

The Who, What and Where of Longidoridae and Trichodoridae

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WHO: LONGIDORIDAE AND TRICHODORIDAE

Longidoridae and Trichodoridae represent the only families of nematodes within the Class Enoplea proven to be plant-parasitic. The Longidoridae are classified within the subclass Dorylaimia (order Dorylaimida, superfamily Dorylaimoidea), while the Trichodoridae belong to the subclass Enoplia (order Triplonchida, superfamily Diphtherophoroidea).

Longidoridae: The family Longidoridae includes some 480 species of the subfamily Longidorinae with six genera: *Longidorus* (144 spp.), *Longidoroides* (13 spp.) and *Paralongidorus* (72 spp.) in the tribe Longidorini, and *Australodorus* (1 sp.), *Paraxiphidorus* (3 spp.) and *Xiphidorus* (8 spp.) in the tribe Xiphidorini and the subfamily Xiphineminae with one genus *Xiphinema* (some 240 spp.). At present, there is no consensus about the status of the genus *Longidoroides* Khan, Chawla and Saha, 1978 (see Decraemer and Coomans, 2007). *Longidorus*, *Paralongidorus* and *Xiphinema* are virus vectors. A wealth of information on *Longidorus*, *Paralongidorus* and *Xiphinema* can be found in papers on polytomous keys and subsequent supplements: *Xiphinema* (Loof and Luc, 1990; Loof and Luc, 1993; Loof et al., 1996), *Longidorus* (Chen et al., 1997; Loof and Chen, 1999) and *Paralongidorus* (Escuer and Arias, 1997) as well as in Coomans et al. (2001), a monography on the genus *Xiphinema* dealing with character analysis, phylogeny and biogeography.

The main diagnostic features of Longidoridae at the genus level are the structure of the odontostyle and odontophore, the structure and position of the guide ring, the shape of the amphidial fovea, shape and size of amphid opening and the position and size of the pharyngeal gland nuclei. Additional features at species level next to morphometric data are the shape and size of the amphidial fovea and opening, the development and structure of the female reproductive system (didelphic, monodelphic, pseudomonodelphic) with uterine differentiation and inclusions in *Xiphinema* and genera of the Xiphidorini, the tail shape in all developmental stages and presence or absence of males. Phylogenetic analyses of the Longidoridae based on sequence data and morphological data were carried out by He et al. (2003). Olivera and Neilson (2004) have a comprehensive review article showing the systematics, virus vector-

ing species and morphological differences among the Longidorid genera, and Decraemer and Coomans (2007) discussed relationships within the family Longidoridae.

Trichodoridae: The Trichodoridae include 100 species and five genera: *Trichodorus* Cobb, 1913, *Paratrachodorus* Siddiqi, 1974, *Monotrachodorus* Andrassy, 1976, *Allotrachodorus* Rodriguez-M, Sher and Siddiqi, 1978 and *Ecuadorus* Siddiqi, 2002. The two largest genera *Trichodorus* (54 spp.) and *Paratrachodorus* (34 spp.) are didelphic in females and occur worldwide. The three remaining genera, *Monotrachodorus* (4 spp., one subspecies), *Allotrachodorus* (6 spp.) and *Ecuadorus* (2 spp.), have fewer species, and females are monodelphic-prodelphic; so far, these three genera have only been recorded from Central America and the northern part of South America.

The main diagnostic characters to differentiate the genera of the Trichodoridae are: in females, (i) the reproductive system (didelphic or monodelphic); (ii) length of vagina, (iii) development of vaginal sclerotized pieces and (iv) presence of advulvar lateral body pores; and in males, (i) presence or absence of caudal alae, (ii) degree of development of copulatory muscles and related habitus and (iii) development of capsule of spicule suspensor muscles (Decraemer and Geraert, 2006). Additional features at species level, apart from morphometric data, are: in females, (i) the vaginal sclerotized pieces (size, shape, orientation, distance), (ii) presence/absence and location of sperm cells; in males and females, structure of sperm cell and nucleus, and in males, (i) the spicules (shape, ornamentation), (ii) number and arrangement of ventromedian cervical papillae and (iii) ventromedian preloacal supplements. Decraemer (1995) gives a comprehensive review of morphological and systematic information on this group.

WHAT: VIRUS VECTORS

The Longidoridae and Trichodoridae are polyphagous root-ectoparasites and are the only plant-parasitic Nematoda that transmit plant viruses. Their associated viruses belong to different virus taxa. Longidorids vector nepoviruses; whereas trichodorids vector Tobraviruses (Taylor and Brown, 1997).

Longidoridae: Of the 38 known nepoviruses, 13 have been proven to be naturally transmitted by Longidoridae: seven by *Longidorus* species, one by *Paralongidorus* and nine by *Xiphinema* species. Thus, only 5% of the known species of Longidoridae have been shown to transmit nepoviruses. The North American *Xiphinema* species, and more specifically the *X. americanum* species group, seems to present the main source of virus vec-

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toring, i.e., three vector species of the *X. non-americanum*-group (*X. index*, *X. diversicaudatum*, *X. italiae*) vs. six putative species of the *X. americanum* group (*X. americanum* s.str., *X. californicum*, *X. bricolense*, *X. intermedium*, *X. revesi*, *X. tarjanense*). In North America, the four nepoviruses cherry rasp leaf, peach rosette mosaic, tobacco ringspot and tomato ringspot are transmitted by members of the *Xiphinema americanum* group of species. These viruses cause substantial damage to a wide range of fruit and vegetable crops (Taylor and Brown, 1997).

Trichodoridae: All tobnaviruses are transmitted by trichodorid vector species. Only the didelphic trichodorid genera possess virus vector species. Out of 54 *Trichodorus* and 34 *Paratrichodorus* species, 7% (four: *T. primitivus*, *T. similis*, *T. cylindricus* and *T. viruliferus*) and 26% (nine: *P. anemones*, *P. divergens*, *P. hispanus*, *P. nanus*, *P. pachydermus*, *P. teres*, *P. tunisiensis*, *P. allius*, *P. minor*, *P. porosus*) are vectors of tobnaviruses, respectively. For Europe, however, the percentages of virus vectors vs. non-vectors are much greater; 67% for *Paratrichodorus* and 27% for *Trichodorus*. Further, in nearly all European countries, vector species and virus are present (Ploeg and Decraemer, 1996). This supports the hypothesis that *Trichodorus* vector/virus association probably evolved in Europe. The presence of these vector species in North America is very restricted and apparently the result of introduction with imported plant material. Similar remarks can be made for *P. pachydermus*, *P. anemones*, *P. teres*, *P. divergens*, *P. hispanus*, *P. nanus* and *P. tunisiensis*, all species whose main occurrence is restricted to Europe and Mediterranean countries. For *P. porosus*, the vector aspect is based on laboratory experiments. The vector species *P. allius* and *P. minor* apparently developed a virus/vector relationship outside Europe and, with *P. minor*, possess a unique association with pepper ringspot virus (PPV) restricted to Brazil, South America.

WHERE: DISTRIBUTION

Longidoridae: Among the genera of Longidoridae, some are considered cosmopolitan, while others have very limited distribution (Coomans 1995). *Longidorus* and *Xiphinema* are taxa with examples found in all inhabited continents. *Australodorus*, *Paraxiphidorus* and *Xiphidorus* are quite limited in distribution, i.e., only South America.

The genus *Longidorus* has been found most frequently in Europe (73 spp.), followed by India (25 spp.), North America (23 spp.), South Africa (18 spp.) and China (13 spp.). In South America, two species have been reported, and in Australia and New Zealand four species. Three North American species have been shown to be serious pests on certain crops in sandy soils, *L. breviannulatus* in the mid-west on corn (*Zea mays*), *L. africanus* on several crops in southern California and *L. americanum* on loblolly pine in Georgia.

The genus *Paralongidorus* (incl. *Longidoroides*) has been reported mainly from India (34 spp.) and South Africa (29 spp.). In Europe, nine species have been recorded, and three from Australia. In the Americas, only two species have been reported, both in North America. Ninety percent of the *Paralongidorus* species were recorded only once or, if several times, then from within a restricted area, 5% from two continents, and no cosmopolitan species has been found.

The genus *Longidoroides* has been reported mainly in India and South Africa. The range of the genera *Australodorus*, *Paraxiphidorus* and *Xiphidorus* is limited to South America, with *Xiphidorus* being the most widely distributed (Argentina, Brazil, Uruguay and Venezuela).

The genus *Xiphinema* is the most diversified genus of the family Longidoridae with both species groups, the *X. americanum*-group and the *non-americanum*-group, occurring worldwide. Lamberti et al. (2000) gave an overview of the geographic distribution of the *X. americanum*-group. A nearly equal number of species has been reported from North America (21) and Asia (22), followed by 17 for Europe, 11 for South America, 10 for Africa and three for Australia. However, 50% or more of the species are considered rare species or of questionable identification. The largest number of common species is found in North America (10) and Europe (8). The biogeographic distribution of the *Xiphinema non-americanum* species group was studied in detail in Coomans et al. (2001). The authors divided the species into four groups: (1) species recorded only once or, when recorded more, only from a restricted area, (2) species recorded in different areas but close to each other or belonging to the same climatic unit, (3) species found in two continents and (4) 'cosmopolitan' species from at least three different continents. *Xiphinema* species appeared far more numerous in tropical areas compared to temperate ones. Sixty-five percent of the *X. non-americanum* group belong to group 1, with the highest diversity recorded from Southeast Africa (53 spp.) and Europe (33 spp.). Only 16% of the species belong to group 2; 8% were recorded from two continents and 10% appear as putative cosmopolitan species. The high number of species recorded from Portugal (19 spp.) and South Africa (40 spp.) might be the result of evolutionary radiation as well as high taxonomic activity.

Trichodoridae: The genus *Trichodorus* is a cosmopolitan genus but predominant in the more temperate regions. *Trichodorus* is widespread in Europe and North America, respectively, with 17 and 20 species recorded. In South Africa, nine species have been recorded, all but one from natural vegetation and all being considered endemic for this region. A similarly high number of species has been recorded from China, but only two species are restricted to this vast country. Former data may be biased by differences in the extension and number of surveys, e.g., we have to take into account that

Europe, North America and South Africa are also the most extensively surveyed regions with more easily assessable published data and reports. Further, the records have to be interpreted with caution because of the results of anthropogenic impact. In Europe, 15 of the 17 species seems to be endemic, while for North America only seven species have been restricted to this continent; a large number of the American records are rare records of introduced European species, the most widely distributed one being *T. primitivus*. Currently, no *Trichodorus* species have been recorded from Australia despite national surveys from crop plants and native vegetation. Only one-fifth of the species appears to occur in former Gondwanaland countries. From this, it can be assumed that the genus probably originated in Laurasia, with the main center of speciation in Europe.

The genus *Paratrichodorus* is also a cosmopolitan genus but mainly present in tropical and subtropical regions. About 75% of *Paratrichodorus* species have been described from former Gondwanaland. This is nicely illustrated by the current distribution for example of *P. lobatus* and *P. porosus*. *Paratrichodorus minor* is the most widely distributed *Paratrichodorus* species, present in most of the surveyed countries in Africa and recorded in Australia, but also in South America, Central America, the West Indies and southern regions of North America.

So far, the monodelphic genera, *Monotrichodorus*, *Allotrichodorus* and recently *Ecuadorus*, have been described only from the Neotropical region, with *Monotrichodorus* being widely recorded to the north and north west of the Amazon Basin (except for *M. propiorifer* (= *M. m. monohystera*) from Para State, Brazil), *Allotrichodorus* only from the southeast of the Basin and restricted to Bahia State and *Ecuadorus* from Trinidad, Bahia State, Brazil, Martinique and Ecuador. Most of these species have been found associated with natural vegetation next to agricultural crops. Their association with native plants supports the theory that the monodelphic trichodorids are endemic to tropical South and Central America. *Ecuadorus*, only known by parthenogenetic females, occupies a somewhat intermediate position between monodelphic (*Allotrichodorus*) and didelphic (*Paratrichodorus*) genera in morphological features and distribution. Prior to the introduction of the genus *Ecuadorus* by Siddiqi (2002), the type species *E. westindicus* had been classified first within the genus *Paratrichodorus*, later within *Allotrichodorus* and was considered *Allotrichodorus westindicus a species incertae sedis* in Hunt (1993).

The discovery of three neotropical genera, *Monotrichodorus*, *Allotrichodorus* and *Ecuadorus*, has clearly demonstrated that parallel evolution in the character number of genital branches in the female reproductive system and corresponding presence/absence of bursa in males (few exceptions) has occurred in the vicariating didelphic and monodelphic genera. Different from

the Longidoridae, no separate tribes have been assigned.

The existence of a transformation series from *P. minor*, *P. caribbensis* to *Ecuadorus westindicus* supports the hypothesis that the monodelphic genera have developed from an ancestral stock just before or after the splitting off of current South America in the Cretaceous period.

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