Revision of the genus *Ditylenchus* Filipjev, 1936: *Ditylenchoides* gen. n. and *Paraditylenchus* gen. n. (Nematoda: Anguinoidea)

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Summary. Using results of the phylogenetic analysis of rRNA gene sequences and morphological data of Anguinoidea, a narrow definition for the genus *Ditylenchus* Filipjev, 1936 is proposed and discussed. Two new genera, *Ditylenchoides* gen. n. with type species, *Ditylenchoides destructor* (Thorne, 1945) gen. n., com. n. and other fourteen species and genus *Paraditylenchus* gen. n. containing the type species, *Paraditylenchus gallaeformans* (Oliveira *et al.,* 2013) gen. n., com. n. are erected. Adults of the genus *Ditylenchoides* gen. n. differs from those of *Ditylenchus* in body length, number of incisures in lateral field, tail terminus shape and types of plant symptoms induced. *Paraditylenchus* gen. n. differs from *Ditylenchus* in body length, post-vulval uterine sac length and bursa length. *Ditylenchus drepanocercus* Goodey, 1953 is transferred to the genus *Zeatylenchus* Zhao *et al.,* 2013 as *Zeatylenchus drepanocercus* (Goodey, 1953) comb. n. New diagnoses for the genera *Ditylenchus* and *Zeatylenchus* are also proposed. Phylogenetic results indicate independent origins of the ability to induce gall formation and tissue swelling in plants within representatives of the superfamily Anguinoidea.
Key words: new genus, phylogeny, stem nematodes, *Zeatylenchus*.

Ditylenchus Filipjev, 1936 is a large complex genus and one of the most taxonomically difficult genera of plant-parasitic nematodes. Its systematic position within the Tylenchida has changed several times, and a great number of former *Ditylenchus* species have been transferred to other genera within suborder Tylenchina as well as to the suborder Hexatylina (Filipjev, 1936; Sumenkova, 1982; Brzeski, 1991; Sturhan & Brzeski, 1991; Siddiqi 2000). The genus *Ditylenchus* is presently considered within the family Anguinidae Nicoll, 1935 (Fortuner & Maggenti, 1987) or within the superfamily Anguinoidea (Nicoll, 1935) Siddiqi, 1980, family Anguinidae, subfamily Anguininae Nicoll, 1935 (Sumenkova, 1982; Siddiqi, 2000).

Over the past years, different authors have proposed different concepts to define this genus and show evolutionary tendencies within it (Paramonov, 1970; Brzeski, 1981, 1991; Fortuner, 1982). The concept of dividing the genus *Ditylenchus* into: 1) pathogen-specific species, and 2) non-specific pathogenic and mycophagous species was proposed by Paramonov (1970). Further, Skarbilovich (1980) also proposed division this genus into two groups: 1) *D. dipsaci* (Kühn, 1857) Filipjev, 1936 and related species, calling it the "dipsacoid group", 2) *D. destructor* Thorne, 1945 and related species calling it the "destructoid group". Presently, two main classifications for *Ditylenchus* and *Ditylenchus*-like nematodes are in use: the first one developed by Fortuner and Maggenti (1987) and the second one by Siddiqi (2000).

Fortuner and Maggenti (1987) proposed a wide definition of the genus *Ditylenchus* with 91 valid species, distinguished three groups with this genus and considered *Nothotylenchus* Thorne, 1941, *Boleodoroides* Mathus, Khan & Prasad, 1966, *Diptenchus* Khan, Chawla & Seshadri, 1969, *Safianema* Siddiqi, 1980 and *Orrina* Brzeski, 1981 as synonyms of *Ditylenchus*. Brzeski (1991) and Sturhan and Brzeski (1991) also accepted this point of view. According to Fortuner and Maggenti

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(1987), the first group of species (*D. dipsaci, D. destructor, D. angustus* (Butler, 1913) Filipjev, 1936, and others) became specialised parasites of above-ground parts of higher plants, the median bulb valve regressed and eventually disappeared completely in the second group of species, and the third group of species became associated with bark beetles.

Siddiqi (2000) distinguished the genus *Ditylenchus* and several other genera: *Nothotylenchus, Safianema*, *Diptenchus* and *Orrina*. Within the genus *Ditylenchus* containing 57 species, Siddiqi (2000) differentiated the *D. dipsaci* group by four incisures in the lateral field, sharply pointed tail tips, and plant-cell feeders that have almost abandoned their primitive trait of fungal feeding. The other group, the *D. triformis* group, includes most *Ditylenchus* species that are basically fungal feeders, with six incisures in the lateral field and a round end tail tip.

The introduction of molecular phylogenetic methods showed a rather complex pattern of Anguinoidea evolution and caused problems with the assignment of known species to certain genera in order to reflect inferred phylogeny. Phylogenetic analysis of partial 28S rRNA gene sequences of some representatives of the order Tylenchida made by Subbotin *et al.* (2006) revealed that in several trees, *D. destructor* did not appear as a sister taxon to the Anguininae. Oliveira *et al.* (2013) using the 28S rRNA gene sequences showed that *Ditylenchus* was a paraphyletic taxon including several evolutionary independent lineages: *i*) *D. dipsaci* and *D. gigas* Vovlas *et al.,* 2011; *ii*) *D. gallaeformans* Oliveira *et al.,* 2013 and *D. drepanocercus* Goodey, 1953; and *iii*) *D. destructor* and *D. halictus* Giblin-Davis *et al.,* 2010. Douda *et al.* (2013) also indicated two clades with *Ditylenchus* species. Based on the analysis of the ITS1 rRNA and 18S rRNA gene sequences, Qiao *et al.* (2016) also noticed that species of *Ditylenchu*s separated into two clades: *i*) *D. destructor*, *D. africanus* Wendt *et al.,* 1995 and *D. myceliophagus* Goodey, 1958; and *ii*) *D. dipsaci* and *D. weischeri* Chizhov *et al.,* 2010. Paraphyly of the genus was also showed by several authors (Shokoohi *et al.,* 2018; Gu *et al.,* 2023; Munawar *et al.,* 2023; Vyshali *et al.,* 2023). However, several authors (Esmaeili *et al.,* 2017a, b; Yaghoubi *et al.,* 2018; Hashemi *et al.,* 2022; Azimi & Abdolkhani, 2023; Zeng *et al.,* 2023) avoided proposing paraphyly of this genus, but considered a wide concept of this taxon for phylogenetic analysis. Thus, the validities, composition and positions of *Ditylenchus*-like nematode taxa have been the subjects of intensive discussions and speculation and, therefore, remain unresolved. Comprehensive morphological and molecular analyses are still needed to understand relationships within these nematode groups and replace the present artificial classification by a natural one that would reflect evolutionary trends.

The modern system of nematode classification should be based on, and reflect, evolutionary relationships among these organisms. Phylogenetic classification may or may not agree with traditional morphological taxonomy, which is based on similarities in structures regardless of ancestry. In this paper, we attempt to resolve some problems of systematics of the Anguinoidea and propose further division of *Ditylenchus* and *Ditylenchus*-like nematodes. Thus, the main goal of this study was to reconstruct phylogenetic relationships within the Anguinoidea with the analyses of relationships of *Ditylenchus* and *Ditylenchus*-like nematodes, and to propose new taxonomic divisions of this group.

MATERIALS AND METHODS

Morphological study. Analysis of morphological and morphometric characters of species belonging to the genera *Ditylenchus*, *Zeatylenchus, Indoditylenchus* Sinha, Choudhury & Baqri*,* 1985, *Pseudhalenchus* Thorne, 1958 and others were made using their published descriptions (Brzeski, 1981, 1991; Fortuner & Maggenti, 1987; Sturhan & Brzeski, 1991; Giblin-Davis *et al.,* 2010; Vovlas *et al*., 2011; Oliveira *et al.*, 2013; Zhao *et al.,* 2013; Esmaeili *et al.,* 2017a, b; Skwiercz *et al.,* 2017; Shokoohi *et al.,* 2018; Yaghoubi *et al.,* 2018; Aliverdi *et al.,* 2021; Hashemi *et al.,* 2022; Azimi & Abdolkhani, 2023; Gu *et al.,* 2023; Munawar *et al.,* 2023; Vyshali *et al.,* 2023; Zeng *et al.,* 2023, and others).

Molecular study. The sequences of the 28S rRNA, ITS of rRNA and 18S rRNA genes of *Ditylenchus* and other representatives of Anguinoidea published in the GenBank (Subbotin *et al.,* 2006; Giblin-Davis *et al.,* 2010; Zhao *et al.,* 2011, 2013; Oliveira *et al.* 2013; Esmaeili *et al.,* 2017a,b; Shokoohi *et al.,* 2018; Yaghoubi *et al.,* 2018; Subbotin & Chizhov, 2019; Aliverdi *et al.,* 2021; Hashemi *et al.,* 2022; Kanzaki *et al.,* 2022; Munawar *et al.,* 2022, 2023; Azimi & Abdolkhani, 2023; Gu *et al.,* 2023; Vyshali *et al.,* 2023; Zeng *et al.,* 2023; Alvarez-Ortega & Subbotin, 2024) were aligned using ClustalX 1.83 (Chenna *et al.,* 2003). Outgroup taxa for each dataset were chosen based on previously published data (Subbotin *et al.,* 2006). Several alignments were created: *i*) D2-D3 of 28 rRNA gene alignment containing sequences of Anguinoidea species; *ii*) partial 18S rRNA gene alignment containing sequences of Anguinoidea species; and *iii*) ITS rRNA gene alignment containing sequences of species from the *Ditylenchoides* gen. n.

The sequence alignments were analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003) with maximum likelihood (ML) using PAUP* 4.0a169 (Swofford, 2003). The BI analysis for each gene was initiated with a random starting tree and was run with four chains for 1.0×10^6 generations. The Markov chains were sampled at intervals of 100 generations. Two runs were performed for each analysis. After discarding burn-in samples and evaluating convergence the remaining samples were retained for further analysis. The topologies were used to generate a 50% majority rule consensus tree. Posterior probabilities (PP) were given on appropriate clades. For testing of alternative topologies in ML, we used the Kishino-Hasegawa (KH), Shimodaira-Hasegawa (SH) and Shimodaira Approximately Unbiased (AU) tests as implemented in PAUP*. Trees were visualised with the TreeView 1.6.6 program (Page, 1996) and drawn with Adobe Illustrator v.10.

RESULTS AND DISCUSSION

Using the results of molecular phylogenetic analysis, morphololological characters and peculiarities of parasitism, two new genera, *Ditylenchoides* gen. n., and *Paraditylenchus* gen. n. are proposed for nematode species previously considered as representatives of the genus *Ditylenchus*.

Because of overlapping morphometric values of diagnostic morphological characters, their limited number, mosaic and parallel evolution, molecular characters play a major role in differentiating and delimiting genera and species

Molecular characterisation and phylogenetic relationships. D2-D3 expansion segments of 28S rRNA gene. The alignment contained 57 sequences of the representatives from Anguinoidea and two sequences of the outgroup taxa and was 844 bp long. All Anguinoidea sequences were distributed with two main clades (I and II, Fig. 1). Clade I consisted of three subclades (a, b, c). Representatives of the genus *Ditylenchus sensu stricto* belonged to the Clade Ib and marked by grey in Figure 1. In the phylogenetic tree, sequences originally identified under generic name '*Ditylenchus*' are kept as such until further clarification.

Partial 18S rRNA gene. The alignment contained 32 sequences of the representatives from Anguinoidea and three sequences of the outgroup taxa and was 987 bp long. The phylogenetic tree contained several clades, but without distinct resolved relationships (Fig. 2).

ITS rRNA gene of *Ditylenchoides* gen. n. The alignment contained 13 sequences of the representatives from *Ditylenchoides* gen. n. and three sequences of the outgroup taxa and was 742 bp long. Phylogenetic relationships of species of *Ditylenchoides* gen. n. are given in Figure 3.

Maximum likelihood testing. The results of ML testing of 28S rRNA and 18S rRNA gene tree topologies indicate two alternative phylogenetic hypotheses: *i*) a sister relationship of *Ditylenchoides* gen. n. with *Ditylenchus*; or *ii*) a sister relationship of *Zeatylenchus* and *Paraditylenchus* gen. n. with *Ditylenchus* (Table 1). All ML tests, except for Shimodaira-Hasegawa test for 18S rRNA gene dataset, rejected the tested alternative topologies.

Phylogenetic analysis of the partial 28S rRNA gene sequences revealed two major clades within Anguinoidea. Clade I consisted of three subclades (a, b, c). Subclade Ia is the only clade that contained representatives with different feeding types and hosts: mycelophagous nematodes (*Ditylenchus*-like nematodes and *Nothotylenchus*), plant-parasitic nematodes inducing necrotic symptoms on fern (*Cotylenchus cleo* Alvarez-Ortega & Subbotin, 2024), plant-parasitic nematodes inducing swelling and galls on hosts (*Orrina phyllobia* (Thorne, 1934) Brzeski, 1981, *Pterotylenchus cecidogenus* Siddiqi & Lenne, 1984), nematodes parasitising fig fruits (*Ficotylus* spp.), and insect associated tylenchids (*Neomisticus* Siddiqi, 1986*, Sychnotylenchus* Rühm, 1956 and *Neoditylenchus* Meyl, 1961). This subclade Ia illustrates evolutionary trends in anguinoids previously noticed by Paramonov (1970) and Siddiqi (1983) from ancestral fungal feeding to parasitism in root and then aerial plant systems, gall inducing or fungal feeding to association with insects. Ryss (2023) proposed that insect vectors in the life cycles of plant-parasitic nematodes are inherited from the ancestral detritivorous nematode associations within the detritus food web, rather than inserted in the dixenic life cycle of the 'nematode-fungus-plant' association.

Phylogenetic analysis of rRNA genes also indicated several independent origins of the ability to induce gall formation and tissue swelling within Anguinoidea: *i*) *Orrina phyllobia* and

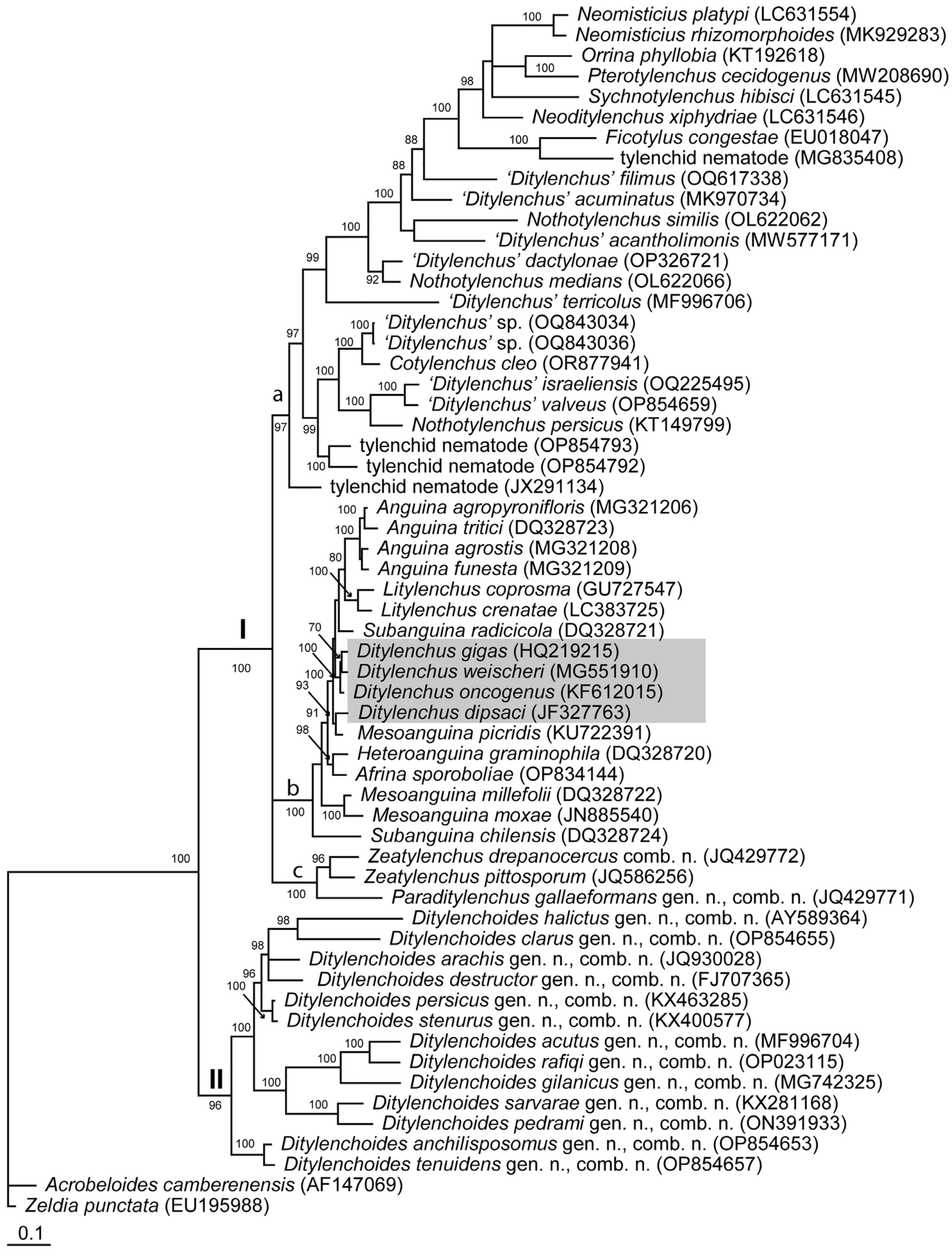

Fig. 1. Phylogenetic relationships within the superfamily Anguinoidea as inferred from Bayesian analysis of the D2-D3 of 28S rRNA gene sequences under the GTR + I + G model. Posterior probabilities greater than 70% are given for appropriate clades. *Ditylenchus sensu stricto* is marked by grey area. *'Ditylenchus'* - *Ditylenchus*-like nematode.

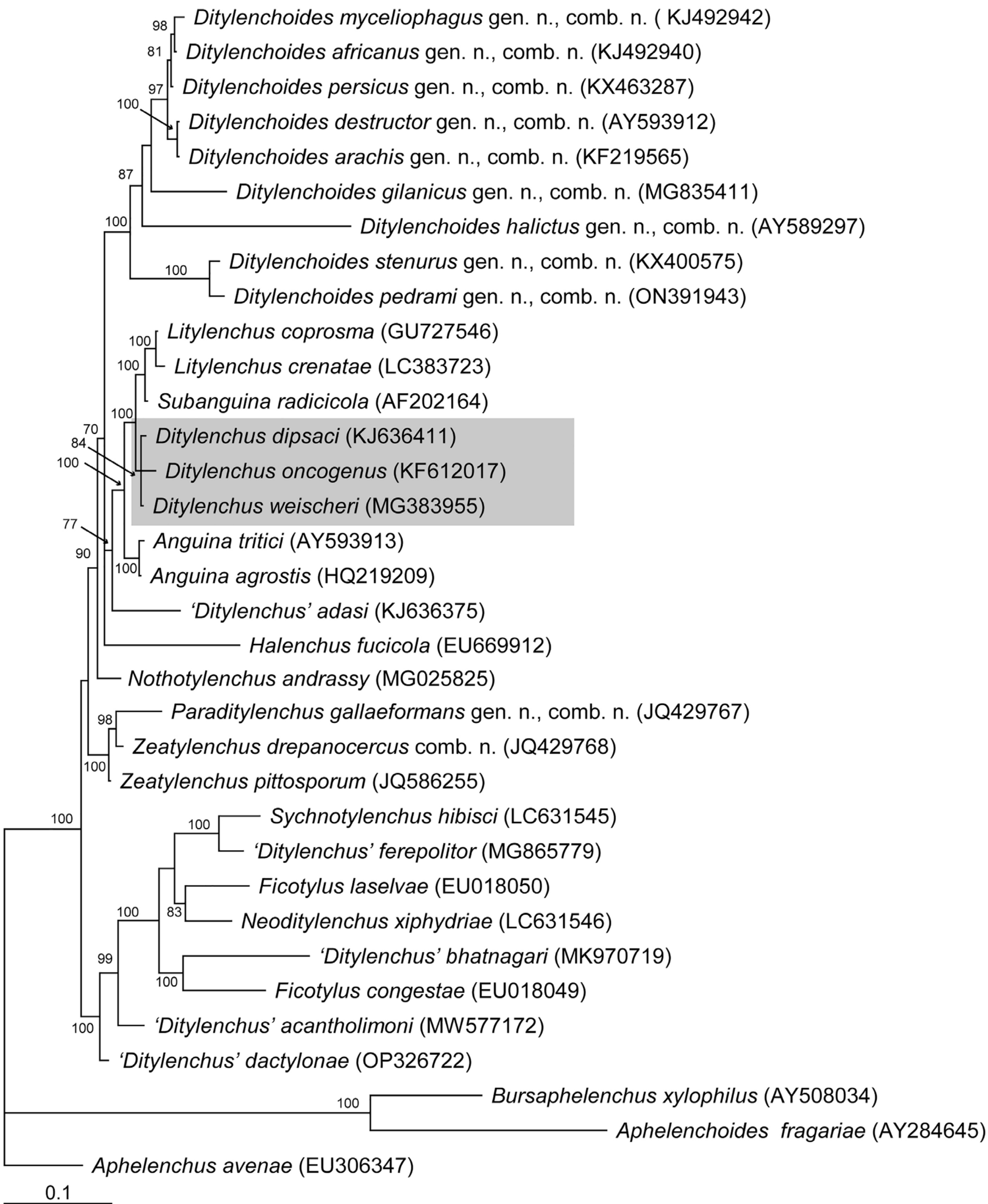

Fig. 2. Phylogenetic relationships within the superfamily Anguinoidea as inferred from Bayesian analysis of the partial 18S rRNA gene sequences under the GTR + I + G model. Posterior probabilities greater than 70% are given for appropriate clades. *Ditylenchus sensu stricto* is marked by grey area. *'Ditylenchus'* - *Ditylenchus*-like nematode.

Pterotylenchus cecidogenus - Clade Ia; *ii*) *Anguina* Scopoli, 1777, related genera and *Ditylenchus sensu stricto* - Clade Ib; *iii*) *Paraditylenchus gallaeformans* comb. n. - Clade Ic and *iv*) *Halenchus fucicola* (de Man & Barton in de Man, 1892) N.A. Cobb in M.V. Cobb, 1933 -

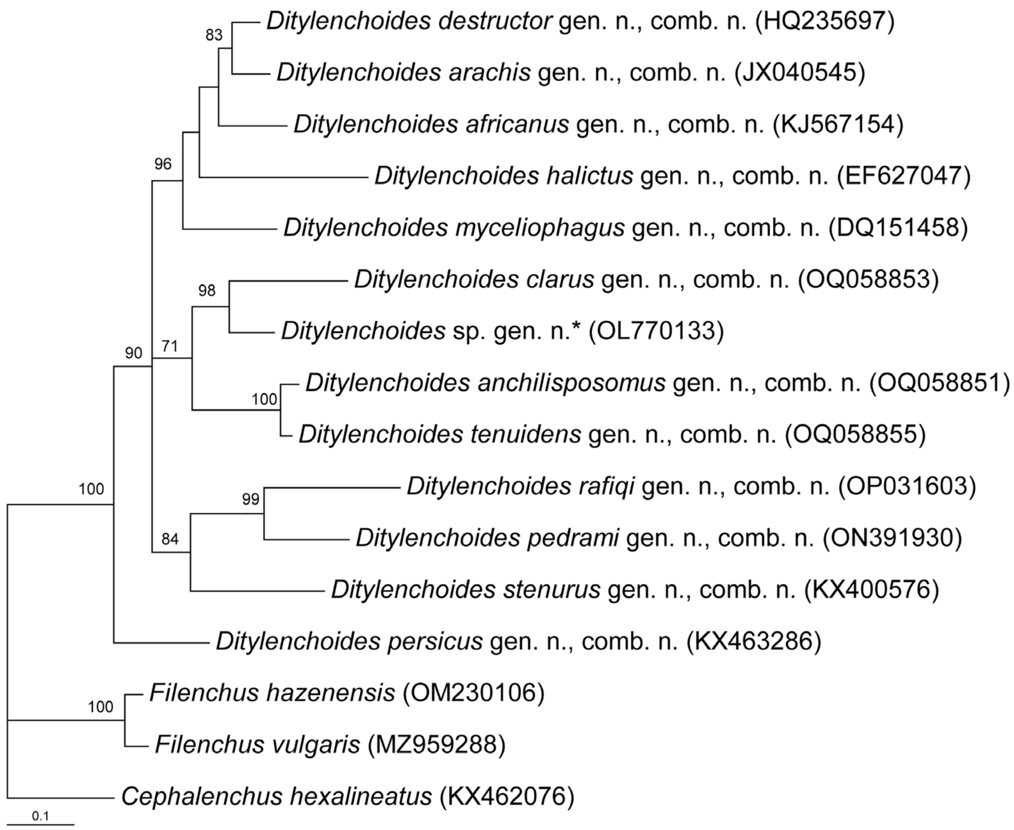

Fig. 3. Phylogenetic relationships within the genus *Ditylenchoides* gen. n. (Clade II) as inferred from Bayesian analysis of the ITS rRNA gene sequences under the GTR + I + G model. Posterior probabilities greater than 70% are given for appropriate clades. * - identified as *Ditylenchus myceliophagus* in the GenBank.

unique position in 18S rRNA gene tree.

The genus *Neomisticius,* previously considered within the family Paurodontidae Thorne, 1941 by Siddiqi (2000), was transferred to the family Anguinidae by Subbotin and Chizhov (2019) and genera *Sychnotylenchus* and *Neoditylenchus* previously considered within the family Sychnotylenchidae Paramonov, 1967 by Siddiqi (2000), were transferred to the family Anguinidae by Kanzaki *et al.* (2022). The present phylogenetic analysis confirmed these changes in classification.

Modified diagnosis for the genera *Ditylenchus sensu stricto* and *Zeatylenchus* are given. Only plant-parasitic nematodes inducing tissue deformation in plants are considered belonging to the genus *Ditylenchus*.

Genus *Ditylenchus* Filipjev, 1936

Diagnosis. Anguinoidea. **Female** body 0.9-2.2 mm, almost straight or slightly curved ventrally, mature adults slender. Lip region continuous, high, cephalic framework moderately sclerotised. Median bulb muscular, with strongly refractive valve. Basal bulb with 0.5 or less overlapping intestine, dorsal and subventral gland nuclei anterior to pharyngeal-intestinal junction. Secretory-excretory pore at posterior half of isthmus to anterior conical or middle part of basal bulb. Lateral field with 4 or rarely 6 incisures. Ovary straight, without distinct flexures, its posterior part with one row of oocytes. Spermatheca elongate, with small sperm cells with nuclei occupying most of cells. Crustaformeria in a form of quadricolumella, four row of four cells each. Vulva is a transverse slit, vagina perpendicular to ventral body wall. Post-vulval uterine sac more than 3 times longer than vulval body diam. Female tail conical with pointed to mucronate terminus. **Male** bursa leptoderan, adanal to subterminal, not reaching tail tip. Testis outstretched. Parasites of higher plants inducing swellings and deformations of plant tissues. Infective stages are juveniles and adults. Distributed in temperate regions.

Type species:

Ditylenchus dipsaci (Kühn, 1857) Filipjev, 1936

Other species:

Ditylenchus angustus (Butler, 1913) Filipjev, 1936

Table 1. Results of tree topology tests and alternative phylogenetic hypotheses.

Alignment / Hypothesis	D2-D3 of 28S rRNA gene				
	-ln L	**Diff-ln L**	**KH**	**SH**	**AU**
ML tree	13742.628	best	-	-	-
Ditylenchoides gen. n. and *Ditylenchus* are sister clades	13800.223	57.595	0.0001*	0.000*	0.000*
Zeatylenchus and *Paraditylenchus* gen. n. are sister clade with *Ditylenchus*	13784.772	42.143	0.0048*	0.001*	0.001*
	Partial 18S rRNA gene				
ML tree	6500.082	best	-	-	-
Ditylenchoides gen. n. and *Ditylenchus* are sister clades	6527.196	27.113	0.0143*	0.079	~0*
Zeatylenchus and *Paraditylenchus* gen. n. are sister clade with *Ditylenchus*	6595.122	95.040	<0.0001*	0.000*	~0*

* $P < 0.05$; KH: Kishino-Hasegawa test using normal approximation, two-tailed test; SH: Shimodaira-Hasegawa test using RELL bootstrap (one-tailed test); AU: Shimodaira Approximately Unbiased test.

Ditylenchus chaerophyllum Karapetian & Mkrtchian, 2000

Ditylenchus dryadis Anderson & Mulvey, 1980

Ditylenchus falcariae (Pogosjan, 1967) Sumenkova, 1982

Ditylenchus galeopsidis Teploukhova, 1968

Ditylenchus gigas Vovlas, Troccoli, Palomares-Rius, De Luca, Liébanas, Landa, Subbotin & Castillo, 2011

Ditylenchus laurae Skwiercz, Kornobis, Winiszewska, Przybylska, Obrepalska-Steplowska, Gawlak & Subbotin, 2017

Ditylenchus oncogenus Vovlas, Troccoli, Palomares-Rius, De Luca, Cantalapiedra-Navarrete, Liebanas, Landa, Subbotin & Castillo, 2016

Ditylenchus paraoncogenus Hashemi, Karegar, Helder, Holterman & Mokaram Hesar, 2022

Ditylenchus sonchophilus Kirjanova, 1958

Ditylenchus tobaensis (Schneider, 1937) Kirjanova, 1951

Ditylenchus weischeri Chizhov, Borisov & Subbotin, 2010

The genus *Ditylenchus* with the type species *Ditylenchus dipsaci* was erected by Filipjev (1936) from representatives of the genus *Tylenchus* Bastian, 1865. Many nematologists considered *D. dipsaci* a collective species or a species complex (Sturhan, 1971; Sturhan & Brzeski, 1991) and molecular analysis confirmed this proposal (Subbotin *et al.,* 2005). Further molecular and morphological analysis lead to descriptions of several new species from the *D. dipsaci* species complex (Subbotin *et al.,* 2005; Vovlas *et al.,* 2011; Skwiercz *et al.,* 2017). Some species are well defined, but others such as *D. galeopsidis, D. falcariae, D. sonchophilus, D. tobaensis* were considered as synonyms of *D. dipsaci* by Brzeski (1991) and Siddiqi (2000). However, these species were considered as valid ones by Sumenkova (1982) and we accepted this point of view.

In this study, we propose a narrower definition of *Ditylenchus* than that used in previous classifications. This genus included only plant-parasitic *Ditylenchus* species. All *Ditylenchus* species induce swellings and deformations of plant tissues. The position of two species assigned by Siddiqi (2000) to the genus *Ditylenchus*: *D. convallariae* Sturhan & Friedman, 1965 and *D. leptosoma* Geraert & Choi, 1990, parasitising plants and inducing symptoms is uncertain and requires detailed analysis and study.

All mycophagous species, including those associated with insects, should be assigned to other known and new genera and some of them are marked on the phylogenetic trees here as *Ditylenchus*-like nematodes. Molecularly, the genus *Ditylenchus* is related to *Heteroanguina ferulae* and *Mesoanguina picridis*.

Differential diagnosis. The genus *Ditylenchus* is similar to the genera *Ditylenchoides* gen. n., *Paraditylenchus* gen. n. and *Zeatylenchus.*

Ditylenchus differs from *Ditylenchoides* gen. n. in number of incisures in lateral field of adults (4, rarely 6 *vs* 6, rarely 4), tail terminus (sharp to pointed or mucronate *vs* mainly conically rounded), plant symptoms induced (swellings and deformations in aerial parts of plant *vs* nonspecific symptoms in under-ground parts of plants or fungal feeders).

Ditylenchus differs from *Paraditylenchus* gen. n. in longer body length for females (0.9-2.2 *vs* 0.5-0.7 mm), post-vulval uterine sac length (more than 3 *vs* 1.4-1.8 times longer than vulval body diam.), bursa length (leptoderan, not reaching tail tip *vs* peloderan, enveloping tail tip).

Ditylenchus differs from *Zeatylenchus* in longer body length for females (0.9-2.2 *vs* 0.45-0.65 mm), adult lip region (continuous and high *vs* offset and low), tail terminus (pointed to mucronate *vs* arcuate, offset on dorsal side, spicate), post-vulval uterine sac length (more than 3 times *vs* 1.0-1.5 times longer than vulval body diam.), plant symptoms induced (swellings and deformations *vs* brown or yellow chlorotic spots in aerial parts of plant).

Genus *Ditylenchoides* gen. n.

Diagnosis. Anguinoidea. **Female** body 0.4-1.9 mm, almost straight or slightly curved ventrally when relaxed. Lip region continuous, high, cephalic framework moderately sclerotised. Median bulb muscular or non-muscular, with indistinct or strongly refractive valve. Basal bulb offset from intestine and compact or irregular, not overlapping intestine or overlapping up to 0.5 body diam. Secretory-excretory pore at middle part of basal bulb, posterior to isthmus. Lateral field mostly with 6 incisures, rarely 4 or 7 incisures. Ovary straight, without distinct flexures, its posterior part with one row of oocytes. Spermatheca elongate, with small sperm cells with nuclei occupying most of cells. Crustaformeria in form of quadricolumella, four rows of four cells each. Vulva is a transverse slit, vagina perpendicular to ventral body wall. Post-vulval uterine sac 0.5-3.1 times longer than the vulval body diam. Female tail conical or subcylindrical, terminus mostly rounded or rarely pointed. **Male** bursa leptoderan, adanal to subterminal, not reaching tail tip. Mostly fungal feeders, parasites of underground plant parts. Some species are associated with insects. Infective stages are juveniles and adults. Distributed in temperate and tropical regions.

Zoobank registration: urn:lsid:zoobank.org:act: B98799E7-1309-44FC-8A18-197A7A 83B8D2

Type species:

Ditylenchoides destructor (Thorne, 1945) gen. n., com. n.

= *Ditylenchus destructor* Thorne, 1945

Other species:

Ditylenchoides acutus (Khan, 1965) gen. n., comb. n.

= *Ditylenchus acutus* (Khan, 1965) Fortuner & Maggenti, 1987

= *Nothotylenchus acutus* Khan, 1965

Ditylenchoides africanus (Wendt, Swart, Vrain & Webster, 1995) gen. n., comb. n.

= *Ditylenchus africanus* Wendt, Swart, Vrain & Webster, 1995

Ditylenchoides anchilisposomus (Tarjan, 1958) gen. n., comb. n.

= *Safianema anchilisposoma* (Tarjan, 1958) Siddiqi, 1980

= *Ditylenchus anchilisposomus* (Tarjan, 1958) Fortuner, 1982

= *Pseudhalenchus anchilisposomus* Tarjan, 1958

Ditylenchoides arachis (Zhang, Liu, Janssen, Zhang, Xiao, Li, Couvreur & Bert, 2014) gen. n., comb. n.

= *Ditylenchus arachis* Zhang, Liu, Janssen, Zhang, Xiao, Li, Couvreur & Bert, 2014

Ditylenchoides clarus (Thorne & Malek, 1968) gen. n., comb. n.

= *Ditylenchus clarus* Thorne & Malek, 1968

Ditylenchoides gilanicus (Yaghoubi, Pourjam, Ye, Castillo & Pedram, 2018) gen. n., comb. n.

= *Ditylenchus gilanicus* Yaghoubi, Pourjam, Ye, Castillo & Pedram, 2018

Ditylenchoides halictus (Giblin-Davis, Erteld, Kanzaki, Ye, Zeng & Center, 2010) gen. n., comb. n.

= *Ditylenchus halictus* Giblin-Davis, Erteld, Kanzaki, Ye, Zeng & Center, 2010

Ditylenchoides myceliophagus (Goodey, 1958) gen. n., comb. n.

= *Ditylenchus myceliophagus* Goodey, 1958

Ditylenchoides pedrami (Azimi & Abdolkhani, 2023) gen. n., comb. n.

= *Ditylenchus pedrami* Azimi & Abdolkhani, 2023

Ditylenchoides persicus (Esmaeili, Heydari, Castillo & Palomares-Rius, 2017) gen. n., comb. n.

= *Ditylenchus persicus* Esmaeili, Heydari, Castillo & Palomares-Rius, 2017

Ditylenchoides rafiqi (Vyshali, Singh Somvanshi, Islam, Kundu & Rahaman Khan, 2023) gen. n., comb. n.

= *Ditylenchus rafiqi* Vyshali, Singh Somvanshi, Islam, Kundu & Rahaman Khan, 2023

Ditylenchoides sarvarae (Shokoohi, Iranpour, Peneva, Elshishka, Fourie & Swart, 2018) gen. n., comb. n.

= *Ditylenchus sarvarae* Shokoohi, Iranpour, Peneva, Elshishka, Fourie & Swart, 2018

Ditylenchoides stenurus (Esmaeili, Heydari, Ziaie & Ye, 2017) gen. n., comb. n.

= *Ditylenchus stenurus* Esmaeili, Heydari, Ziaie & Ye, 2017

Ditylenchoides tenuidens (Gritsenko, 1971) gen. n., comb. n.

= *Ditylenchus tenuidens* Gritsenko, 1971

Differential diagnosis. The genus *Ditylenchoides* gen. n. is similar to the *Ditylenchus*, *Indoditylenchus* and *Pseudhalenchus.*

Ditylenchoides gen. n. differs from *Ditylenchus* in number of incisures in lateral field of adults (6, rarely 4 *vs* 4, rarely 6), tail terminus (mainly conically rounded *vs* sharp to pointed or mucronate), plant symptoms induced (not specific symptoms in underground parts of plants or fungal feeders *vs* swellings and deformations in aerial parts of plant).

Ditylenchoides gen. n. differs from *Pseudhalenchus* in pharyngeal gland lobe length (short or abutting *vs* pharyngeal lobe long and equal to or greater than 3 body diameters).

Ditylenchoides gen. n. differs from *Indoditylenchus* in tail shape (conical to subcylindroid *vs* filiform to elongate-conical).

Ditylenchoides gen. n. is a highly morphologically and molecularly diverged genus belonging to Anguinoidea. The plant-parasitic species, *Ditylenchoides destructor*, was selected as the type species of the proposed genus *Ditylenchoides* gen. n. The genus *Ditylenchoides* gen. n. is well distanced from the *Ditylenchus* and other Anguinoidea genera in the combination of its biological, molecular and morphological characters. All species are fungal feeders and some infect underground plant parts. *Ditylenchoides* gen. n. contains the larger number of species in the superfamily. This number will likely be increased after molecular characterisation of other known *Ditylenchus*-like nematodes and descriptions of new species.

Genus *Paraditylenchus* gen. n.

Diagnosis. Anguinoidea. **Female** body 0.5-0.7 mm, almost straight to slightly arcuate. Lip region continuous, high, cephalic framework moderately sclerotised. Median bulb muscular, with strongly refractive valve. Basal bulb usually abutting, offset from intestine or slightly overlapping intestine. Secretory-excretory pore at isthmus level. Lateral field with 4 incisures. Ovary straight, without distinct flexures, its posterior part with one row of oocytes. Spermatheca elongate, with large sperm cells which nuclei occupying most of cell. Crustaformeria in form of quadricolumella, four rows of four cells each. Vulva a transverse slit, vagina perpendicular to ventral body wall. Post-vulval uterine sac 1.4-1.8 times longer than vulval body diam. Female tail conical, terminus pointed to minutely rounded. **Male** bursa enveloping tail tip (peloderan). Parasites of aerial parts of plants, causing swellings on leaves, inflorescences, and stems. Infective stages unknown. No data about associations with insects or fungi. Distributed in tropical region.

Zoobank registration: urn:lsid:zoobank.org: act:75213879-ABC1-439C-80F6-7E5CB4B F4E01

Type and only species:

Paraditylenchus gallaeformans (Oliveira, Santin, Seni, Dietrich, Salazar, Subbotin, Mundo-Ocampo, Goldenberg & Barreto, 2013) gen. n., comb. n.

= *Ditylenchus gallaeformans* Oliveira, Santin, Seni, Dietrich, Salazar, Subbotin, Mundo-Ocampo, Goldenberg & Barreto, 2013.

Differential diagnosis. The genus *Paraditylenchus* gen. n. is morphologically similar to the genera *Ditylenchus* and *Zeatylenchus.*

Paraditylenchus gen. n. differs from *Ditylenchus* in shorter body length for females (0.5-0.7 *vs* 0.9-2.2 mm), post-vulval uterine sac length (1.4-1.8 *vs* more than 3 times longer than the vulval body diam.), and bursa length (peloderan, enveloping tail tip *vs* leptoderan, not reaching tail tip).

Paraditylenchus gen. n. differs from *Zeatylenchus* in female tail terminus (pointed to minutely rounded *vs* terminus arcuate, offset on dorsal side), spicate bursa length (peloderan *vs* adanal), number of lateral field incisures (4 *vs* 3), and plant symptoms induced (swellings and deformations *vs* brown or yellow chlorotic spots in aerial parts of plant).

Genus *Zeatylenchus* Zhao, Davies, Alexander & Riley, 2013

Diagnosis. Anguinoidea. **Female** body 0.45-0.65 mm, almost straight, slender to semi-obese. Lip region offset and low, cephalic framework moderately sclerotised. Median bulb muscular or non-muscular, with weak valve. Lateral field with 3 incisures. Basal bulb offset from intestine and compact or irregular, slightly overlapping intestine. Secretory-excretory pore at stylet knob or isthmus level. Ovary straight, without flexures, its posterior part with one row of oocytes. Spermatheca elongate. Crustaformeria in form of quadricolumella, four rows of four cells each. Vulva a transverse slit, vagina perpendicular to ventral body wall. Post-vulval uterine sac 1.0-1.5 times longer than vulval body diam. Female tail conical, terminus arcuate, offset on dorsal side, spicate.

Male bursa adanal, not reaching tail tip. Sperms amoeboid. Parasites of leaves of higher plants, causing brown or yellow chlorotic spots. Infective stages are juveniles and adult females. No data about associations with insects and fungi. Distributed in temperate and tropical regions.

Type species:

Zeatylenchus pittosporum Zhao, Davies, Alexander & Riley, 2013

Other species:

Zeatylenchus drepanocercus (Goodey, 1953) comb. n.

= *Ditylenchus drepanocercus* Goodey, 1953

Differential diagnosis. The genus *Zeatylenchus* is similar to the genera *Ditylenchus* and *Litylenchus* Zhao *et al.,* 2011.

Zeatylenchus differs from *Ditylenchus* in shorter body length for females (0.45-0.65 *vs* 0.9-2.2 mm), adult lip region (offset and low *vs* continuous and high), tail terminus (terminus arcuate, offset on dorsal side, spicate *vs* pointed to mucronate), post-vulval uterine sac length (1.0-1.5 times *vs* more than 3 times longer than vulval body diam.), plant symptoms induced (brown or yellow chlorotic spots *vs* swellings and deformations in aerial parts of plant).

Zeatylenchus differs from *Litylenchus* in tail terminus (terminus arcuate, offset on dorsal side, spicate *vs* bluntly rounded or pointed, sometimes with mucro) and bursa length (adanal *vs* peloderan).

In this study, we attempted to use the morphological and molecular data presently available for the superfamily Anguinoidea for proposal of a natural classification of this group. Considerable work still remains to understand phylogenetic patterns across the Anguinoidea and propose natural division of *Ditylenchus*-like nematodes in known and new genera.

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С.А. Субботин и А.Ю. Рысс. Ревизия рода *Ditylenchus* Filipjev, 1936: *Ditylenchoides* gen. n. и *Paraditylenchus* gen. n. (Nematoda: Anguinoidea).

Резюме. На основе результатов филогенетического анализа последовательностей генов рРНК и морфологических данных некоторых представителей надсемейства Anguinoidea предложено узкое определение рода *Ditylenchus* Filipjev, 1936. Предложено два новых рода, *Ditylenchoides* gen. n. с типовым видом *Ditylenchoides destructor* (Thorne, 1945) gen. n., comb. n. и еще четырнадцати видами и *Paraditylenchus* gen. n. с типовым видом *Paraditylenchus gallaeformans* (Oliveira *et al.,* 2013) gen. n., comb. n. Взрослые особи рода *Ditylenchoides* gen. n. отличается от особей *Ditylenchus* длиной тела, количеством инцизур в боковом поле, формой кончика хвоста и и симптомами, индуцируемыми на растениях. *Paraditylenchus* gen. n. отличается от *Ditylenchus* длиной тела, длинами задней матки и бурсы. *Ditylenchus drepanocercus* Goodey, 1953 переведен в род *Zeatylenchus* Zhao *et al.* 2013 как *Zeatylenchus drepanocercus* (Goodey, 1953) comb. n. Предложены также новые диагнозы для родов *Ditylenchus* и *Zeatylenchus*. Филогенетические результаты указывают на независимое происхождение способности индуцировать образование галлов и искривлений органов растений у представителей надсемейства Anguinoidea.
