

Phylogeny of the Longidoridae

August Coomans¹

Zoology Institute, University of Gent, K.L. Ledeganckstraat 35, B-9000 Gent, Belgium.

Accepted for publication 20 December 1995

Summary. The longidorid ancestor is reconstructed on the basis of primitive characters encountered in extant species of the family. The present distribution and morphology of the various genera are related to the geological history of the continents to trace the area of origin as well as the evolution within the family. The cladogram of the Longidoridae is amended and two possible classifications are proposed on the basis of the cladogram.

Key words: Distribution, evolution, geological history, Gondwanaland, *Longidoroides*, *Longidorus*, Oceania, *Paralongidorus*, *Paraxiphidorus*, *Xiphidorus*, *Xiphinema*.

Introduction: the longidorid ancestor

The Longidoridae are believed to have originated from an ancestor close to Pungentinae (Coomans, 1985). Such an ancestor was characterized by: a long and slender body; an offset amalgamated lip region with 6+10 small papillae; stirrup-shaped amphids with a wide slit-like aperture just behind the lip region; an elongate cheilostome and 'double' guiding ring; a very long, needle-like odontostyle possessing a 'forked' base and strong odontophore forming a sclerotized cone with three inner cores opening posteriorly before the swollen base; eight well developed stylet protractors necessary for operating the protrusion of the extremely long spear; four pairs of poorly developed stylet retractors and three pharyngeal retractors diverging to four bands prior to their attachment to the body wall; anterior part of pharynx slender and flexible with circular lumen and weak radial musculature; basal part of pharynx expanded with triradial lumen and strong radial musculature, with only three glands, one large dorsal and two smaller ventrosublateral ones, DN larger than SN and at a distance behind DO, SN about halfway along the expanded part and much anterior to SO; gonochoristic; female reproductive system didelphic-amphidelphic, each branch composed of a reflexed ovary, bipartite oviduct, sphincter, unipartite uterus of about the same length as the oviduct; male reproductive system typically dorylaimoid; relatively few, spaced ventromedian supplements; rectal glands

reduced; tails of both sexes similar and elongate; ectoparasitic on root tips.

The characterization of the longidorid ancestor is based on the following considerations:

1. *Body length and shape:* the vast majority of present day longidorids have a long and slender body, only a few species are less than 2 mm in length.

2. *Lip region:* all longidorids have amalgamated lips; an offset lip region is more primitive than a contiguous one.

3. *Anterior sensilla:* always 6+10, either slightly protruding as papillae (primitive) or flush with the lip contour, showing pores in SEM.

4. *Amphids:* as in other dorylaims, the stirrup-shaped fovea with wide slit-like aperture just behind the lip region is the primitive type.

5. *Anterior feeding apparatus or stomodeum:* the stoma and the pharynx (oesophagus) constitute the most typical feature of the family. The **cheilostome** is long to extremely long, resulting in a backward position of the guiding ring. In other dorylaims with posteriorly located guide ring, the guiding sheath is folded anteriorly from the fixed guide ring, giving rise to a so called **double guiding ring** (Goodey, 1961; Coomans, 1964). Hence, this condition is regarded as primitive for longidorids since all species have a very long stylet. The latter is composed of a needle-like **odontostyle** with either a 'furcate' ('forked') or a non-'furcate' base, and an odontophore with or without flanges. The so called furcate or forked base of the odontostyle is due to an optical section through a collar-like extension (Roggen *et al.*, 1967; Swart & Heyns, 1987b; Cho & Robbins, 1990), it is typical for dorylaims and therefore represents the primitive condition. The **odontophore** is variously developed,

¹This paper is an expanded version of an invitational Plenary talk presented at the First English Language International Symposium of the Russian Society of Nematology held in St. Petersburg, Russia, 23rd to 30th September 1995.

but always shorter than the odontostyle. It is sclerotized and consists of a closed anterior part with first a ventral core and two subdorsal cores further back. The cores open in the posterior region of the odontophore, resulting in three (1 dorsal, 2 ventro-sublateral) cuticular radii which may form more or less developed terminal extensions at the base of the odontophore, the flanges. The flanged condition is found in *Xiphinema*, *Xiphidorus*, *Paraxiphidorus*, some *Paralongidorus* and some *Longidorus*. Because it is widespread in the family, but also for functional reasons, it is considered to represent a plesiomorphy. Indeed, the longer the cheilostome, the more resistance is met with upon protraction of the stylet and the stronger the odontophore base has to be (Coomans, 1985; Cho & Robbins, 1990). This is best achieved with flanges because they provide a larger surface area for the insertion of the radial muscles; the latter transmit the traction exerted by the stylet protractor muscles to the cuticular odontophore (Robertson & Taylor, 1975).

In dorylaims there are typically eight **stylet protractors** (Coomans, 1964) and this number is also found in longidorids, but at the base of the odontophore, where these muscles are attached to the basal lamina of the pharynx, the number varies from six to eight (Wright, 1965; Wright *et al.*, 1983; Jacobs *et al.*, 1987). The **stylet retractors** are reduced in comparison with those of other dorylaims. This is correlated with the extreme elongation of the anterior feeding apparatus and especially with the structure of the odontophore (see above), onto which these retractors normally attach about halfway along its length. The full complement of four pairs of (rather poorly developed) stylet retractors has so far only been found in one *Xiphinema* species (Jacobs *et al.*, 1987). Some *Paralongidorus* and *Longidorus* species have four single stylet retractors, while other species of both these genera seem to lack stylet retractors completely (Taylor & Robertson, 1971; Jacobs *et al.*, 1987).

Whether stylet retractors are present or absent, stylet retraction is mainly or exclusively carried out by the **pharyngeal retractors**. These muscles are present in other dorylaims as well (Lippens *et al.*, 1974; Lippens, 1975), but are better developed in longidorids due to the elongation and special structure of the anterior feeding apparatus. The pharyngeal retractors attach to the basal lamina surrounding the slender part of the pharynx, either over a long distance (longitudinal attachment) or over a short one (transverse attachment) (Robertson & Taylor, 1975), depending on the structure of the slender part of the pharynx (see below). The longitudinal attachment is typical for Dorylaimida, hence considered as plesiomorphic. The muscles form

three bands, splitting up to four (rarely five) when they diverge to the body wall where they attach opposite the anterior end of the pharyngeal bulb. The longitudinal attachment has been found in *Xiphinema*, *Paralongidorus* and *Longidorus*, the transverse attachment has only been found in a few *Longidorus* species (Robertson & Taylor, 1975; Jacobs *et al.*, 1987).

The **slender part of the pharynx** is a flexible tube with circular lumen, forming a posterior loop when the stylet is in the retracted position. The cuticular lining of the lumen is composed of rigid rings alternating with weaker ones (Swart & Heyns, 1987b). Radial muscles are present throughout the length of the slender pharynx in species with longitudinal attachment of the pharyngeal retractors, while they are restricted to two short areas, one anterior at the base of the odontophore and one posteriorly, in species with transverse attachment of the pharyngeal retractors (Robertson & Taylor, 1975; Jacobs *et al.*, 1987).

The **expanded part of the pharynx** or pharyngeal bulb has, except in its anteriormost part, a triradiate lumen. The cuticular lining forms six longitudinal rows of triangular platelets (one pair per sector). Prominent radial muscles attach to these platelets; their contraction opens the lumen. Peripheral muscles on the outside of the bulb act as springs and are stretched by contraction of the radial muscles, they mediate the closing of the lumen (Robertson & Taylor, 1975; Seymour, 1984; Robertson *et al.*, 1987). The general structure of the bulb is as in other dorylaims, but little detailed information is available on the peripheral muscles in other families. The bulb contains only three glands due to the disappearance of the anterior pair of ventrosublateral glands. The reduction of the anterior pair has already started in the Pungentinae (see Coomans, 1985).

Although there are other dorylaims with a needle-like stylet (e.g. *Longidorella*, *Xiphinemella*, *Californidorus*) or a slender anterior pharynx with circular lumen, the combination as found in longidorids is unique and considered to represent an autapomorphy of the family. This is also true for the pharyngeal bulb with elaborate dorsal gland and only the second pair of ventrosublateral glands developed.

6. The *reproductive systems* of primitive longidorids probably were typically dorylaimoid and simple in structure. This situation can be found in all genera. Males have rather few supplements and reduced rectal glands, but due to lack of information on the closest outgroups it is not possible to conclude whether this reduction is an autapomorphy or not.

7. As explained elsewhere, long *tails* in both sexes are generally considered as the primitive condition in dorylaims.

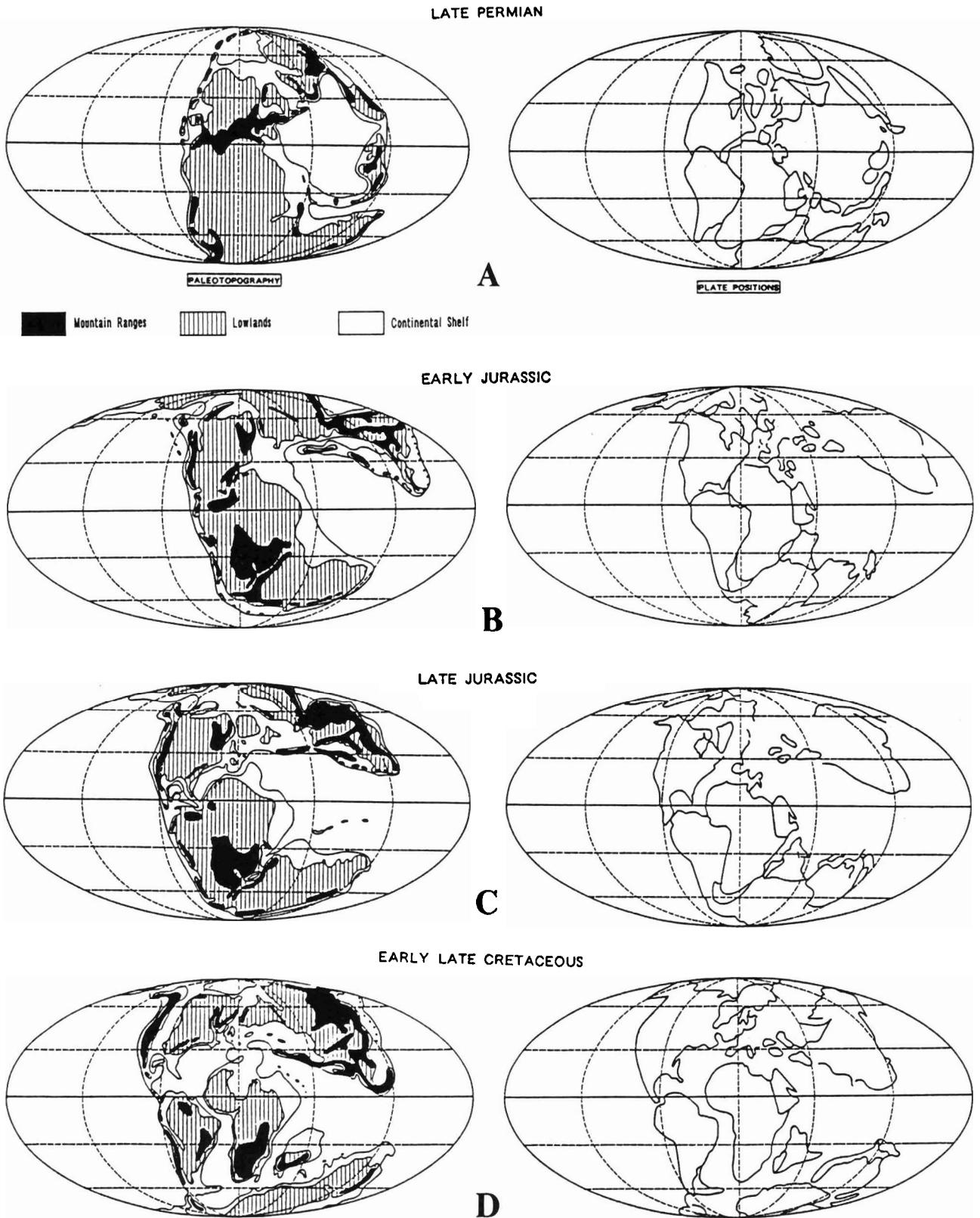


Fig. 1. Generalized paleotopography and continental positions. A: The Late Permian, about 255 million years BP.; B: The Early Jurassic, about 195 my. BP.; C: The Late Jurassic, about 152 my. BP.; D: The Early Late Cretaceous, about 94 my. (redrawn from Behrensmeier, A.K. *et al.*, 1992. *Terrestrial Ecosystems Through Time*. The University of Chicago Press, Chicago and London; after C.R. Scotese and the PaleoMap Project, University of Texas, Arlington).

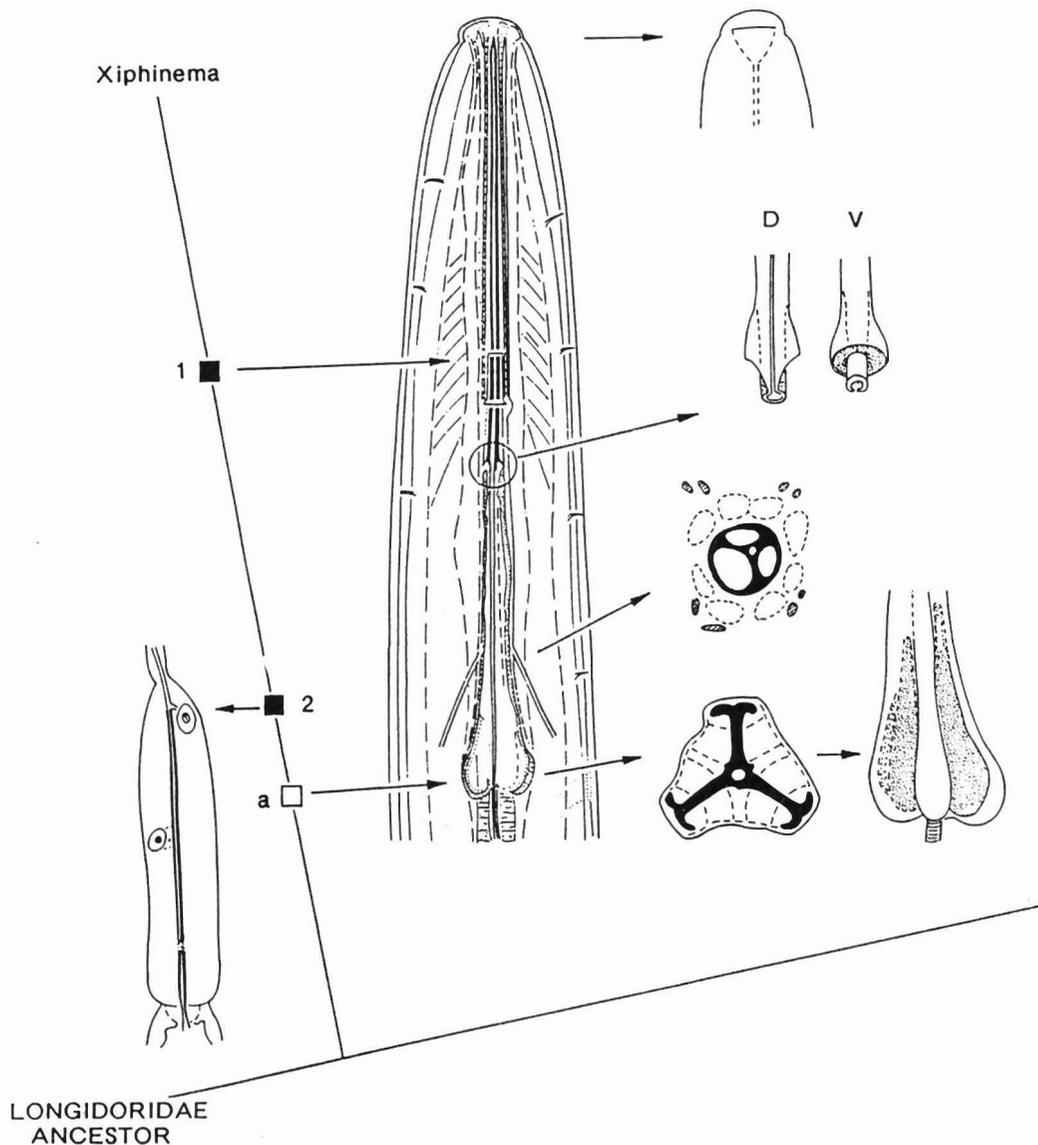


Fig. 2. The genus *Xiphinema* as first off-shoot of the cladogram. 1: Cheilostome retractor muscles (= dilatores buccae); 2: DN opposite DO; a: Strong stylet with anchor-shaped flanges. Black squares represent apomorphies, white squares are possible apomorphies omitted in the full cladogram.

Evolution within the Longidoridae

The origin of the Longidoridae and especially of *Xiphinema* is probably correlated with the *Glossop-teris*-flora of Gondwanaland during the Permian period (280-225 my BP). These seed ferns became the dominant land plants after a huge glaciation in southern Gondwanaland which even affected present day India.

In the late Permian (Fig. 1A) Gondwanaland was separated from present day North America by a wide mountain range. The longidorid ancestor probably originated in the northern part of Gondwanaland, corresponding with the present West-, North- and Central Africa and the northern half of South Amer-

ica. This part of Gondwanaland then occupied a tropical position and has been a primary area of evolution for many plant and animal taxa (Raven & Axelrod, 1974).

The genus *Xiphinema* soon expanded its range to the more southern parts of Gondwanaland, including present southern South America, southern Africa, India, Madagascar, Antarctica and Oceania. This southern expansion was probably correlated with the northward shift of the land masses. However, during the early Jurassic (Fig. 1B) a large part of central and southern Africa had become a mountainous area, leaving only a narrow rim in the South and the East of present day Africa, as well as Madagascar and India as lowlands. Another mountain range separated

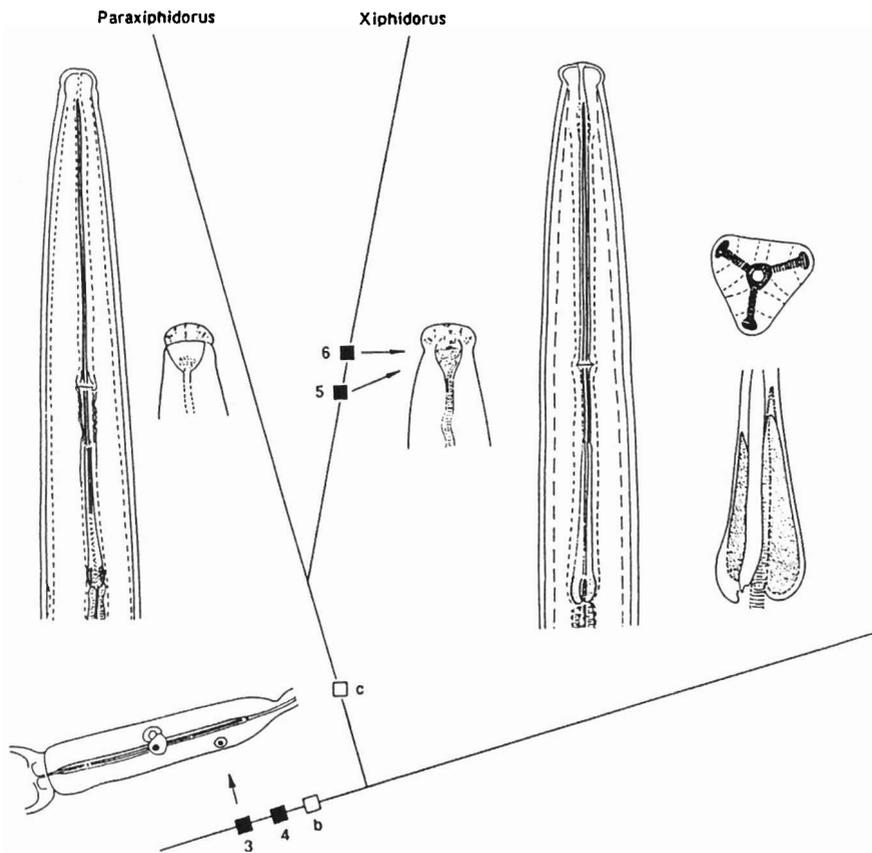


Fig. 3. The sister branch defined by two apomorphies: 3 - DN smaller than SN; 4 - single guide ring; and possibly also by a weaker stylet surrounded by a more flexible cheilostome wall (b); and the second off-shoot (*Paraxiphidorus* and *Xiphidorus*) possibly defined by a short guiding sheath (c). *Xiphidorus* characterized by 5 - non-stirrup-shaped amphids and 6 - pore-like amphid openings.

Antarctica and Oceania from the remainder of Gondwanaland, except for a northern connection via present day India. This, together with the southern position, may have hampered a further spread into this area, explaining the paucity of longidorids in present Oceania.

At the other side, the mountain range between North America and Gondwanaland partly broke up, leading to lowland connections along the western and eastern ends of the range. These connections, however, disappeared in the late Jurassic (Fig. 1C).

During the Jurassic, other longidorids may have appeared in association with the more diverse flora, already including angiosperms (cf. Cornet, 1993). First came *Paralongidorus*, in the eastern and northern parts of Gondwanaland. Its present distribution is still there as well as in Europe which was invaded much later. '*Longidoroides*' must have had its origin in the eastern part of Gondwanaland, when at that time Africa and India were still connected. The radiation of '*Longidoroides*' was limited and its later dispersal confined to southern and Southwest Africa (1 species in Namibia), with the possibility for some

dispersal to South America through the then existing connection between Southwest Africa and South America. Although neither *Paralongidorus* nor '*Longidoroides*' have thus far been found in Madagascar, we anticipate their presence there. Finally, *Longidorus* also originated before the split up of Gondwanaland in the eastern part of it (e.g. see the distribution of *L. pisi*). It became the most successful genus of the three. It spread in all directions except towards South America and radiated most in Laurasia, especially in Europe. The present distribution of the *Paralongidorus* - '*Longidoroides*' - *Longidorus* complex indicates that either it originated shortly before or just after the break up of Gondwanaland. In the first case it did not disperse in a western direction prior to the break up. The few specimens belonging to the complex, reported so far from Central and South America probably represent introductions. This may also be true for the occasional occurrence of a *Paralongidorus* in the USA.

Since *Paraxiphidorus* and *Xiphidorus* are confined to South America it can be safely assumed that they originated in that continent after the split up of

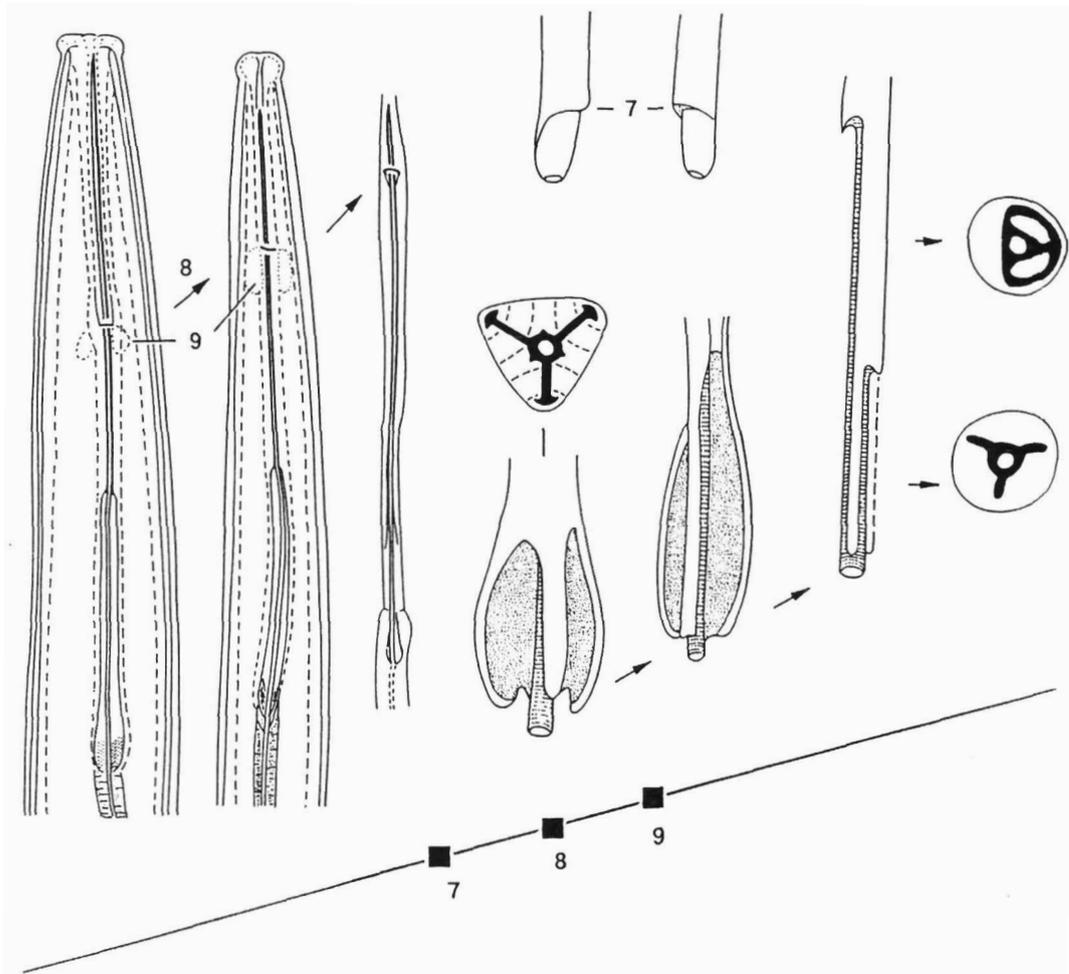


Fig. 4. The sister branch defined by three apomorphies: 7 - non-furcate base of the odontostyle; 8 - guide ring around first or second third of odontostyle; 9 - guiding system with compensation sacs. In this branch there is a reduction of the flanges.

Gondwanaland during the Cretaceous period about 100 million years ago (Fig. 1D).

Cladogram of the Longidoridae

In 1985 a cladogram for the family was proposed on the basis of available information (Coomans, 1985). Subsequently, new data from TEM and SEM studies has been accumulated and a new genus has been described. In general the 1985 cladogram is still valid and therefore reference can be made to the above cited paper for the basic principles. Here I discuss the main points and make the necessary emendations.

Xiphinema is the only genus with a 'double' guiding ring when the stylet is fully retracted (a plesiomorphic character, see above); it is clearly separated from other genera by two autapomorphies (Fig. 2): the presence of cheilostomal retractor muscles (*dilatores buccae*) and the position of DN

(opposite DO). Although cheilostomal retractor muscles are probably a further elaboration of *dilatores buccae* muscles in more primitive dorylaims, such a development is unique for *Xiphinema*. Species of *Xiphinema* have well developed flanges at the base of the odontophore, but flanged odontophores occasionally occur in other genera too, i.e. in species with a posteriorly located guide ring. Tail shape varies from filiform to short rounded, it may be similar in both sexes or it may be sexually dimorphic. The genus *Xiphinema* has a cosmopolitan distribution.

All other longidorid genera are derived from an ancestor with the following two apomorphies: a posterior but single guide ring when the stylet is fully retracted (a secondary condition in Longidoridae) and DN smaller or at most equal in size to SN. Cheilostome retractor muscles are absent. Tails of both sexes are similar and short.

From this ancestor an evolutionary line emerged which retained all the primitive characters present in

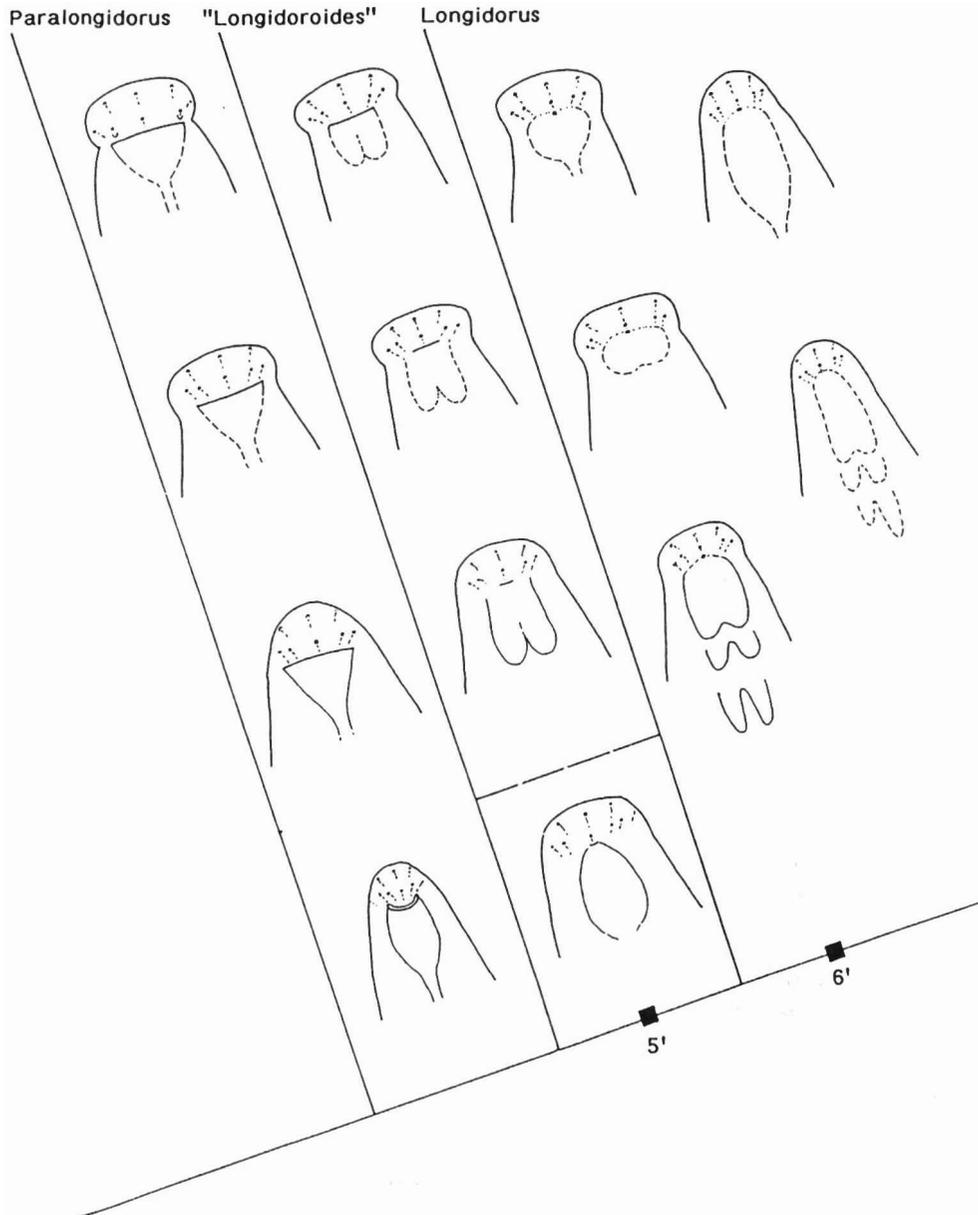


Fig. 5. The *Paralongidorus* - 'Longidoroides' - *Longidorus* complex comprises primitive forms with offset lip region and stirrup-shaped amphids with wide slit-like openings, intermediate species and the most derived ones with contiguous lip region and lobed pouch-like amphids with pore-like openings. The non-stirrup-shaped amphids and the pore-like openings are clear apomorphies (5' and 6').

Paraxiphidorus, but developed differently shaped amphids with minute openings as in *Xiphidorus* (Fig. 3). Both genera are restricted to South America.

The sister line is characterized by at least three synapomorphies: a non-furcate base of the odontostyle (remnants of the collar can still be observed in some species of *Paralongidorus* and *Longidorus*), a shortening of the cheilostome and a stylet guiding system with compensation sacs (Fig. 4). Males have a higher number of ventromedian supplements (up to 20) so that the posterior-most ones occur within the spicula range and even may be arranged in a double row. Ventromedian supplements within the

spicula range are exceptional in *Xiphinema* (e.g. several species of the *X. americanum* group, *X. pachydermum*, *X. macrostylum*, 1 male of *X. ensiculiferum*), but in species in this sister line it is common. This branch is represented by the *Paralongidorus* - 'Longidoroides' - *Longidorus* complex. The most primitive condition is found in *Paralongidorus*, a genus mainly occurring in Gondwanaland countries, except for South America; it is also absent in North America. All species of the complex with stirrup-shaped amphids having wide apertures are considered to belong to this genus. However, this is a sympleiomorphy rather than a synapomorphy, hence there

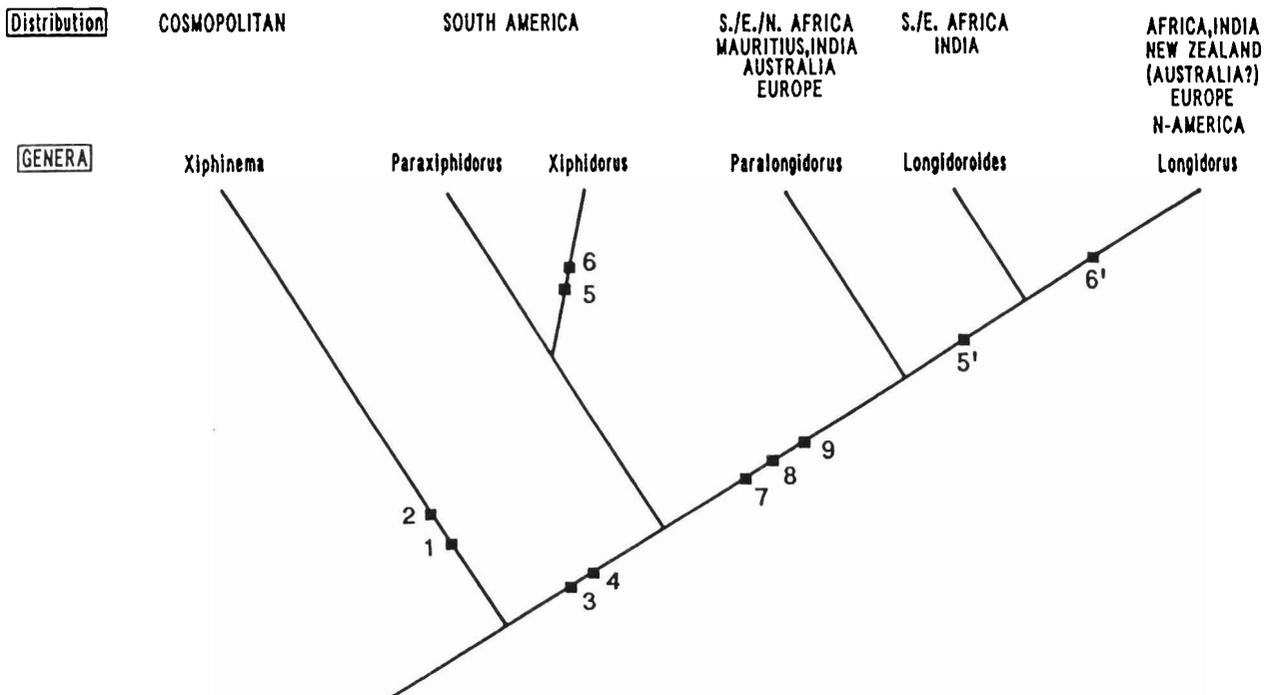


Fig. 6. Amended cladogram of the family Longidoridae based on the following apomorphies: 1 - cheilostome retractor muscles (*dilatatores buccae*); 2 - DN opposite DO; 3 - DN < or at most = SN; 4 - single guide ring; 5 - non-stirrup-shaped amphids; 6 - pore-like amphid openings; 7 - non-furcate base of odontostyle; 8 - guide ring around first or second third of odontostyle; 9 - guiding system with compensation sacs; 5-5' and 6-6': parallel evolution.

is no evidence for monophyly. The other forms of the complex are characterized by one or two apomorphies: either they possess a pouch-like amphidial fovea with slit-like apertures ('*Longidoroides*') or a pouch-like fovea with pore-like apertures (*Longidorus*) (Fig. 5).

Recently, *Longidoroides* was synonymized with *Paralongidorus* (Siddiqi *et al.*, 1993). This action was based on a new interpretation of the amphid structure of *P. sali*, the type species of the genus *Paralongidorus*. A study of type material of this species has not convinced me that the interpretation of the fovea presented by Siddiqi *et al.* is correct. In the specimens that I have seen the fovea was rather long, with convex sides, but without the posterior extensions illustrated in Fig. 3, O in Siddiqi *et al.* Whatever the status of *Longidoroides* (genus, subgenus or simply a species-group within *Paralongidorus*) it represents an intermediate condition between *Paralongidorus* species with typical amphids and *Longidorus* species with pouch-like amphids and pore-like openings. However, the exact shape of the fovea is often difficult to observe and a small slit is not much different from a pore. A revision of the complex based on a reappraisal of commonly used characters and the addition of new ones (such as the small flaps behind the

cephalic sensilla - see Swart & Heyns, 1987a) may either better define genera or show that the complex is just one variable genus.

Out of 46 or 48 species of *Paralongidorus*, 20 were described from India, 14 or 16 from southern Africa (including 1 from Mauritius and 1 from Namibia), 5 from Europe, 1 from Niger, 1(?) from Senegal, 1 from Algeria, 1 from Pakistan and 3 from Australia.

Out of 14 or 17 '*Longidoroides*' species 6 have been described from India, 7 or 10 (problematic species: *hooperi*, *clavicaudatus* - probably belonging to *Paralongidorus* - and *strelitziae* - probably a *Longidorus*) from South Africa and 1 from Malawi. The recently described *P. duncani* from Senegal fits in this group.

Out of almost 100 *Longidorus* species, 36 have been described from Europe and 37 occur on this continent; 16 or 17 from southern Africa (including 1 from Mauritius) and 18 or 19 occur in the area; 14 from India, 9 from North America and a 10th species (*L. africanus*) was probably imported; 3 from the Near-East and 3 more occur in the region; 1 from Central Africa, 1 from New Zealand and 1 from the West Indies.

On the basis of the cladogram (Fig. 6), the following classifications can be proposed:

Family Longidoridae	
A	B
Subfam. Xiphinematinae	Subfam. Xiphinematinae
Genus <i>Xiphinema</i>	Genus <i>Xiphinema</i>
Subfam. Longidorinae	Subfam. Xiphidorinae
Tribe Xiphidorini	
Genera <i>Paraxiphidorus</i> <i>Xiphidorus</i>	Genera <i>Paraxiphidorus</i> <i>Xiphidorus</i>
Tribe Longidorini	Subfam. Longidorinae
Genera <i>Paralongidorus</i> ' <i>Longidoroides</i> ' <i>Longidorus</i>	Genera <i>Paralongidorus</i> ' <i>Longidoroides</i> ' <i>Longidorus</i>

Classification A reflects better the phylogenetic relationships, classification B relies on Nelson's sequencing convention (Nelson, 1974). In classification A Xiphidorini vicariate with Longidorini whereas in B Xiphidorinae vicariate with Longidorinae.

REFERENCES

- Cho, M.R. & Robbins, R.T. 1990. Scanning electron microscopy of *Xiphinema*, *Longidorus* and *Californidorus* stylet morphology. *Journal of Nematology* 22: 162-169.
- Coomans, A. 1964. Stoma structure in members of the Dorylaimina. *Nematologica* 9 (1963): 587-601.
- Coomans, A. 1985. A phylogenetic approach to the classification of the Longidoridae (Nematoda: Dorylaimida). *Agriculture, Ecosystems and Environment* 12: 335-354.
- Cornet, B. 1993. Dictyo-like leaf and flowers from the late triassic tropical Newark supergroup rift zone, U.S.A. *Modern Geology* 19: 81-99.
- Goodey, J.B. 1961. The nature of the spear guiding apparatus in Dorylaiminae. *Journal of Helminthology*, R.T. Leiper Supplement: 101-106.
- Jacobs, P.J.E., Heyns, J., Coomans, A. & Loots, G.C. 1987. Studies on the ultrastructure of the pharyngeal region in Longidoridae (Nematoda). *Nematologica* 33: 199-212.
- Lippens, P.L. 1975. Ultrastructure of Dorylaimidae. In: *Nematode Vectors of Plant Viruses*. (F. Lamberti, C.E. Taylor and J.W. Seinhorst, Eds.) pp. 159-176. London, New York, Plenum Press.
- Lippens, P.L., Coomans, A., De Grisse, A.T. & Lagasse, A. 1974. Ultrastructure of the anterior body region in *Aporcelaimellus obtusicaudatus* and *A. obscurus*. *Nematologica* 20: 242-256.
- Nelson, G.J. 1974. Classification as an expression of phylogenetic relationships. *Systematic Zoology* 22: 344-359.
- Raven, P. & Axelrod, D.I. 1974. Angiosperm biogeography and past continental movements. *Annals Missouri Botanical Garden* 61: 539-673.
- Robertson, W.M. & Taylor, C.E. 1975. The structure and musculature of the feeding apparatus in *Longidorus* and *Xiphinema*. In: *Nematode Vectors of Plant Viruses*. (F. Lamberti, C.E. Taylor and J.W. Seinhorst, Eds.) pp. 179-194. London, New York, Plenum Press.
- Robertson, W.M., Topham, P.B. & Smith, P. 1987. Observations on the action of the oesophageal pump in *Longidorus* (Nematoda). *Nematologica* 33: 43-54.
- Roggen, D.R., Raski, D.J. & Jones, N.O. 1967. Further electron microscopic observations of *Xiphinema index*. *Nematologica* 13: 1-16.
- Seymour, M.K. 1984. Action of the feeding pump in *Longidorus caespiticola* Hooper. *Nematologica* 29: 65-77.
- Siddiqi, M.R., Baujard, P. & Mounport, D. 1993. Descriptions of *Paratylenchus pernoxius* sp.n. and *Paralongidorus duncani* sp.n. from Senegal, and the synonymization of *Longidoroides* with *Paralongidorus*. *Afro-Asian Journal of Nematology* 3: 81-89.
- Swart, A. & Heyns, J. 1987a. Comparative morphology of the head regions of some longidorid nematodes from South Africa using the SEM. *Phytophylactica* 19: 99-101.
- Swart, A. & Heyns, J. 1987b. Morphological study of longidorid nematode stylets using the SEM. *Phytophylactica* 19: 103-106.
- Taylor, C.E. & Robertson, W.M. 1971. Ultrastructure of the guide ring and guiding sheath in *Xiphinema* and *Longidorus*. *Nematologica* 17: 303-307.
- Wright, K.A. 1965. The histology of the oesophageal region of *Xiphinema index* Thorne & Allen, 1950 as seen with the electron microscope. *Canadian Journal of Zoology* 43: 689-700.
- Wright, K.A., Carter, R.F. & Robertson, W.M. 1983. The musculature of the anterior feeding apparatus of *Xiphinema* species (Nematoda: Dorylaimoidea). *Nematologica* 29: 49-64.

Сoomans A. Филогения Longidoridae.

Резюме. На основании анализа примитивных признаков, выявляемых у ныне живущих видов, восстановлен облик предка лонгидорид. Морфология и современное зоогеографическое распространение видов лонгидорид поставлены в соответствие с геологической историей континентов, что позволило выявить центры их происхождения и пути эволюции в пределах семейства. Предложена кладограмма семейства Longidoridae, а на ее основе - две возможных классификационных схемы.