javanica* Treub, 1885
 = *Tylenchus (Heterodera) javanicus* (Treub, 1885) Cobb, 1890
 = *Anguillulajavanica* (Treub, 1885) Laverigne, 1901
 = *M. javanicajavanica* (Treub, 1885) Chitwood, 1949
 = *M. javanicabauruensis* Lordello, 1956
 = *M. bauruensis* (Lordello, 1956) Esser, Perry and Taylor, 1976
 = *M. lordelloi* da Ponte, 1969
 = *M. lucknowica* Singh, 1969
M. jianyangensis Yang, Hu, Chen and Zhu, 1990
 = *M. jianyangensis* Zhu, Lan, Hu, Yang and Wang, 1991 (= objective junior homonym)
M. jinanensis Zhang and Su, 1986
M. kikuyensis De Grisse, 1961
 = *Spartonema kikuyense* (De Grisse, 1961) Siddiqi, 2000
M. konaensis Eisenback, Bernard and Schmitt, 1995
M. kongi Yang, Wang and Feng, 1988
M. kralli Jepson, 1984
M. lini Yang, Hu and Zhu, 1988
M. lopezi Humphreys-Pereira, Flores-Chaves, Gómez, Salazar, Gómez-Alpizar and Elling, 2014
M. luci Carneiro, Correa, Almeida, Gomes, Mohammad Deimi, Castagnone-Serenio and Karssen, 2014
M. lusitanica Abrantes and Santos, 1991
M. mali Itoh, Ohshima and Ichinohe, 1969
 = *M. ulmi* Marinari-Palmisano and Ambrogioni, 2001
M. maritima Jepson, 1987
M. marylandi Jepson and Golden in Jepson, 1987
M. megadora Whitehead, 1968
M. megatyla Baldwin and Sasser, 1979
M. mersa Siddiqi and Booth, 1991
 = *M. (Hypsoperine) mersa* Siddiqi and Booth, 1991
M. microcephalus Cliff and Hirschmann, 1984 (original spelling microcephala)
M. microtyla Mulvey, Townshend and Potter, 1975
M. mingnanica Zhang, 1993
M. minor Karssen, Bolk, van Aelst, van den Beld, Kox, Korthals, Molendijk, Zijlstra, van Hoof and Cook, 2004
M. moensi Le, Nguyen, Nguyen, Liébanas, Nguyen and Trinh, 2019
M. morocciensis Rammah and Hirschmann, 1990
M. naasi Franklin, 1965
M. nataliei Golden, Rose and Bird, 1981
M. oleae Archidona-Yuste, Cantalapiedra-Navarrete, Liébanas, Rapoport, Castillo and Palomares-Rius, 2018
M. oryzae Maas, Sanders and Dede, 1978
M. oteifai Elmiligy, 1968 (original spelling oteifae)
M. ottersoni (Thorne, 1969) Franklin, 1971
 = *Hypsoperine ottersoni* Thorne, 1969
 = *Hypsoperine (Hypsoperine) ottersoni* (Thorne, 1969) Siddiqi, 1986
M. ovalis Riffle, 1963
M. panyuensis Liao, Yang, Feng and Karssen, 2005
M. pakistanica Shahina, Nasira, Salma, Mehreen and Bhatti, 2015
M. paranaensis Carneiro, Carneiro, Abrantes, Santos and Almeida, 1996
M. partityla Kleynhans, 1986
M. petunia Charchar, Eisenback and Hirschmann, 1999

M. phaseoli Charchar, Eisenback, Charchar and Boiteau, 2008
M. pini Eisenback, Yang and Hartman, 1985
M. piperi Sahoo, Ganguly and Eapen, 2000
M. pisi Charchar, Eisenback, Charchar and Boiteau, 2008
M. platani Hirschmann, 1982
M. propora Spaull, 1977
= *Hypsoperine propora* (Spaull, 1977) Siddiqi, 1986
= *Hypsoperine (Hypsoperine) propora* (Spaull, 1977) Siddiqi, 1986
M. querciana Golden, 1979
M. salasi Lopez-Chaves, 1985
M. sasseri Handoo, Huettel and Golden, 1994
M. sewelli Mulvey and Anderson, 1980
M. silvestris Castillo, Vovlas, Troccoli, Liébanas, Palomares-Rius and Landa, 2009
M. sinensis Zhang, 1983
M. spartelensis Ali, Tavoillot, Mateille, Chapuis, Besnard, Bakkali, Cantalapiedra-Navarrete, Liébanas, Castillo and Palomares-Rius, 2015
M. spartinae (Rau and Fassuliotis, 1965) Whitehead, 1968
= *Hypsoperine spartinae* Rau and Fassuliotis, 1965
= *Spartonema spartinae* (Rau and Fassuliotis, 1965) Siddiqi, 1986
= *Hypsoperine (Spartonema) spartinae* (Rau and Fassuliotis, 1965) Siddiqi, 1986
M. subarctica Bernard, 1981
M. suginamiensis Toida and Yaegashi, 1984
M. tadshikistanica Kirjanova and Ivanova, 1965
M. thailandica Handoo, Skantar, Carta and Erbe, 2005
M. trifoliophila Bernard and Eisenback, 1997
M. triticoryzae Gaur, Saha and Khan, 1993

M. turkestanica Shagalina, Ivanova and Krall, 1985

M. vandervegeti Kleynhans, 1988

Species inquirendae

M. marioni (Cornu, 1879) Chitwood and Oteifa, 1952

= *Anguillula marioni* Cornu, 1879

= *Heterodera marioni* (Cornu, 1879) Marcinowski, 1909

= *M. goeldi* Lordello, 1951 (= *nomennovum* for *M. marioni*)

M. megriensis (Poghossian, 1971) Esser, Perry and Taylor, 1976

= *Hypsoperine megriensis* Poghossian, 1971

= *Hypsoperine (Hypsoperine) megriensis* (Poghossian, 1971) Siddiqi, 1986

M. poghossianae Kirjanova, 1963

= *M. acronea* apud Poghossian, 1961

M. vialae (Laverigne, 1901) Chitwood and Oteifa, 1952

= *Anguillula vialae* Laverigne, 1901

= *Heterodera vialae* (Laverigne, 1901) Marcinowski, 1909

Nomina nuda

M. californiensis Abdel-Rahman, 1981

M. carolinensis Fox, 1967

M. goeldii Santos, 1997

M. panyuensis Liao, 2001

M. Zhanjiangensis Liao, 2001

Diagnostic compendium for second-stage juveniles and males of *Meloidogyne* species.

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in μm . L. L. refers to the number of lateral lines in the males (Tables 1-8).

Table 1 Group 1 (group 1 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 16-27 μm long, subcylindrical, its terminus broad and rounded at tip (Fig. 1; G1).

Species name	J2		Male (♂)			
	Stylet length	DGO	L. L.	Stylet length	DGO	Spicules
<i>M. brevicauda</i>	14 - 15	4.0	4	19 - 21	3.0	34 - 43
<i>M. fanzhiensis</i>	8 - 11	3.1 - 4.2	4	10 - 14	4.2 - 7.3	21 - 29
<i>M. indica</i>	10 - 14	?	4	16	3.0 - 4.0	30
<i>M. oleae</i>	11 - 13	2.5 - 3.5	4	13 - 18	4.0 - 6.0	21 - 32
<i>M. nataliei</i>	22 - 23	3.0 - 4.3	5	28 - 29	4.0 - 6.5	41 - 44
<i>M. propora</i>	16 - 19	2.0 - 3.0	4 to 7	18 - 23	5.0	32 - 35

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in μm . L. L. refers to the number of lateral lines in the males.

Table 2 Group 2 (groups 2 + 3 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 28 - 40 µm long (except in *Meloidogyne artiella* and *Meloidogyne manganica* is 22 µm and in *Meloidogyne microtyla* is 44 µm), its terminus broad, gradually tapering with a rounded hyaline part, and generally without any marked cuticular constrictions in the hyaline region (Fig. 1; G2).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. acronea</i>	10 - 15	2.2 - 4.5	4	16 - 20	2.1 - 7.2	24 - 36
<i>M. africana</i>	12 - 18	3.0	4, 5	19 - 22	4.0 - 6.0	26 - 35
<i>M. artiella</i>	14 - 16	2.5 - 4.5	4, 5	17 - 27	5.0 - 7.0	25 - 30
<i>M. cirricauda</i>	8 - 11	2.5 - 3.0	4	21 - 24	3.0 - 5.0	32 - 40
<i>M. coffeicola</i>	9 - 11	3.1 - 3.8	4	23 - 26	5.0	20 - 29
<i>M. kikuyensis</i>	12 - 15	3.5 - 5.0	4	17 - 20	4.5 - 6.0	31 - 35
<i>M. mali</i>	9 - 15	3.0 - 6.0	4	17 - 23	4.8 - 13.0	21 - 38
<i>M. microtyla</i>	11 - 12	2.5 - 3.5	4	18 - 20	4.0	28 - 30
<i>M. manganica</i>	9 - 10	2.0 - 3.0	4	23	5.0	37
<i>M. suginamiensis</i>	12 - 15	3.0 - 5.0	4	17 - 21	4.0 - 8.0	24 - 37
<i>M. vandervegti</i>	10 - 12	4.2 - 5.3	4 to 7	22 - 27	3.3 - 7.6	35 - 44

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 3 Group 3 (group 9 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 45 - 58 µm long, irregularly tapering, ending in a finely rounded tip (Fig. 1; G3).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. jianyangensis</i>	13 - 17	2.1 - 3.7	4	19 - 26	2.5 - 3.5	26 - 34
<i>M. jinanensis</i>	10 - 14	3.2 - 5.3	4	17 - 24	4.0 - 5.6	21 - 35
<i>M. megadora</i>	10 - 15	2.3 - 5.0	4 to 6	18 - 23	4.0 - 8.3	25 - 43
<i>M. microcephalus</i>	9 - 13	2.5 - 3.8	4	19 - 28	2.9 - 7.9	24 - 39

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 4 Group 4 (groups 4 + 5 + 6 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 40 - 50 µm long, ending in a broadly rounded tip; usually with a deep (sometimes more than one) constrictions along the hyaline region (Fig. 1; G4).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. ardenensis</i>	9 - 15	2.0 - 4.0	4, 5	17 - 28	3.0 - 5.0	28 - 38
<i>M. camelliae</i>	11 - 12	3.0 - 4.5	4, 5	21 - 24	4.0 - 7.0	33 - 39
<i>M. caraganae</i>	13 - 16	3.6 - 4.8	4	19 - 21	5.2 - 6.6	29 - 33
<i>M. carolinensis</i>	11 - 13	3.0 - 4.7	4	17 - 22	1.9 - 5.2	27 - 35
<i>M. chitwoodi</i>	9 - 11	2.6 - 3.9	4	18 - 19	2.2 - 3.4	26 - 29
<i>M. christiei</i>	10 - 12	3.5 - 4.7	4	17 - 19	3.5 - 5.3	24 - 26
<i>M. decalineata</i>	11 - 14	4.0	10	19 - 20	4.0	33 - 37
<i>M. donghaiensis</i>	12 - 15	3.0 - 6.0	4, 5	22 - 25	2.5 - 6.1	31 - 43
<i>M. ethiopica</i>	9 - 14	2.0 - 3.0	4, 5	14 - 24	2.0 - 3.5	29 - 42
<i>M. fallax</i>	10 - 11	3.2 - 3.8	4, 5	19 - 21	3.2 - 5.7	22 - 30
<i>M. floridensis</i>	10 - 11	2.5 - 3.0	4	17 - 23	2.5 - 3.5	23 - 35
<i>M. hispanica</i>	9 - 13	2.2 - 5.3	4, 5	20 - 25	1.4 - 7.9	28 - 41
<i>M. incognita</i>	9 - 15	2.1 - 4.0	4	20 - 26	1.7 - 4.7	29 - 40
<i>M. izalcoensis</i>	12 - 13	3.0 - 4.0	4 to 6	23 - 26	4.0 - 7.0	27 - 35
<i>M. kongi</i>	12 - 14	3.9 - 5.8	4	22 - 24	5.8 - 7.5	33 - 38
<i>M. lusitanica</i>	13 - 16	3.5 - 4.5	4	21 - 27	4.0 - 6.0	32 - 45
<i>M. megatyla</i>	14 - 17	4.2 - 5.9	4	22 - 26	4.2 - 6.3	29 - 37
<i>M. oteifai</i>	11 - 13	3.0	4 to 6	19 - 23	3.0 - 4.5	29 - 37
<i>M. paranaensis</i>	13 - 14	4.0 - 4.5	4	20 - 27	3.5 - 5.5	22 - 38
<i>M. partityla</i>	10 - 15	1.7 - 5.6	4, 5	17 - 21	2.3 - 5.3	27 - 35
<i>M. pini</i>	11 - 14	3.1 - 4.4	4	18 - 23	2.3 - 7.0	21 - 35
<i>M. querciana</i>	10 - 12	2.6 - 4.3	4, 5	19 - 20	2.2 - 2.8	32 - 33
<i>M. silvestris</i>	12 - 14	2.0 - 4.0	4	24 - 27	5.3 - 6.7	29 - 38
<i>M. subarctica</i>	13 - 15	2.9 - 4.8	4 to 6	17 - 20	4.1 - 5.8	33 - 37
<i>M. turkestanica</i>	13 - 16	3.0	4	16 - 19	4.0	25 - 34

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 5 Group 5 (group 7 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 44 - 60 µm long, ending in a finely rounded to pointed tip, usually with more than one constrictions along the hyaline region (some individuals of *Meloidogyne ichinohei* have a short triangular hyaline tail part) (Fig. 1; G5).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. actinidia</i>	13 - 15	3.5	4	20 - 26	2.6 - 5.9	21 - 33
<i>M. arabicida</i>	9 - 15	2.0 - 4.7	4	16 - 22	3.0 - 5.0	19 - 36
<i>M. arenaria</i>	10 - 13	2.4 - 4.1	4	20 - 28	2.4 - 8.0	22 - 39
<i>M. baetica</i>	13 - 14	3.0 - 5.0	4	16 - 19	3.5 - 5.5	24 - 36
<i>M. chosena</i>	11 - 13	2.8 - 4.8	4	17 - 21	3.5 - 4.2	22 - 32
<i>M. citri</i>	11 - 12	3.7	4	25	5.0	39
<i>M. cruciani</i>	10 - 12	3.2 - 3.6	4 to 7	19 - 24	3.2 - 7.9	29 - 38
<i>M. cynariensis</i>	11 - 13	3.0 - 3.4	Male unknown			
<i>M. daklakensis</i>	11 - 16	2.0 - 5.0	4	17 - 20	4.0 - 7.0	28 - 34
<i>M. dimocarpus</i>	11 - 15	2.2 - 3.8	4	15 - 23	4.5 - 5.8	25 - 40
<i>M. enterolobii</i>	10 - 13	2.8 - 4.5	4	19 - 26	3.2 - 5.8	26 - 32
<i>M. exigua</i>	9 - 14	2.6 - 5.0	4 or more	14 - 22	3.0 - 6.5	20 - 37
<i>M. fujianensis</i>	13 - 14	4.0	4	22 - 25	4.0 - 8.0	31 - 39
<i>M. ichinohei</i>	10 - 13	3.6 - 6.4	7, 8	16 - 18	6.1 - 6.9	33 - 34
<i>M. inornata</i>	10 - 13	2.5 - 3.5	4 to 6	20 - 25	4.0 - 5.0	26 - 38
<i>M. javanica</i>	10 - 12	2.0 - 5.0	4	15 - 25	4.0 - 6.0	25 - 38
<i>M. konaensis</i>	12 - 14	4.2 - 5.9	4, 5	20 - 27	5.0 - 8.4	22 - 36
<i>M. lini</i>	14 - 17	5.0	10 to 12	15 - 20	6.0	31 - 47
<i>M. lopezi</i>	9 - 13	2.4 - 3.6	4	22 - 24	1.9 - 3.4	29 - 38
<i>M. luci</i>	12 - 14	2.3 - 3.3	4	21 - 23	2.5 - 4.5	24 - 35
<i>M. minor</i>	7 - 10	2.5 - 3.2	4 to 6	17 - 19	3.2 - 4.4	23 - 28
<i>M. moensi</i>	9 - 12	2.9 - 4.1	4, 5	14 - 16	3.0 - 4.8	21 - 28
<i>M. ovalis</i>	?	?	4	18 - 23	3.0 - 5.0	31 - 38
<i>M. pakistanica</i>	10 - 14	2.0 - 4.0	6	20 - 25	4.0 - 6.0	29 - 33
<i>M. panyuensis</i>	13 - 15	3.0 - 4.5	4, 5	22 - 26	5.0 - 7.0	25 - 35
<i>M. petunia</i>	9 - 11	2.8 - 4.0	4	21 - 26	1.3 - 3.4	28 - 37
<i>M. phaseoli</i>	10 - 12	2.9 - 4.2	4	20 - 26	3.8 - 5.9	28 - 40
<i>M. piperi</i>	11 - 13	3.0 - 4.0	Male unknown			
<i>M. pisi</i>	10 - 11	2.5 - 4.2	4	19 - 26	4.2 - 8.4	27 - 37
<i>M. platani</i>	11 - 13	2.7 - 4.0	4 to 8	19 - 24	2.3 - 4.5	25 - 32
<i>M. tadshikistanica</i>	12	3.0	4	22 - 25	5.0 - 5.4	27 - 37
<i>M. thailandica</i>	10 - 11	2.5 - 3.5	4	17 - 20	2.5 - 5.0	25 - 38
<i>M. triticoryzae</i>	11 - 13	2.0 - 3.0	4	17 - 19	3.0 - 4.0	26 - 32

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 6 Group 6 (group 8 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 53 - 65 µm long, ending in a broadly rounded tip, its hyaline region with more or less parallel sides (Fig. 1; G6).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. aberrans</i>	16 - 17	3.0 - 3.9	11 to 15	18 - 20	3.8 - 5.3	23 - 37
<i>M. aquatilis</i>	10 - 12	2.0 - 4.0	4	13 - 16	3.0 - 4.0	24 - 26
<i>M. graminis</i>	9 - 13	2.0 - 4.0	4	13 - 19	1.7 - 5.0	27 - 34
<i>M. hapla</i>	10 - 13	2.5	4	17 - 23	3.0 - 6.0	20 - 31
<i>M. haplanaria</i>	9 - 12	1.8 - 3.6	4	17 - 22	3.7 - 6.4	36 - 42
<i>M. maritima</i>	12 - 13	2.5 - 3.6	4	18 - 23	2.5 - 3.6	26 - 35
<i>M. marylandi</i>	10 - 14	1.8 - 3.1	Male unknown			
<i>M. morocciensis</i>	11 - 13	3.0 - 4.4	4	23 - 26	3.5 - 6.2	31 - 39

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 7 Group 7 (groups 10 + 11 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 67 - 75 µm long, ending in a finely rounded to pointed tip, sometimes with fine but marked clavate tip (Fig. 1; G7).

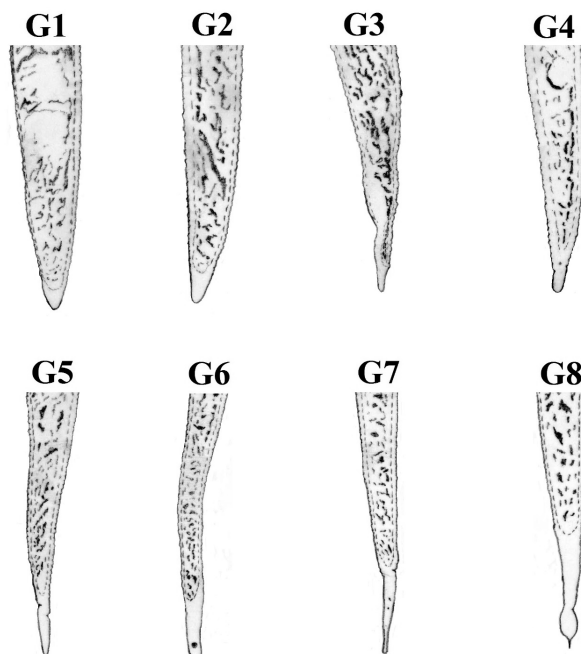
Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. aegracyper</i>	10 - 12	2.7 - 4.8	4	14 - 17	3.0 - 3.3	22 - 25
<i>M. dunensis</i>	11 - 13	1.5 - 3.0	4 to 6	16 - 22	2.5 - 4.5	29 - 38
<i>M. duytsi</i>	10 - 12	3.2 - 3.8	4	19 - 20	3.8 - 5.1	24 - 27
<i>M. graminicola</i>	9 - 13	2.6 - 3.6	4 to 8	15 - 17	2.8 - 5.8	23 - 29
<i>M. hainanensis</i>	10 - 15	4.7 - 5.2	4 to 8	17 - 20	5.2 - 7.8	29 - 36
<i>M. kralli</i>	10 - 12	3.0 - 4.5	4 to 8	18 - 20	3.5 - 6.0	22 - 28
<i>M. mersa</i>	13 - 16	6.0 - 8.0	4 to 12	20 - 23	6.0 - 9.0	35 - 39
<i>M. naasi</i>	13 - 15	2.0 - 3.0	4	16 - 19	2.0 - 4.0	25 - 30
<i>M. oryzae</i>	14 - 15	3.0	4 to 8	19 - 20	4.0 - 5.0	25 - 34
<i>M. ottersoni</i>	13 - 15	4.0	4	14 - 16	3.0	19 - 23
<i>M. salasi</i>	9 - 13	2.1 - 5.3	4 to 6	12 - 22	2.8 - 5.9	18 - 35
<i>M. sewelli</i>	11 - 12	7.0 - 8.0	4	18 - 20	5.0 - 6.0	28 - 30
<i>M. sinensis</i>	17 - 19	3.7 - 5.8	4	24 - 32	4.0 - 8.0	27 - 40
<i>M. trifoliophila</i>	11 - 14	2.9 - 4.6	8 to 12	17 - 19	3.4 - 6.7	27 - 34

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

Table 8 Group 8 (group 12 in Jepson, 1987) for second-stage juveniles and males of *Meloidogyne* species. J2 tail 79 - 100 µm long, ending in a terminal process (except in *Meloidogyne sasseri*) (Fig. 1; G8).

Species name	J2		Male (♂)			
	Stylet	DGO	L. L.	Stylet	DGO	Spicules
<i>M. californiensis</i>	11 - 13	1.0 - 3.0	4	18 - 28	2.0 - 6.0	20 - 40
<i>M. sasseri</i>	13 - 15	1.5 - 4.5	4	19 - 22	3.0 - 4.0	30 - 36
<i>M. spartelensis</i>	13 - 15	1.5 - 3.0	4	17 - 20	2.5 - 4.0	25 - 31
<i>M. spartinae</i>	14 - 17	4.0 - 6.0	4	17 - 21	3.5 - 7.0	25 - 40

The stylet length, dorsal gland orifice distance from stylet base (DGO) and spicules length are in µm. L. L. refers to the number of lateral lines in the males.

**Figure 1** Tail terminus shape in second-stage juveniles (J2s) of *Meloidogyne* species based on the grouping given in the present study (redrawn from Jepson, 1987).

Discussion

The present study has updated the list of *Meloidogyne* species, including some recently described species and a few species which have not appeared in other lists. Moreover, a diagnostic compendium is presented based on the most important diagnostic characters in J2s and males. Such grouping of species in a diagnostic compendium may be helpful in characterization of several species; however, problems in accurate identification of species particularly those in groups 4 and 5 still remain. As stated in Hunt and Handoo (2013), some of the described species are undoubtedly junior synonyms of common, highly variable species. For instance, it may be inferred that certain species in group 4 such as *M. floridensis*, *M. hispanica* and *M. izalcoensis*, and even in group 5 (e. g., *M. enterolobii* and *M. dimocarpus*) could not be easily distinguished from *incognita*, solely based on morphological characters of J2s and males. Although, the diagnostic morphological characters of females, particularly perineal pattern, could be added for better characterization of certain species, intraspecific variation and a large increase in the number of nominal species taking their toll on its utility, particularly for the inexperienced eye (Hunt and Handoo, 2009). Nevertheless, providing diagnostic compendia based upon the features of females may be useful as a supplementary aid completing the present study.

Molecular and biochemical characterization may be considered as additional options to make more precise identifications, as well as to confirm or refute the status of the nominal species. As a wise approach, an integrative taxonomy of the species encompassing their multigene phylogeny, similar to the work conducted for *M. nataliei* (Álvarez-Ortega *et al.*, 2019), is highly recommended to clarify exact intrageneric structure of the genus *Meloidogyne*. Significant advances in sequencing technologies also could provide more detailed information about the intraspecific variation among the problematic taxa (Rashidifard *et al.*, 2019), to finally

address the taxonomic problems in root-knot nematodes.

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فهرست گونه‌های جنس *Meloidogyne* Göldi, 1887 و گروه‌بندی گونه‌ها براساس ویژگی‌های ریخت‌شناختی لارو سن دو و نر

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چکیده: نماتدهای ریشه گرهی *Meloidogyne* spp. که در تمام مناطق دنیا حضور دارند، به‌عنوان مهم‌ترین گروه نماتدهای انگل گیاهی مطرح هستند و قادرند به تمام گونه‌های گیاهان عالی آسیب وارد سازند. پژوهش حاضر فهرست روزآمد شده ۱۰۵ گونه معتبر جنس *Meloidogyne* را به‌همراه فهرست مترادف‌ها و آرایه‌های نامعتبر ارائه داده است. هم‌چنین گروه‌بندی گونه‌ها براساس ویژگی‌های مهم ریخت‌شناختی لارو سن دو (شکل دم، طول دم، طول استایلت و محل ریزش غده پشتی مری) و نماتد نر (تعداد شیارهای جانبی، طول استایلت، محل ریزش غده پشتی مری و طول اسپیکول‌ها) انجام شده است.

واژگان کلیدی: شناسایی، ریخت‌شناسی، نماتدهای ریشه گرهی، فهرست گونه‌ها، آرایه‌بندی، *Meloidogyne*