

The genus *Dorylaimoides* Thorne & Swanger, 1936 (Nematoda : Dorylaimida). 1. Taxonomy and variability

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Summary – A general revision of different aspects of the morphology and taxonomy of the genus *Dorylaimoides* Thorne & Swanger, 1936 is presented. Variability of the morphological features is described and illustrated, and their taxonomic value is briefly discussed. The taxonomical position of the genus, its relationships with other genera and its intrageneric taxonomy are likewise treated. A list of the species is also given.

Résumé - Le genre *Dorylaimoides* Thorne & Swanger, 1936 (Nematoda : Dorylaimida). 1. Taxinomie et variabilité - Une révision générale des différents aspects de la morphologie et de la taxonomie du genre *Dorylaimoides* Thorne & Swanger, 1936 est présentée. La variabilité des caractéristiques morphologiques est décrite et illustrée, et leur valeur taxonomique est discutée brièvement. La position taxonomique du genre, ses relations avec d'autres genres et la taxonomie intragénérique sont également traitées. Une liste des espèces est donnée.

Key words : *Dorylaimoides*, nematodes, taxonomy.

Dorylaimoides Thorne & Swanger, 1936 is one especially interesting dorylaimid nematode genus due to its intricate taxonomy and its relatively wide morphological variability. At present, it contains more than 60 species, some of which have been described from a small number of specimens or have been poorly illustrated; other species are known from several localities and present significant intraspecific variability mainly affecting the morphology of the tail and the female genital system but also other features.

In Andalucía Oriental (Southeastern Spain) the genus appears well distributed and diversified. Very recently we have examined (Peralta & Peña Santiago 1995a, b, c) some eighty populations collected from very different habitats (forest, brushwood, cultures, meadow, etc.), and including fourteen different species. In our opinion, this Spanish material constitutes a good representation of the genus due to the number of species, but mostly because of the morphological variability observed among these species. The information so obtained has led us to undertake a more general revision of the morphology and the taxonomy of the genus, which is presented below.

Notes on general morphology

General aspect : Body length varying strongly, ranging from 0.7 to 3.0 mm but very rarely exceeding 2 mm; frequently around 1 mm. Shape cylindrical, tapering to the anterior end which becomes about one-third of the

body diameter at neck base; tapering also, towards the posterior extremity more or less according to the tail shape. In general, body slender since de Man's "a" ratio usually varies from 30 to 40 but may exceed the latter value. After fixation, habitus more or less ventrally curved to C- or J-shaped; almost always the male presents a more curved posterior body region than the female.

Cuticle : Under optical microscopy it is possible to distinguish two layers: outer layer thin, constant in thickness along the entire body; fine and transverse surface striations normally present but some interspecific variability exists since inconspicuous as well as clear striation can occur; inner layer always thicker than the outer one, widening visibly at the caudal region.

Lateral chord and pores : A relatively narrow lateral chord (in Spanish material varying from one-tenth to one-seventh of the midbody diameter) always obvious, its margins appearing clear and including a granular or amorphous content, although in some species the existence of glandular bodies is easily perceptible. Lateral pores fine and located in a simple row, frequently very inconspicuous.

Lip region : A wide interspecific variability can be observed (see Fig. 1 A-C) : the lip region is often somewhat angular and offset from the adjacent body by a depression or a more or less deep constriction; however, practically continuous and more rounded in some species. Lips almost always amalgamated, with the outer

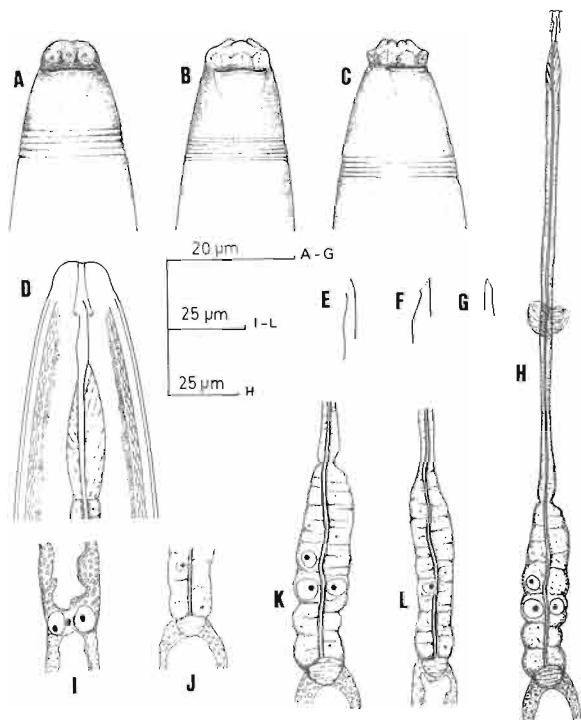


Fig. 1. A-C: Lip region in surface lateral view (A: *Dorylaimoides rotundicephalus*; B: *D. hispanicus*; C: *D. grandis*); D: Lip region in median lateral view (*D. rotundicephalus*); E-G: Odontostyle (E: *D. rotundicephalus*; F: *D. grandis*; G: *D. hispanicus*); H: Pharynx (*D. striatus*); I: Intestine-prerectum junction (*D. hispanicus*); J: Cardia (*D. rotundicephalus*); K, L: Pharyngeal basal bulb (K: *D. striatus*; L: *D. teres*).

part normally rounded but sometimes angular and the inner part frequently elevated and even forming perioral liplets. Labial and cephalic papillae with the typical (6 + 6 + 4) distribution for dorylaims and easily perceptible by their often clear innervation since they are generally not raised above the head contour.

Amphid: Amphid opening at the level of the cephalic depression or constriction (the base of the lip region), or immediately behind, and generally occupying more than half of the corresponding body diameter. **Fovea** cup-like and more rarely stirrup-like; **fusus** located near the odontophore base, more clearly visible in dorsal or ventral view.

Cheilostome and guiding ring: Oral aperture followed by a cylindrical or truncate conical cavity (cheilostome) whose walls appear sometimes slightly refractive and somewhat thickened in the perioral area; length of the cavity 2-3 times its maximum width; guiding ring always simple and conspicuous since it is relatively thick and refractive.

Stylet: The stylet morphology (Fig. 1 D) is one of the characteristic features of the genus. The odontostyle is

relatively robust and its length (ventral side) varies from half to scarcely more than the lip region width (Fig. 1 E-G). Aperture always well visible and occupying 25-33 % of the total stylet length. In lateral view, the ventral side of the odontostyle appears practically straight and with the anterior end dorsally bent; dorsal side somewhat sigmoid and in all cases longer than the ventral one. Odontophore presenting a typical ventral curvature and surrounded by a somewhat hyaline tissue; odontophore always longer than the odontostyle but its precise length difficult to establish since it joins the pharyngeal lining without a clear transition.

Digestive system: Pharynx consisting of a slender anterior part and a basal bulb (Fig. 1 H); the former begins with a somewhat thickened portion which becomes more slender at level of the nerve ring, then widens slightly again until the junction with the bulb. Both parts of the pharynx clearly distinguishable since the anterior part expands always abruptly (Fig. 1 K, L) into the basal bulb and a more or less pronounced constriction can mark the separation. Pharyngeal bulb typically cylindrical and relatively short, occupying one-fourth to one-third of the total neck length (in *D. subhasi* the bulb represents 43-45 % of the total neck length, an exceptional percentage in the genus). Nuclei and outlets of the pharyngeal glands always easily visible; DN and S₂N in general clearer than S₁N; these are situated somewhat behind the middle of the DN-S₂N distance. Cardia hemispherical or rounded conoid (Fig. 1 J), relatively small and often surrounded by intestinal tissue. Intestine a simple tube without special modifications; cells number low; cells characterized by a granular aspect and prominent nucleus. Transition between the intestine and the prerectum generally marked off by three guard cells (Fig. 1 I). Prerectum length variable even in the same species or population and ranges from three to ten anal body widths. Rectum (in females) a short tube equal to or scarcely longer than the anal body diameter.

Female genital system: An interesting interspecific variability can be noted in its morphology (Fig. 2 A, D): two ovaries or only the posterior one, can exist. Didelphic species with two similar genital branches each consisting of ovary, oviduct, sphincter and uterus. In species with only the posterior ovary developed, the posterior genital tract is similar to a genital branch of the didelphic species and the anterior one is normally reduced to a more or less developed uterine sac (monodelphic-opisthodelphic species *sensu lato*). *D. limnophilus* is the only species with the anterior sac practically absent (monodelphic-opisthodelphic species *sensu stricto*). Moreover, in a few species, termed by us (Peralta & Peña Santiago, 1995b) pseudodidelphic-opisthodelphic, the anterior tract appears to be constituted by a sphincter, a vestigial oviduct with solid appearance, and even a small cell mass resembling a rudimentary ovary; we prefer the terminology pseudodidelphic *versus* pseudomonodelphic (*cf.* Cohn & Sher, 1972) because these

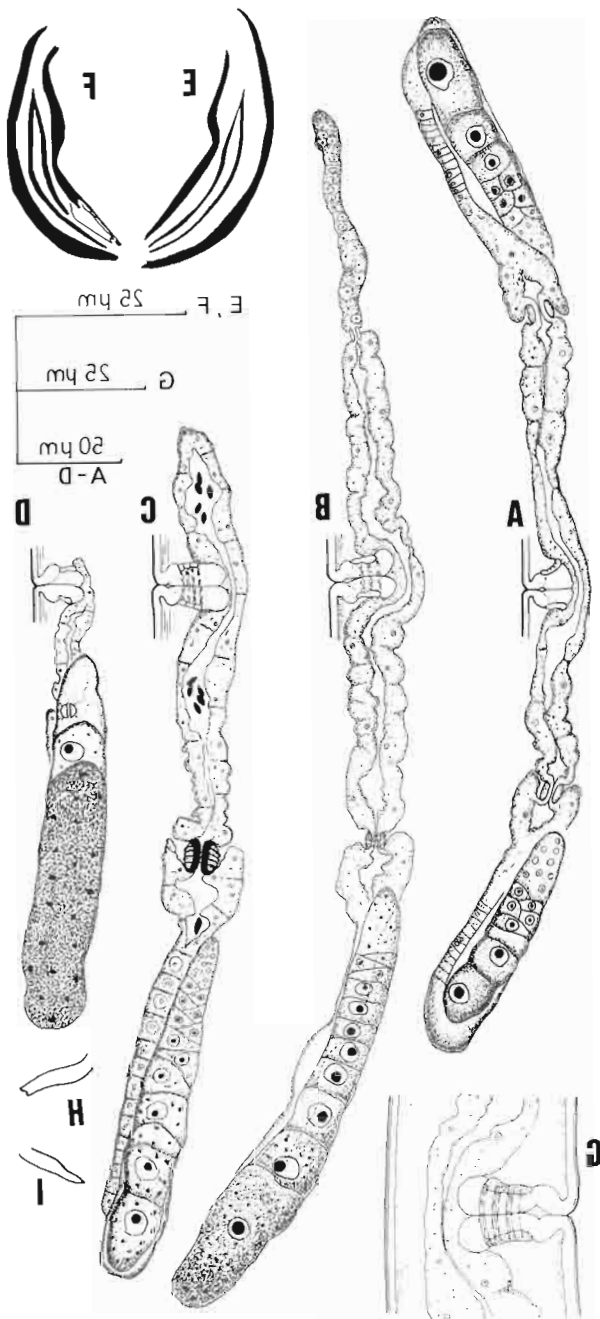


Fig. 2. A-D: Female genital system. A: *Didelphic* species (*Dorylaimoides teres*); B: *Pseudodidelphic-opisthodelphic* species (*D. rotundicephalus*); C: *Monodelphic-opisthodelphic* species sensu lato (*D. grandis*); D: *Monodelphic-opisthodelphic* species sensu stricto (*D. limnophilus*); E, F: Spicules (E: *D. arcuatus*; F: *D. hispanicus*); G: Vagina (*D. paraconfusus*); H, I: Lateral guiding pieces (H: *D. paraconfusus*; I: *D. grandis*).

species present both genital tracts (genital tubes) although the anterior one is reduced or not functional. Ovary almost always medium sized, reaching the oviduct-uterus junction but rarely continuing past it; oocytes situated first in two or more rows and then in a single row. Oviduct joining the ovary subterminally and consisting of a slender part with cubic or prismatic cells and a generally well developed *pars dilatata*. A prominent sphincter, often with a more refractive inner part surrounded by the circular musculature, separates oviduct and uterus. Uterus a tube shorter and wider than the oviduct but without special modifications. Vagina cylindrical (Fig. 2 G) or somewhat pyriform and extending over half or scarcely less than the corresponding body diameter; its wall adjacent to the vulva composed of inner body cuticle extending inwards and widening in this region, the other part of the wall encircled by a more or less developed musculature. Vulva, in all cases in which it was observed in frontal view, a transverse slit.

Male genital system: Following the general dorylaim pattern and consisting of two opposed testes leading into a common *vas deferens* which joins the ejaculatory duct, the ejaculatory duct opens into the rectum and together they form the cloaca whose surface opening is the cloacal opening. The system does not have special taxonomic interest since it presents only very little morphological variation; however, the secondary sexual organs composed of the copulatory apparatus (spicules and lateral guiding pieces) and genital papillae (supplements), although rather constant in the genus, are useful in distinguishing the species. Spicules more or less ventrally curved (Fig. 2 E, F) and consisting of a poorly developed head, a blade and a prominent median piece; main variation affects size (19-56 μm) and the more or less slender aspect. Lateral guiding pieces relatively small, almost straight or sigmoid (Fig. 2 H, I), and with the tip acute or more frequently bifurcate. Supplements mammiform differing scarcely among the species; in addition to the adanal pair, a series of one to twelve regularly spaced ventromedian papillae is present beginning normally at the level of the spicules, but with some interspecific, or even intraspecific variability.

Tail: General morphology (size and shape mainly) extremely variable in the genus (Fig. 3). However, within a particular species, both sexes have tails practically identical, except that the male tail is often somewhat shorter and more ventrally curved than in females. Intraspecific variability of the caudal region in general small (it should be pointed out that most species are known from only one or a few populations and from a small number of specimens), but interspecific variation is very large. Tail frequently filiform in the genus, practically straight or slightly ventrally curved but in many cases tip dorsally recurved; from this filiform shape, all transitions can be found to a very short hemispherical one.

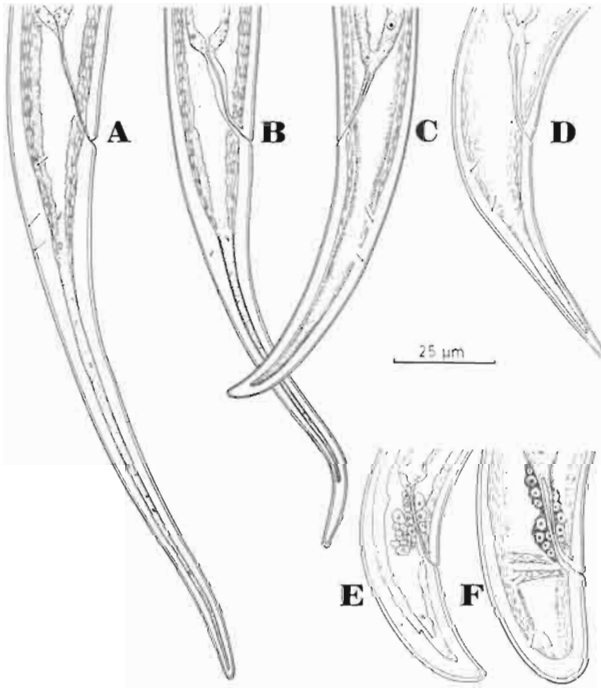


Fig. 3. Intragenetic variability of the tail morphology in several Spanish species of the genus *Dorylaimoides*. A: *D. grandis*; B: *D. limnophilus*; C: *D. arcuatus*; D: *D. sp.*; E: *D. baeticus*; F: *D. rotundicephalus*.

Taxonomical considerations

EVOLUTIVE TRENDS IN THE GENUS AND INTRAGENETIC TAXONOMY

Dorylaimoides seems to be a diversified genus with a large amount of polymorphism in several morphological qualitative and quantitative features. To determine the direction of changes produced during the evolutionary history is an intricate problem. However, the most important diagnostic features can be determined and their plesiomorphic and apomorphic character states can be investigated.

A rounded lip region, continuous with the adjacent body (see *D. parateres*, *D. brevidens* or *D. constrictoides*) could be interpreted as an apomorphic state against the angular and offset lip region (see *D. grandis*), which can be considered as plesiomorphic, but several grades of cephalic differentiation can be found making the interpretation more difficult.

A slender and relatively long odontostyle (equal to or somewhat longer than lip region width; see *D. parateres*, *D. teres* or *D. ornatus*) is surely plesiomorphic *vs* a broad and relatively short odontostyle (equal to or scarcely more than half of the lip region width; see *D. grandis* or *D. angustus*) but, here again, there is a continuous range of possibilities between the two extremes which, moreover,

are rather close, varying from 3 μm (minimum) to 11 μm (maximum).

The existence of a constriction between the two parts of the pharynx must be considered as the apomorphic state as compared to absence of constriction, in spite of the fact that the two states can be found within the same species and even the same population.

It seems that a tendency towards the reduction of the anterior genital branch exists inside the genus. Consequently, a didelphic system must be considered plesiomorphic with respect to the opisthodelphic system *sensu stricto*, which is considered apomorphic. In this context, the species presenting a pseudodidelphic-opisthodelphic or opisthodelphic *sensu lato* genital system can be interpreted as intermediate steps in the process of reduction. The fact that the pseudodidelphic-opisthodelphic condition is only rarely found can indicate (Coomans, *in litt.*) that it is a transitional situation which is probably selected out rapidly; indeed, whereas such a long branch with "annex" does not seem to serve any useful function, a short uterine sac can store sperm and is important for ovejector formation. In any case, under a taxonomical point of view, it is useful (*cf.* Southey, 1973) to consider and distinguish the degree of reduction of the anterior genital tract with two clear possibilities: only uterine sac or uterus, sphincter and more or less developed oviduct and ovary.

It is possible to accept that the morphology of the tail presents a clear evolutive tendency from a more primitive filiform shape towards an apomorphic state with short rounded aspect. However, between these two extremes, we find almost all the intermediate possibilities of shape and size whose interpretation is more difficult due to the numerous different cases and the intraspecific variability observed within each one of these cases. We propose a tentative hypothesis in which from the filiform tail (plesiomorphic state) three basically different models can be derived (short rounded, conical and regularly ventrally curved, and conical with the ventral side straight or dorsally bent at the tip) which are considered apomorphic states, and this evolutive pattern has repeated itself several times in different species and in different moments of the evolutionary history of the group. The same apomorphic character state presented by different species could be thus due to convergence. This would mean that similar species may have arisen from different ancestors.

A genus containing a high number of species poses a challenge to taxonomists who may try to split it in order to make the identification and classification of the species easier. However, in our opinion, species should be clustered in natural groups (based on their evolutionary history) which then can be identified as subgenera or other taxa. Other tentatives based on artificial and speculative characters should be avoided.

As mentioned above, we think that, at the present and except for a few cases which will be commented upon

- = *Dorylaimoides* (*Shamimonema*) Jairajpuri & Ahmad, 1992
- = *Dorylaimoides* (*Arcidorylaimoides*) Jairajpuri & Ahmad, 1992
- = *Dorylaimoides* (*Tarjania*) Jairajpuri & Ahmad, 1992

DIAGNOSIS

Slender nematodes of medium size, almost always 1-2 mm long. Habitus ventrally curved, to C-shaped. Outer cuticle relatively thin and with fine transverse striations. Inner cuticle thicker than the outer layer. Lateral chord very narrow. Odontostyle asymmetrical, ventral side shorter than the dorsal one and practically straight but dorsally bent at its anterior end; dorsal side longer and somewhat sigmoid. Odontophore usually arcuate or angular, involved by the pharynx. Guiding ring simple. Pharynx consisting of a slender and weakly muscular anterior part expanding more or less abruptly into a basal bulb. Pharyngeal bulb cylindrical and occupying one-fourth to one-third of the total neck length. Female genital system didelphic, pseudodidelphic-opisthodelphic or opisthodelphic. Vulva transverse. Male genital system diorchic. Spicules dorylaimoid, 19-56 µm long. Lateral guiding pieces small. One to twelve ventromedian supplements regularly spaced and beginning usually into the range of the spicule. Tail similar in both sexes: filiform, conical-elongated, conical, conoid or hemispherical.

TYPE SPECIES

- D. teres* Thorne & Swanger, 1936
- = *D. (Dorylaimoides) teres* Thorne & Swanger, 1936

OTHER SPECIES

- D. akon* Goseco, Ferris & Ferris, 1976
- = *D. (Longidorylaimoides) akon* Goseco, Ferris & Ferris, 1976
- D. angustus* Sauer, 1967
- = *D. (Shamimonema) angustus* Sauer, 1967
- D. arcuatus* Siddiqi, 1964
- = *D. (Arcidorylaimoides) arcuatus* Siddiqi, 1964
- = *D. rusticus* Timm, 1964
- = *D. intermedius* Thorne, 1964
- D. arcuicaudatus* Baqri & Jairajpuri, 1969
- = *D. (Dorylaimoides) arcuicaudatus* Baqri & Jairajpuri, 1969
- D. ariasae* Loof, 1990
- D. baeticus* Peralta & Peña Santiago, 1991
- D. brevidens* Thorne, 1964
- = *D. (Tarjania) brevidens* Thorne, 1964
- D. buccinator* Sauer, 1967
- = *D. (Dorylaimoides) buccinator* Sauer, 1967
- D. bulbosus* (Brzeski & Szczygiel, 1961) Szczygiel, 1965
- = *Tarjania bulbosa* Brzeski & Szczygiel, 1961
- = *D. (Tarjania) bulbosa* (Brzeski & Szczygiel, 1961) Szczygiel, 1965

- D. chamoliensis* Ahmad & Jairajpuri, 1983
- = *D. (Dorylaimoides) chamoliensis* Ahmad & Jairajpuri, 1983
- D. chathamii* Yeates, 1979
- = *D. (Dorylaimoides) chathamii* Yeates, 1979
- D. confusus* Peralta & Peña Santiago, 1995
- D. constrictoides* Goseco, Ferris & Ferris, 1976
- = *D. (Tarjania) constrictoides* Goseco, Ferris & Ferris, 1976
- D. constrictus* Baqri & Jairajpuri, 1969
- = *D. (Arcidorylaimoides) constrictus* Baqri & Jairajpuri, 1969
- D. conurus* Thorne, 1939
- D. cylindricaudatus* Peralta & Peña Santiago, 1991
- D. dactylurus* Heyns, 1963
- = *D. (Shamimonema) dactylurus* Heyns, 1963
- D. elaboratus* Siddiqi, 1965
- = *D. (Longidorylaimoides) elaboratus* Siddiqi, 1965
- D. elegans* (de Man, 1880) Thorne & Swanger, 1936
- = *Dorylaimus elegans* (de Man, 1880)
- = *D. (Digidorylaimoides) elegans* (de Man, 1880) Thorne & Swanger, 1936
- D. elongatus* Husain & Khan, 1968
- = *D. (Arcidorylaimoides) elongatus* Husain & Khan, 1968
- D. enodis* Goseco, Ferris & Ferris, 1976
- = *D. (Dorylaimoides) enodis* Goseco, Ferris & Ferris, 1976
- D. filicaudatus* Jana & Baqri, 1981
- = *D. (Longidorylaimoides) filicaudatus* Jana & Baqri, 1981
- D. grandis* Peralta & Peña Santiago, 1995
- D. hispanicus* Peralta & Peña Santiago, 1995
- D. ilyasi* Ahmad & Jairajpuri, 1980
- = *D. (Tarjania) ilyasi* Ahmad & Jairajpuri, 1980
- D. indicus* Jairajpuri, 1965
- = *D. (Dorylaimoides) indicus* Jairajpuri, 1965
- D. kalingus* Ahmad & Jairajpuri, 1983
- = *D. (Shamimonema) kalingus* Ahmad & Jairajpuri, 1983
- D. lepidus* Timm, 1964
- = *D. (Longidorylaimoides) lepidus* Timm, 1964
- D. leptura* Siddiqi, 1965
- = *D. (Longidorylaimoides) leptura* Siddiqi, 1965
- D. leptus* Husain & Khan, 1968
- = *D. (Digidorylaimoides) leptus* Husain & Khan, 1968
- D. limnophilus* (de Man, 1880) Loof, 1964
- = *Dorylaimus limnophilus* de Man, 1880
- = *Thornenema limnophilum* (de Man, 1880) Andrassy, 1959
- = *D. (Tarjania) limnophilus* (de Man, 1880) Loof, 1964
- = *Dorylaimoides riparius* Andrassy, 1962
- = *D. (Tarjania) riparius* Andrassy, 1962
- D. longicaudatus* (Imamura, 1931) Thorne & Swanger, 1936

- = *Dorylaimus elegans* var. *longicaudatus* Imamura, 1931
 = *D. (Longidorylaimoides) longicaudatus* (Imamura, 1931) Thorne & Swanger, 1936
D. longiurus Siddiqi, 1965
 = *D. (Tarjania) longiurus* Siddiqi, 1965
D. loofi Baqri & Khera, 1979
D. malabaricus Ahmad & Jairajpuri, 1982
 = *D. (Longidorylaimoides) malabaricus* Ahmad & Jairajpuri, 1982
D. micoletzkyi (de Man, 1921) Thorne & Swanger, 1936
 = *Dorylaimus micoletzkyi* de Man, 1921
 = *D. (Digidorylaimoides) micoletzkyi* (de Man, 1921) Thorne & Swanger, 1936
 = *D. pakistanensis* Siddiqi, 1964
 = *D. (Digidorylaimoides) pakistanensis* Siddiqi, 1964
D. mitis Sauer, 1967
 = *D. (Shamimonema) mitis* Sauer, 1967
D. modestus Siddiqi, 1965
 = *D. (Tarjania) modestus* Siddiqi, 1965
D. ornatus Peralta & Peña Santiago, 1995
D. paraconfusus Peralta & Peña Santiago, 1995
D. parateres Siddiqi, 1964
 = *D. (Dorylaimoides) parateres* Siddiqi, 1964
D. parvus Thorne & Swanger, 1936
 = *D. (Longidorylaimoides) parvus* Thorne & Swanger, 1936
 = *D. riparius* apud Loof, 1964
D. paulbuchneri Meyl, 1956
 = *D. (Longidorylaimoides) paulbuchneri* Meyl, 1956
D. pretoriensis Heyns, 1963
 = *D. (Shamimonema) pretoriensis* Heyns, 1963
D. reversus Thorne, 1964
 = *D. (Tarjania) reversus* Thorne, 1964
D. rotundicephalus Peralta & Peña Santiago, 1995
D. saueri Baqri & Jairajpuri, 1969
 = *D. (Arcidorylaimoides) saueri* Baqri & Jairajpuri, 1969
D. siddiqii Baqri & Khera, 1979
D. similis Thorne, 1964
 = *D. (Longidorylaimoides) similis* Thorne, 1964
D. striatus Peralta & Peña Santiago, 1995
D. subhasi Jana & Baqri, 1981
 = *D. (Tarjania) subhasi* Jana & Baqri, 1982
D. thecolaimus Heyns, 1963
 = *D. (Dorylaimoides) thecolaimus* Heyns, 1963
D. thornei (Jairajpuri, 1964) Siddiqi, 1969
 = *Leptonema thornei* Jairajpuri, 1964
 = *Shamimonema thornei* (Jairajpuri, 1964) Chawla, Khan & Prasad, 1965
 = *D. (Shamimonema) thornei* (Jairajpuri, 1964) Siddiqi, 1969
D. venustus Andrassy, 1959
 = *D. (Tarjania) venustus* Andrassy, 1959
D. websteri Sauer, 1967
 = *D. (Dorylaimoides) websteri* Sauer, 1967

SPECIES INQUIRENDAE

- D. microdentatus* Altherr, 1968 [probably not *Dorylaimoides*]
D. pari Mahajan, 1973 [a prodelpic species]
D. stenodorus Altherr, 1953 [described in base to a single male]
D. thienemanni (Schneider, 1937) Jairajpuri, Ahmad & Dhanachand, 1980
 = *Dorylaimus thienemanni* Schneider, 1937
 = *Thornenema thienemanni* (Schneider, 1937) Andrassy, 1959
 = *D. (Tarjania) thienemanni* (Schneider, 1937) Jairajpuri, Ahmad & Dhanachand, 1980

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