# A reappraisal of Tylenchina (Nemata). 5. The family Dolichodoridae Chitwood, 1950 (1)

# Michel Luc\* and Renaud Fortuner\*\*

Muséum national d'Histoire naturelle, Laboratoire des Vers, 61, rue de Buffon, 75005 Paris, France and California Department of Food and Agriculture, Analysis and Identification (Nematology), 1220 N Street, Sacramento, CA 95814, USA.

# SUMMARY

The family Dolichodoridae is redefined. It includes only two genera: Dolichodorus and Neodolichodorus. Brachydorus is considered a genus inquirendum. Position of Dolichodoridae, in Tylenchoidea, is discussed.

#### RESUMÉ

Réévaluation des Tylenchina (Nemata). 5. La famille des Dolichodoridae Chitwood, 1950

La famille des Dolichodoridae est redéfinie; elle est limitée aux deux genres Dolichodorus et Neodolichodorus. Brachydorus est considéré comme un genus inquirendum. La position des Dolichodoridae à l'intérieur des Tylenchoidea est discutée.

Chitwood (1950) created the subfamily Dolichodorinae under Criconematidae. As described by Chitwood, this family is a motley assembly of genera sharing a single character: a long spear (Chitwood wrote: "Stylet shaft greatly elongated"; actually in all the concerned genera, it is the cone which is elongated). Chitwood placed Criconema, Criconemoides and Hemicycliophora in the subfamily Criconematinae; Paratylenchus and Cacopaurus in Paratylenchinae, and Dolichodorus and Belonolaimus in Dolichodorinae. This latter subfamily was said to differ from the other two ones by a cuticle coarsely striated with three or more lateral lines, and by females with two genital branches. The caudal alae are terminal in Dolichodorus and adanal in Belonolaimus.

Loof (1958) in reviewing Chitwood's (1950) Criconematidae, pointed out that *Dolichodorus* "does not show any close affinities to other genera". Loof (1958) rejected the subfamily Dolichodorinae, and he assigned *Belonolaimus* to Hoplolaiminae and *Dolichodorus* to Tylenchinae.

Skarbilovich (1959) agreed with Chitwood's (1950) concept of Dolichodorinae and raised the subfamily to family rank.

Goodey (1963) and Paramonov (1967) consider only *Dolichodorus* in the subfamily Dolichodorinae, under

Hoplolaimidae. These two authors gave to the family Hoplolaimidae a wide definition, and included in it the subfamilies Hoplolaiminae, Rotylenchoidinae, Belonolaiminae, Dolichodorinae, Pratylenchinae and Nacobbinae. Allen and Sher (1967) assigned Dolichodorinae to Tylenchidae. It should be noted that these authors gave to the family Tylenchidae about the same generic content as Goodey's or Paramonov's Hoplolaimidae.

Siddiqi (1970) rediagnosed the family Dolichodoridae, and enlarged its definition to include in it the subfamilies Tylodorinae Paramonov, 1967 (Tylodorus), Dolichodorinae (Dolichodorus, and the newly described genus Brachydorus), Trophurinae Paramonov, 1967 (Trophurus, Macrotrophorus), and Tylenchorhynchinae Eliava, 1964 (Tylenchorhynchus, Nagelus, Geocenamus, Merlinius).

Golden (1971) on the contrary restricted Dolichodoridae/Dolichodorinae to the genera *Dolichodorus* and *Brachydorus*.

Andrássy (1976) followed Golden's concept, but he splited *Dolichodorus* into *Dolichodorus s. str.* and *Neodolichodorus* Andrássy, 1976 (21 days later Siddiqi (1976) created the genus, *Plesiodorus*, a junior objective synonym of *Neodolichodorus*).

Fotedar and Handoo (1978) also had a narrow concept

<sup>(1)</sup> This article is part of a study on the classification of Tylenchina by the present authors, E. Geraert (Rijksuniversiteit, Gent, Belgie), and A. R. Maggenti and D. J. Raski (University of California, Davis, USA).

<sup>\*</sup> Nematologist from ORSTOM.

<sup>\*\*</sup> Associate in the Division of Nematology, University of California, Davis, CA 95616, USA.

of Dolichodoridae; they divided it into two subfamilies Dolichodorinae (Dolichodorus, Brachydorus and Neodolichodorus) and a new subfamily Dolichorhynchinae with Dolichorhynchus, because in this genus the caudal alae somewhat resemble those of Dolichodorus.

Siddiqi (1986) again proposed to give a wide content to the Dolichodoridae, with eight subfamilies (Dolichodorinae, Meiodorinae, Tylenchorhynchinae, Macrotrophurinae, Trophurinae, Merliniinae, Telotylenchinae and Belonolaiminae) and 29 genera. He also elevated the family to the rank of superfamily, Dolichodoroidea, with the two families Dolichodoridae and Psilenchidae.

This history of dolichodorids may appear as confuse and erratic. The different opinion of the various authors can be summarized as follows:

- the first concept (Chitwood, 1950) was based mainly on the long stylet, a character that has no value at suprageneric level, and little value even at generic level;
- the subsequent authors may be divided into three groups: *i)* those who considered the peculiarities of *Dolichodorus s. lat.* to be such as to warrant restricting the family to this genus and its closest relatives; *ii)* those who considered the reinforcement of the labial sclerotization as a primary character and placed Dolichodorinae in Hoplolaimidae (or in Tylenchidae if Hoploplaiminae was considered at subfamily level); *iii)* those who estimated that the structure of the glandular part of the oesophagus, pyriform and not overlapping the intestine, was a primary character, and consequently grouped *Dolichodorus* with *Tylenchorhynchus* and related genera; Siddiqi (1986) followed this last interpretation, but he also placed *Belonolaimus* and related genera with a long oesophageal overlap in Dolichodoridae.

Elongation of the stylet is not a reliable family criterion, because it occurred several times in otherwise unrelated groups in Tylenchina. In *Macrotrophurus* (Tylenchidae), in *Belonolaimus* et aff. (Belonolaimidae), and in *Gracilacus, Hemicriconemoides*, etc. (Criconematidae), the elongation of the stylet is similar to that of dolichodorids. It affects mostly the cone, and there is a correlated modification of the corpus, with procorpus enlarged and more or less fused with the median bulb, and enlarged median bulb valve. These modifications are a mechanical consequence of the elongation of the stylet, and they cannot be used independantly of the latter character to argue for a systematic relationship between the forms listed above.

Reinforcement of labial sclerotization may follow different paths. In the dolichodorids, both the basal plate and the internal part of the labial arches are strengthened. In those belonolaimids with strong labial framework (Carphodorus and some Morulaimus), the basal plate remains thin. In other families (hoplolaimids, criconematids), the labial arches are never thickened. These differences point to probable parallel evolution for this character.

The elongation of the oesophageal glands, and their overlap of the intestine result from an increase in size of the glands, unrelated to any change in structure. This phenomenon occurred many times in the order, within the same family, the same genus, and even the same species.

The definition of the family Dolichodoridae cannot rely on such superficial resemblances. *Dolichodorus* and its closest relatives do have some very distinctive characteristics, i. e., male tails with trilobed caudal alae, female tails undergoing a symmetrical, axial regression, and columned uterus with four rows of cells. While resemblances with other taxa in Tylenchina can be found for every one of these characters, the description of dolichodorids is distinctive enough to warrant their placement into a separate family, Dolichodoridae.

The family DOLICHODORIDAE Chitwood, 1950

# Diagnosis

Tylenchina. Tylenchoidea. Large slender nematodes with cylindroid bodies. No secondary sexual dimorphism. Lateral field with three or four lines. Deirids absent. Labial region distinctly off-set, annulated (rarely smooth). Labial sclerotization strong, with a very thick basal plate and thick arches. Amphids apertures seen as small slits. Stylet generally well developed (up to 150 μm); cone markedly longer than shaft. Oesophagus with procorpus fused with the median bulb, strong valve, short isthmus and pyriform glandular region not overlapping the intestine. Female tail rounded to hemispherical, or with spike-like extension, rarely elongateconoid. Female with two genital branches; columned uterus with four rows of cells; vagina vera heavily sclerotized. Male caudal alae terminal, wing-like, trilobed. Amphimictic reproduction. Obligate migratory ectoparasites of plants roots.

Type genus

Dolichodorus Cobb, 1914

OTHER GENUS

Neodolichodorus Andrássy, 1976 = Plesiodorus Siddiqi, 1976

GENUS DUBIUM

Brachydorus de Guiran & Germani, 1968

The relation between Dolichodoridae and related families in Tylenchina have been discussed by Maggenti et al., (1987).

# Description of Dolichodoridae

Female vermiform; body length from 1 to 3.5 mm. Lip region high, generally rounded, off-set, often with deep incisure; generally provided with numerous but conspicuous annuli (rarely few or no annuli); in end-on view, lip region roughly quadrangular to conspicuously four-lobed, always with dorsal and ventral longitudinal grooves; labial disc most often prominent; with SEM, lateral labial sectors reduced or absent; homologous subventral and subdorsal labial sectors generally distinct from each other. Amphids apertures slit-like, directed either dorso-ventrally or laterally. Cuticle thick, deeply annulated; in some cases the annuli anterior to the level of excretory pore are notably wider than the other body annuli. Lateral field areolated or plain. Phasmids pore-like, on tail or at level just anterior to anus. Caudalids and cephalids present. No deirids. Stylet guide, long, tubular. Stylet basal knobs rounded, laterally or posteriorly directed, without anterior processes. DGO close to the base of stylet. Procorpus most generally more or less barrel-shaped to accommodate coiled oesophageal lumen, amalgamated with the median bulb (cylindrical and non amalgamated in Brachydorus and species of other genera with short stylet); oesophagointestinal valve strongly developped. Intestine generally provided with fasciculi; posterior part of intestine may or may not overlap the rectum. Spermatheca well developped most generally provided with sperms. Vagina vera variously slecrotized; no vulval flaps; no epiptygmata.

Male tail short, conical pointed. Spicules strong, nearly straight or slightly curved, flanged or not; gubernaculum without titillae, protrusible or not.

Generally found in wet soils.

# Genera in Dolichodoridae

### Dolichodorus Cobb, 1914

DIAGNOSIS. Dolichodoridae.

Female: Labial region rounded, striated, offset, roughly quadrangular to prominently four lobed in en face view; labial disc more often prominent; subdorsal and subventral lip sectors distinct; lateral lip sectors reduced or absent. Amphid aperture small slit laterally directed. Stylet long (50 to 160 μm), strong. Lateral field with three lines, areolated. Tail hemispherical-spiked, rarely conoid. Phasmids postanal.

Male: Spicules most generally with prominent flanges. Gubernaculum apparently protruding.

#### TYPE SPECIES

Dolichodorus heterocephalus Cobb, 1914

#### OTHER SPECIES

- D. aestuarius Chow & Taylor, 1978
- D. aquaticus Doucet, 1986
- D. cobbi Golden, Handoo & Wehunt, 1986
- D. grandaspicatus Robbins, 1982
- D. kishansinghi Jairajpuri & Rahmani, 1979
- D. longicaudatus Doucet, 1981
- D. marylandicus Lewis & Golden, 1981
- D. minor Loof & Sharma, 1975
- D. miradvulvus Smart & Khuong, 1985
- D. nigeriensis Luc & Caveness, 1963
- D. profundus Luc, 1960
- D. pulvinus Khan, Seshadri, Weischer & Mathen, 1971
- D. silvestris Gillespie & Adams, 1962
- D. similis Golden, 1958

# Neodolichodorus Andrássy, 1976 = Plesiodorus Siddigi, 1976

### **DIAGNOSIS**

Female: Labial region rounded, striated (rarely smooth), weakly offset, rounded to roughly quadrangular in en face view; labial disc generally not prominent; amphid aperture small slit dorso-ventrally directed. Lateral field with four lines. Stylet long (50-140  $\mu m$ ), strong. Tail short, hemispherical, rarely conical. Phasmids adanal or slightly anterior to anus.

Male: Spicules not or weakly flanged. Gubernaculum apparently not protruding.

# TYPE SPECIES

Neodolichodorus obtusus (Allen, 1957) Andrássy, 1976

- = Dolichodorus obtusus Allen, 1957
- = Plesiodorus obtusus (Allen, 1957) Siddiqi, 1976

# OTHER SPECIES

- N. adelaidensis (Fisher, 1964) Siddigi, 1977
  - = Dolichodorus adelaidensis Fisher, 1964
  - = Plesiodorus adelaidensis (Fisher, 1964) Siddiqi, 1976
- N. arenarius (Clark, 1963) Siddiqi, 1977
  - = Dolichodorus arenarius Clark, 1963
  - = Plesiodorus arenarius (Clark, 1963) Siddiqi, 1976
- N. brevistilus (Heyns & Harris, 1973), Siddiqi, 1977
  - = Dolichodorus brevistilus Heyns & Harris, 1973
  - = Plesiodorus brevistilus (Heyns & Harris, 1973) Siddiqi, 1976

N. cassati (Luc & Dalmasso, 1971) Siddiqi, 1977

- = Dolichodorus cassati Luc & Dalmasso, 1971
- = Plesiodorus cassati (Luc & Dalmasso, 1971), Siddiqi, 1976

N. leiocephalus Doucet, 1981

- N. rostrulatus (Siddiqi, 1976) Siddiqi, 1977
  - = Plesiodorus rostrulatus Siddiqi, 1976

Brachydorus de Guiran & Germani, 1968 (genus dubium)

# **DIAGNOSIS**

Dolichodoridae. Labial region rounded, slightly offset, roughly quadrangular in end-on view, not annulated. Amphid apertures not known (no available SEM study). Stylet short (20-35  $\mu$ m); procorpus cylindrical not amalgamated with metacorpus. Lateral field with four incisures, not areolated. Female tail elongated (c' = 3.8-7.8), extremity pointed. Male tail short, conical. Spicules not flanged. Gubernaculum protruding.

### TYPE SPECIES

Brachydorus tenuis de Guiran & Germani, 1968

#### OTHER SPECIES

B. swarupi Koshy, Raski & Sosamma, 1981

### RELATIONSHIP BETWEEN GENERA

It has been pointed out earlier (Luc & Dalmasso, 1971) that the species in *Dolichodorus* can be divided into two groups : *i)* species with female tail spicate and lateral field with three lines; *ii)* species with female tail hemispherical and lateral field with four lines.

The second group was proposed as a new genus, Neodolichodorus Andrássy, 1976 (= Plesiodorus Siddiqi, 1976). More differential characters were discussed in successive emendations of the diagnoses, i. e. labial region more prominently off-set and face view more distinctly four-lobed in Dolichodorus; vaginal sclerotization symmetrical in Dolichodorus vs asymmetrical in Neodolichodorus; spicules with a more developed flange and gubernaculum protruding in Dolichodorus, vs spicules no or slightly flanged and gubernaculum not protruding in Neodolichodorus.

Some of these characters are not absolutely constant in the two genera, as for exemple the type of vaginal sclerotization. However, an additional difference does exist between them: the slit-like amphid aperture is laterally directed in *Dolichodorus* but it is dorsoventrally directed in *Neodolichodorus*.

Consequently the two genera are here considered to be distinct and valid. Note that female tail shape in *Dolichodorus* (hemispherical with spicate terminus) is very similar to that of J3 in *Neodolichodorus*, as observed by Luc, Coomans and Sarr (1987) in *N. rostrulatus*, in which the female tail is hemispherical.

When described by de Guiran & Germani (1968), Brachydorus, with type and only species B. litoralis, clearly differed from all species then known in Dolichodorus s. lato by four characters: i) a notably shorter body (at most 1.3 mm vs at least 1.8 mm in Dolichodorus s. 1.); ii) a considerably shorter stylet (at most 23  $\mu$ m vs at least 79  $\mu$ m in Dolichodorus s. l.); iii) a long conical female tail (c' = 5.5-7.8) vs a short tail hemispherical or with a spicate terminus in Dolichodorus s. l. (c' at most = 3.2); iv) a lip area smooth vs lip area with conspicuous annuli in Dolichodorus s. l. These characters were largely sufficient to justify a new genus.

The description of *Brachydorus swarupi* Koshi, Raski & Sosamma, 1981 generally agrees with the definition of the genus. However in this species the body length reaches 2.3 mm, the stylet is somewhat longer (up to 35  $\mu$ m) and the female tail shorter (c' = 3.8-5) than in the type species.

Subsequently new species have been described in the genera *Dolichodorus* and *Neodolichodorus*, that do not quite fit the description given for either one: *D. longicaudatus* share all the characters of *Dolichodorus*, but the tail long (c' = 3.8-5) and conical pointed, resembles that of *Brachydorus*; *N. leicocephalus* has lip region not annulated, a character which was considered specific for *Brachydorus*; *D. brevistilus* possesses a stylet only 50-60 µm long, and procorpus is cylindrical, not amalgamated with metacorpus. *D. aestuarius* and *D. pulvinus* show a lip region rounded instead of four-lobed, resembling *Neodolichodorus* or *Brachydorus*.

Because of these intermediate species, *Dolichodorus*, *Neodolichodorus* and *Brachydorus* appear very close to one another. Unfortunately no data could be obtained on the structure of amphid aperture in *Brachydorus*, a character that could have been of primary importance for deciding on the taxonomic status of this genus.

Until it is possible to study the face view of *Brachydorus* with SEM, it seems best to consider this genus a *genus dubium* in Dolichodoridae.

# POSITION OF DOLICHODORIDAE IN TYLENCHOIDEA

With only two valid genera, the family Dolichodoridae is the smallest in the suborder Tylenchina. It sheds some interesting lights on the evolution within the suborder, and it also represents a transition from the "prototylenchid" type, parallel to that shown by the Belonolaimidae.

Dolichodoridae retains many ancestral characters as defined by Luc et al. (1987): all species are ectoparasitic

on plant roots; all species are apparently amphimictic (males are present and numerous in each species and spermathecae contain sperms); no tendency exists for the females to become obese; there is no sexual dimorphism (no regression of the oesophagus and/or male stylet); the glandular part of the oesophagus remains pyriform and abutting the intestine; the oesophago-intestinal valve is prominent; phasmids are punctiform; all females have two functional genital branches equally developped and the columned uterus consists of four rows of cells.

Some derived characters are constantly seen in all members of the family, i. e., the disappearance of the deirids, the elongation of the stylet, and the reinforcement of the cephalic framework.

Other derived characters are seen in some species, i. e., the shortening of the tail; when present, this shortening always follows a symmetrical axial mode. The amphid apertures are of two types: rather long lateral slits or semi-circular dorso-ventrally directed slits.

The family also is characterized by the body annulation generally strong with a lateral field well marked and a thick cuticle; the characteristic cephalic sclerotization (see Luc, Coomans & Sarr, 1987 on *Neodolichodorus rostrulatus*); the tendency to regression or disappearence of the lateral lip sectors, coupled with a more or less pronounced incisure between homologous dorsal and ventral lip sectors, and in the subsequent lip region annuli, resulting of a four-lobed shape of the labial area; the heavy sclerotization of the *vagina vera*, and the trilobed caudal alae coupled with robust spicules and gubernaculum.

# REFERENCES

- ALLEN, M. W. & SHER, S. A. (1967). Taxonomic problems concerning the phytoparasitic nematodes. A. Rev. Phytopath., 5: 247-264.
- ANDRASSY, I. (1976). Evolution as a basis for the systematization of nematodes. London, Pitman Publishing, 288 p.
- CHITWOOD, B. G. (1950). An outline classification of the nematodes. In: Chitwood, B. G. & Chitwood, M. B. (Eds). *An introduction to nematology. I. Anatomy*. Baltimore, USA, Monumental Printing Co: 12-27.
- FOTEDAR, D. N. & HANDOO, Z. A. (1978). A revised scheme of classification to order Tylenchida Thorne, 1949 (Nematoda). J. Sci. Univ. Kashmir, 3 (1975): 55-82.

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- GOLDEN, A. M. (1971). Classification of the genera and higher categories in the order Tylenchida (Nematoda). In: Zuckerman, B. M., Mai, W. F. & Rohde, R. A. (Eds). Plant Parasitic Nematodes. Vol. 1. Morphology, Anatomy, Taxonomy and Ecology. New York & London, Academic Press: 191-232.
- Goodey, T. (1963). Soil and Freshwater Nematodes (2d Ed., rev. J. B. Goodey). London, Methuen & Co, xvi + 544 p.
- DE GUIRAN, G. & GERMANI, G. (1968). Brachydorus tenuis n. g., n. sp. (Nematoda: Dolichodorinae), associé à Ravenala madagascariensis sur la côte est malgache. Nematologica, 14: 447-452.
- Loof, P. A. A. (1958). Some remarks on the status of the subfamily Dolichodorinae, with description of *Macrotrophurus arbusticola* n. g., n. sp. (Nematoda: Tylenchidae). *Nematologica*, 3: 301-307.
- LUC, M., COOMANS, A. & SARR, E. (1987). Redescription of Neodolichodorus rostrulatus (Siddiqi, 1976) Siddiqi, 1977 (Nematoda: Tylenchina). Revue Nématol., 10: 29-37.
- Luc, M. & Dalmasso, A. (1971). Dolichodorus cassati n. sp. (Nematoda: Tylenchida). Annls Zool. Ecol. anim., 3: 97-101.
- Luc, M., Maggenti, A. R., Fortuner, R., Raski, D. J. & Geraert, E. (1987). A reappraisal of Tylenchina (Nemata). 1. For a new approach of the taxonomy of Tylenchina (Nemata). Revue Nématol., 10: 127-134.
- MAGGENTI, A. LUC, M., RASKI, D. J., FORTUNER, R. & GERAERT, E. (1987). A reappraisal of Tylenchina (Nemata). 2. Classification of the suborder Tylenchina (Nemata: Diplogasteria). Revue Nématol., 10: 135-142.
- Paramonov, A. A. (1967). [A critical review of the suborder Tylenchina (Filip'jev, 1934) (Nematoda : Secernentea)]. Akad. Naul SSSR Trudy gel'mint. Lab., 18: 78-101.
- SIDDIQI, M. R. (1970). On the plant-parasitic genera *Merlinius* gen. n. and *Tylenchorhynchus* Cobb and the classification of the families Dolichodoridae and Belonolaimidae n. rank. *Proc. helminth. Soc. Wash.*, 37: 68-77.
- SIDDIQI, M. R. (1976). New plant nematode genera Plesiodorus (Dolichodorinae), Meiodorus (Meiodorinae subfam. n.), Amplimerlinius (Merliniinae) and Gracilancea (Tylodorinae grad. n.). Nematologica, 22: 390-416.
- SIDDIQI, M. R. (1986). Tylenchida Parasites of Plants and Insects. Slough, UK, Commonw. Inst. Parasitol.: IX + 645 p.
- SKARBILOVICH, T. S. (1959). On the structure of nematodes order *Tylenchida* Thorne, 1949. *Acta parasit. pol.*, 7: 117-132.