The Virus-Vector and Damage Potential, Morphometrics and Distribution of Paralongidorus maximus

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Abstract: Paralongidorus maximus was tested as a vector for 20 viruses. Nine were recovered directly from *P. maximus,* an indication that they had ingested the virus, but there was no correlation between the ingestion and transmission of these viruses. Raspberry ringspot (English and Scottish strains), arabis mosaic, and strawberry latent ringspot viruses were recovered from the roots of bait plants grown in pots together with virus infected plants and *P. maximus.* Under the experimental conditions, these four viruses may have been transmitted by *P. maximus.* Sixteen of these viruses were not transmitted by *P. maximus.* None were transmitted when *P. maximus* was extracted between the infector and bait plants. The authors conclude that *P. maximus* is not likely to be a vector, under field conditions, of any of the presently known nematode-transmitted viruses. A new site is reported for *P. maximus* in a forest nursery in Angus, Scotland where it was causing considerable damage to 3- and 4-year-old Scots pine (*Pinus sylvestris*). Morphometrically, this population (which was used in the virus tests) is very similar to populations from Germany and other parts of Britain. Geographical distribution of this species is restricted to western Europe, where it is widely distributed, and to only three sites in the British Isles. *Key Words: Xiphinema diversicaudatum, X. index, X. vuittenezi, Longidorus elongatus, L. macrosoma, Trichodorus* spp., root galls, host range, nematode.

Paralongidorus maximus (Bütschli) Siddiqi was first described as *Dorylaimus maximus* in 1874 by Bütschli (2) from a single female specimen found in garden soil in Kiel, Germany. It was transferred to the genus *Longidorus* (14) and subsequently to *Paralongidorus* by Siddiqi in 1964 (17) after the erection of that genus by Siddiqi et al. (18). Apart from its large size (averaging 10 mm), it can be distinguished from all other Longidorids by its prominent, rounded, offset lip region and large amphidial apertures which extend almost across the width of the head.

In Great Britain, *P. maximus* had been recorded only twice, from Suffolk and from Eastern Scotland (1, 12). However, a third site was discovered in 1974 in a forest nursery in Angus, Scotland where it occurred in moderately high numbers around the roots of 3- to 4-year old ,poorly growing Scots pine (*Pinus sylvestris* L.).

Interest in this species is several-fold: it, being visible to the naked eye, is the largest member of the family Longidoridae to be found in Europe (6, 16, 19, 21). It has a wide host range and a pathogenic association has been established for many plants (19, 20, 21). Taxonomically, it falls between two virus-vector genera (*Xiphinema* and *Longidorus*) but it has not previously been reported as a vector of plant viruses.

Weischer et al. (27, 28, 29) observed *P. maximus* associated with several unidentified grapevine viruses in Germany. Several attempts were made to transmit these viruses by *P. maximus,* but no indubitable transmissions could be obtained. They concluded that it was improbable that *P. maximus* was a vector for the grapevine-viruses they tested.

Our study was undertaken to determine the virus-vector potential of *P. maximus* and its distribution and pathogenic effect in the forest nursery in Scotland; and to compare morphometrically the Scottish and European populations. A report on the European distribution of this species is also given.

MATERIALS AND METHODS

Viruses and Nematodes: The 20 viruses used for the transmission experiments are set out in Table 1 with their abbreviations. Nematode species used were as follows: *Paralongidorus maximus*—from Scots pine in a forest nursery in Angus, Scotland; *Xiphinema diversicaudatum* (Micol.) Thorne—from elder (*Sambucus nigra* L.) near Dundee, Scotland; *Xiphinema index* Thorne and Allen—from a glasshouse culture beneath fig (*Ficus carica* L.) (originally

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TABLE 1. Viruses used in transmission tests.

Nematode-vector group	Virus	Strain	Abbreviation used in test
Xiphinema	Grapevine chrome mosaic	Type	GCMV
	Grapevine fanleaf	Italian	GFLV
	Strawberry latent ringspot	Type	SLRV
	Tobacco ringspot	Arkansas	TRSV
	Tomato ringspot	Wisconsin	TomRSV
Xiphinema and *Longidorus*	Arabis mosaic	Type	AMV
	Brome mosaic	Wild Type	BMV
	Carnation ringspot	Type	CRSV
	Cherry leaf roll	Cherry	CLRV(C)
	" " "	Golden elderberry	CLRV(G)
	" " "	Rhubarb	CLRV(R)
	Raspberry ringspot	English	RRV(E)
	" "	Scottish	RRV(S)
Longidorus	Artichoke Italian latent	Type	AILV
	Prunus necrotic ringspot	Cherry	PNRV(C)
	" " "	Hop	PNRV(H)
	Tomato black ring	Scottish	TBRV(S)
	" " "	German	TBRV(G)
Trichodorus	Pea early browning	British	PEBV
	Tobacco rattle	PRN	TRV

from an Italian population); *Xiphinema vuittenezi* Luc, Lima, Weischer and Flegg—from Colmar, France; *Longidorus elongatus* (de Man) Thorne and Swanger—from pasture soil near Coupar Angus, Scotland; *Longidorus macrosoma* Hooper—from a glasshouse culture beneath raspberry (*Rubus idaeus* L.) and originally from Bury St. Edmunds, England; and *Trichodorus* spp.— a mixed population comprised of *Trichodorus velatus, Paratrichodorus pachydermus* and *T. primitivus* in a ratio 3:2:1 from a forest nursery near Perth, Scotland.

All of these nematode populations were determined to be virus-free by bait testing with *Petunia hybrida* Vilm., *Chenopodium quinoa* Willd., *Cucumis sativus* L., *Stellaria media* (L.) Vill., and *Nicotiana clevelandii* A. Gray, and by assaying the roots after 4 weeks on *C. quinoa* and *N. clevelandii.*

Nematode extraction procedures: Soil from a forest nursery containing *P. maximus* was placed in 50-kg plastic bins and planted with Sitka spruce [*Picea sitchensis* (Bong.) Carr.]. The extraction procedure was a modification (4) of the Cobb (3) sieving and decanting technique. Quantities of soil (400 gm) were suspended in 4.5 liters of water, and after 20 sec the supernatant was poured into water within a semi-submerged 125-μm aperture sieve. The nematodes and residue retained on the sieve were washed off into water within a semi-submerged 90-μm nylon sieve and this fraction was placed in a water-filled Baermann funnel. Nematodes were collected from funnels after 15 h and counted. Extracting nematodes over water resulted in survival of greater numbers of nematodes during the experiments.

Nematodes for morphometric studies were heat killed at 60 C for 2 min, fixed in TAF, and mounted in glycerin.

Growing conditions: A soil mix developed at the Scottish Horticultural Research Institute was used in all tests with one exception: it consisted of a 2:1 mix of steam-sterilized, air-dried loam and sand with an aggregate and particle size $> 1{,}410$ μm and < 149 μm. This mix gave a medium suitable for good plant growth, nematode activity, and slow water loss, and it facilitated clean root and nematode recovery. The sand only was used in one test and, by using the extraction technique with only the 90-μm sieve, almost 100% nematode recovery was achieved. This method allowed rapid extraction, counting, and reinoculation of the nematodes.

All tests were made in temperature-controlled cabinets (22), and 25-ml plastic pots, which were plunged into moist sand contained in plastic-stacking boxes, were used. A plate-glass top minimized water loss and provided a more stable amount of humidity within the boxes. The cabinets were in the glasshouse, and supplementary mercury vapor lamps maintained a minimum 16-h day length.

Vector and virus host selection: Seven host plants for the viruses were tested as hosts for *P. maximus*. Five seedlings each of *Stellaria media* (L.) Vill., *Petunia hybrida* Vilm., *Chenopodium quinoa* Willd., *Nicotiana clevelandii* A. Gray., *Cucumis sativus* L., *Hordeum vulgare* L., and *Lycopersicon esculentum* Mill. were inoculated with 10 nematodes/pot. The nematodes and root galls were counted after 3 weeks. Although *P. maximus* feeding caused galls (Fig. 1-A) on all plants tested, greatest galling occurred on *C. quinoa*. From this information and knowledge of the virus host ranges, the following plant-virus combinations were selected for the transmission experiments: *C. quinoa* for GFLV, GCMV, CLRV, and SLRV; *P. hybrida* for AMV, CRSV, RRV, AILV, and TBRV; *C. sativus* for TRSV, TomRSV, PNRSV, and bait only for PEBV and TRV; *L. esculentum* for acquisition only for TRV; *N. clevelandii* for acquisition only for PEBV; and *H. vulgare* for BMV.

Transmission experimentation: Three-week-old acquisition plants were transplanted into pots, and after 3 days, their leaves were dusted with corundum and

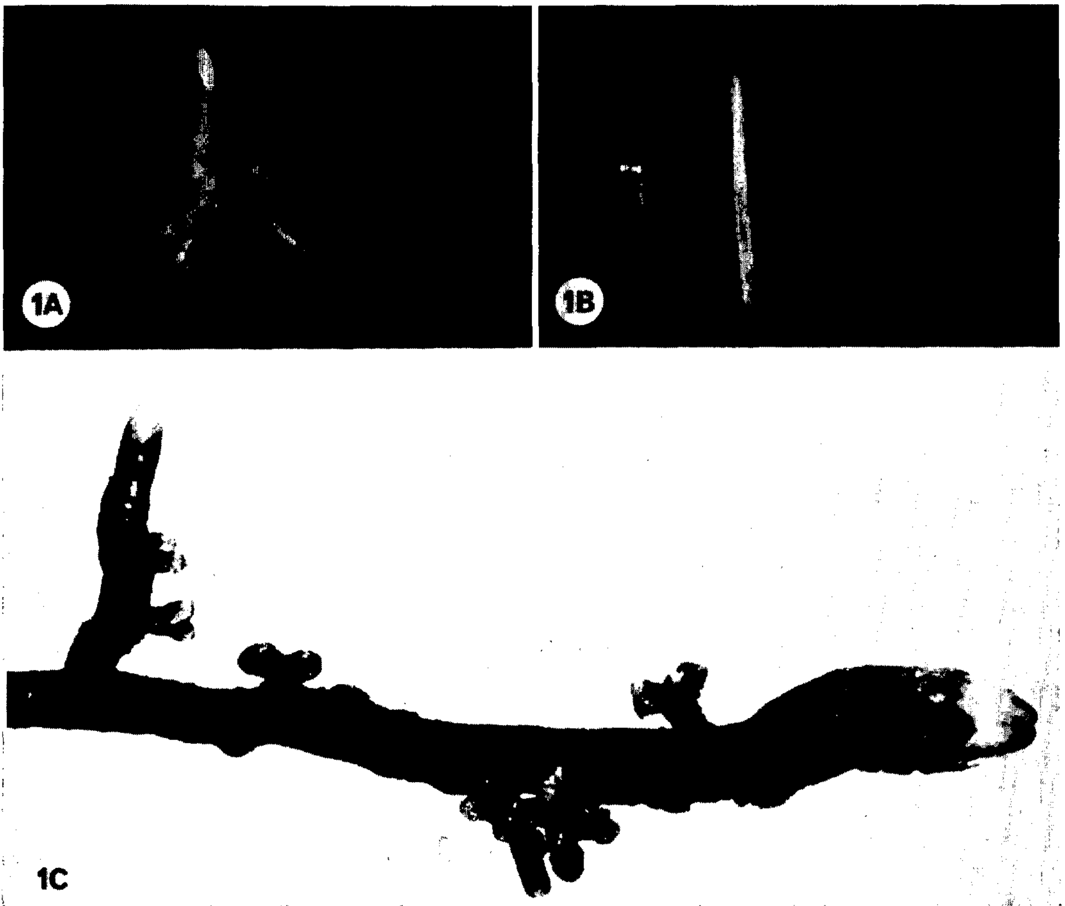

FIG. 1-(A-C). *A, B)* Root galling induced by the feeding of *Paralongidorus maximus* on Petunia hybrida. Note new laterals growing from the root gall. *C)* Root galls induced by the feeding of *P. maximus* on *Pinus sylvestris* growing in a forest nursery in Angus, Scotland. Note the swollen tips, reduced number, and truncated appearance of the laterals.

inoculated with sap from a virus-infected plant. Thirty to fifty nematodes were added to the pots 3-5 days later and allowed an acquisition access period (AAP) of 4 weeks.

Following the AAP, the nematodes were tested in two ways to determine their ability to transmit the virus. One group of nematodes was extracted from the pots, counted, and added to another set of pots. The second group of nematodes was left in the original pots from which the acquisition plants were removed and 3-week-old virus-free bait plants were transplanted to both series of pots. Galls were counted on all acquisition plant roots; then the roots were ground and inoculated onto *C. quinoa* indicator plants to confirm virus infection.

Nematode-free controls were of three types: *(i)* the supernatant from nematodes was collected after the AAP and was added to bait plants growing in sterile soil; *(ii)* the acquisition and bait plants were grown concurrently in the same pot; and *(iii)* the acquisition and bait plants were grown consecutively in the same soil.

In both tests, the nematodes were allowed an inoculation-access period (IAP) on the bait plants of 4 weeks. Following this, the nematodes were extracted and counted. After a thorough washing, the bait plant's roots were examined under a stereoscopic microscope to check that no nonattached roots or nematodes remained and the number of galls were counted. The roots were then ground separately and inoculated onto *C. quinoa* indicator plants.

Virus within the nematodes was assayed, following both the AAP and IAP, by hand-picking groups of five active nematodes with full intestines and placing them in a drop of phosphate buffer solution (pH 6.9) in a spot-plate well. A small quantity of celite was added to make a paste; the nematodes were ground in this paste and inoculated onto *C. quinoa* indicator plants with a clean glass rod. Preliminary tests demonstrated that grinding the nematodes in this manner gave complete break up of the body without prior cutting. The spot-plate, glass-rod technique was also used to assay small quantities of plant roots.

Wherever possible, the known nematode vector species for the virus being tested was included in the trial as a control to ascertain that transmission was possible under the existing experimental conditions. All vectors tested were treated similarly.

Nursery sampling: The distribution of *P. maximus* in the forest nursery was determined from samples consisting of 5-cm diam cores 10 cm in depth. The vertical distribution was investigated by taking 5 samples from 20 different sites throughout the nursery. After the vertical distribution was established, a transect was conducted across a decline area and soil samples were taken at 10- to 20-cm depths from around roots of measured trees growing in every third row (70-cm intervals).

Geographical distribution: Since the geographical distribution of *P. maximus* appears to be restricted to Europe, the base map of Europe, as produced by the European Invertebrate Survey (10), was used to pot the distribution to 50 km squares throughout Europe. A comprehensive literature survey and records from samples taken by the present authors contributed to the compilation of the distribution map (Fig. 2).

RESULTS AND DISCUSSION

Virus transmission: No virus transmission occurred in the tests in which *P. maximus* was extracted between the AAP and the IAP. Sixteen of the viruses were not recovered from the bait-plant roots in tests in which the bait plants followed the acquisition plants in the same pot with *P. maximus* (Table 2) but RRV(E), RRV(S), AMV, and SLRV were recovered from some of the bait-plant roots in these tests. In all tests, the nematodes fed sufficiently to cause galls, an indication that the nematodes could have acquired or inoculated virus during feeding. Nine of the 20 viruses tested were recovered directly from *P. maximus,* an indication that the nematodes had ingested these viruses (Table 3). Known vectors successfully transmitted their associated viruses (Table 2), an action which demonstrated that transmission was possible under the experimental conditions. It is therefore concluded that *P. maximus* is not a vector of 16 of the 20 viruses tested.

In the tests in which *P. maximus* was not extracted between the AAP and the IAP, the results for the four viruses which were recovered from some of the bait-plant roots are less conclusive as the bait plants

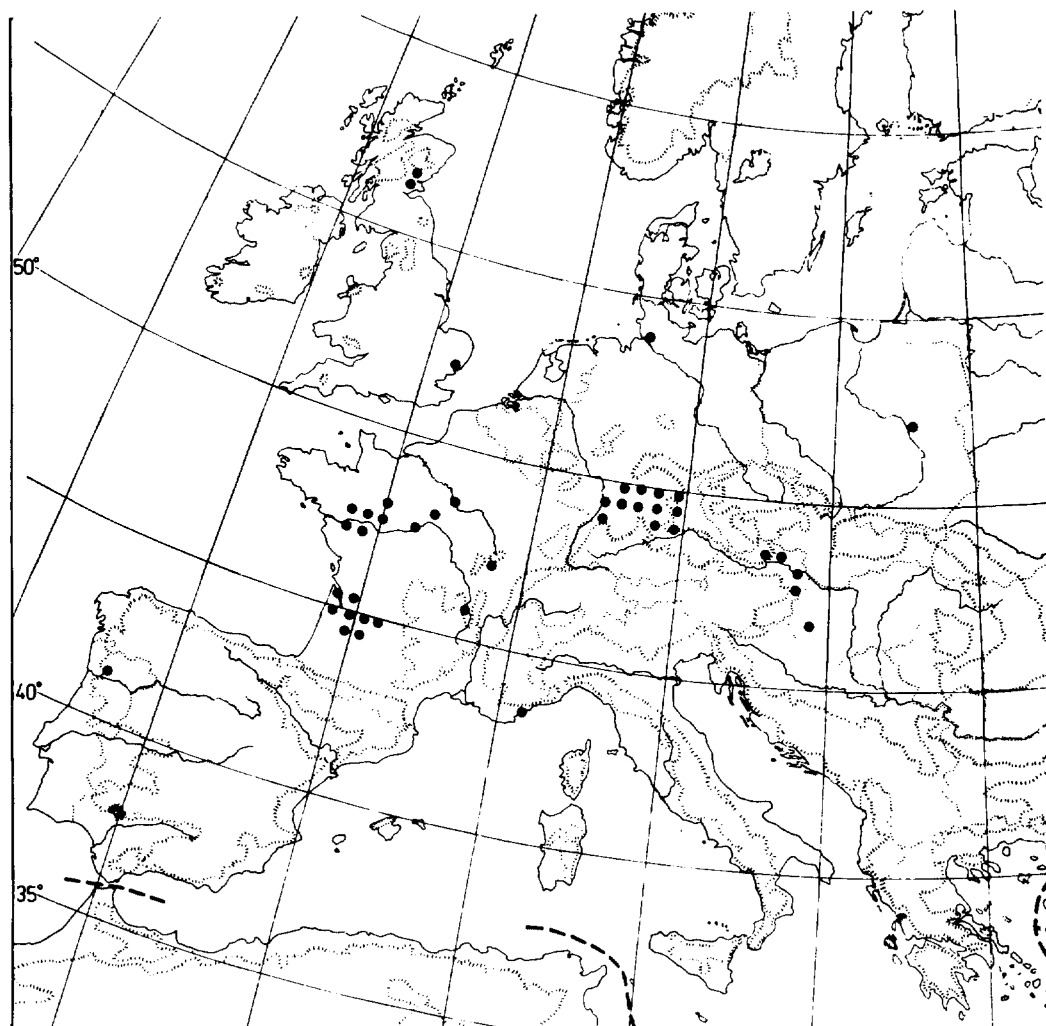

FIG. 2. Distribution of *Paralongidorus maximus* in western Europe and the British Isles.

were not tested for systemic movement of virus, and contamination could have been responsible for these results. Contamination by old infected root material is thought improbable because care was taken to inspect and remove all old root material found adhering to the bait-plant roots. Also, the controls in which *P. maximus* was not present were all negative.

It has been demonstrated that virus infectivity of vector nematodes decreased with increased time in Baermann funnels (25). This decreased infectivity does not seem to be the reason for lack of transmission by extracted *P. maximus.* No transmission occurred even when the nematodes were removed from the acquisition plants and immediately placed on bait plants without being passed through a funnel. The fact that virus transmission occurred only when *P. maximus* was left undisturbed, and then only at low rates, suggests that virus particles may have been transferred as short-term surface contaminants of the mouth parts. This relationship has been proposed by others (5, 23, 24) to explain similar results with other virus-nematode combinations. Virus particles may lodge in a nonspecific manner in the esophageal lumen of *Xiphinema* and *Longidorus* (24) to allow for occasional transmission of an unnaturally associated virus. Although this transmission may occur in *P. maximus,* our results suggest that some

TABLE 2. Virus transmission by nematodes which were: (1) not extracted and (2) extracted from the soil between the acquisition and bait plant tests.

Nematode-vector group virus	Paralongidorus maximus		Controls		
	Non-extracted	Extracted	Nematode spp.	Non-extracted	Extracted
Xiphinema					
GFLV	0/10[a]	0/20	*X. index*	—	2/6
GCMV	0/10	0/18	*X. index*	—	0/6
			X. vuittenezi	—	0/10
SLRV	2/20	0/15	*X. diversicaudatum*	—	10/10
TRSV	0/10	0/10	—	—	—
TomRSV	0/10	0/10	—	—	—
Xiphinema and *Longidorus*					
AMV	3/20	0/17	*X. diversicaudatum*	—	17/17
CLRV(C)	0/10	0/8	—	—	—
CLRV(R)	0/9	0/8	—	—	—
CLRV(G)	0/10	0/8	—	—	—
CRSV	0/10	0/5	*L. macrosoma*	—	0/3
			X. diversicaudatum	—	4/5
BMV	0/10	0/10	*X. diversicaudatum*	—	7/9
RRV(E)	5/20	0/17	*L. elongatus*	4/5	7/15
RRV(S)	5/20		*L. elongatus*	5/5	5/5
Longidorus					
AILV	0/10	0/8	—	—	—
PNRSV(C)	0/10	0/10	*L. macrosoma*	—	0/10
PNRSV(H)	0/10	0/10	—	—	—
TBRV(B)	0/10	0/10	*L. elongatus*	0/5	0/5
TBRV(S)	0/10	0/10	*L. elongatus*	3/5	5/5
Trichodorus					
PEBV	0/10	0/10	*Trichodorus* spp.	0/8	0/8
TRV	0/10	0/10	*Trichodorus* spp.	4/10	0/8

[a]Numerator is the total number of bait plants infected; denominator is the number tested.

specificity is involved as this phenomenon occurred with only certain of the viruses tested. It is not known if this specificity is an artifact of the virus, nematode, or a combination of both. Electron microscope examination of these questionable virus-nematode relationships may help answer this question.

Seven of the viruses tested have been reported to be vectored by both *Xiphinema* and *Longidorus* species. The majority of the viruses directly recovered from *P. maximus* also fall into this group (Table 2 and 3). Nine of the viruses were recovered directly from *P. maximus* and, apart from being a useful indicator that the nematodes had had access to the virus, the results also indicated that differences exist in the composition of the digestive fluids in the guts of *Longidorus, Paralongidorus,* and *Xiphinema.* No viruses were directly recovered from any of the *Xiphinema* species but four were recovered from *Longidorus.* These four viruses did not correspond with the nine viruses recovered from *P. maximus* since TBRV(S) was directly recovered from *L. elongatus* but TBRV(G) was not; the reverse combination was true with *P. maximus.* The fact that certain viruses cannot be recovered directly suggests they are destroyed in the gut upon ingestion or, less likely, by compounds released upon grinding of the nematode body. Since it is only the nucleic acid of nepoviruses that is important in the initiation of infection (13), this component is probably where specificity of the destruction lies. Further discussion of this is beyond the scope of this paper, but further work along these lines would provide clues to the digestive processes of these species and the type of food being utilized by them.

Tests reported here as controls confirm reported transmission of BMV (15) and

TABLE 3. Viruses recorded directly from nematodes fed for 3 weeks on infected plants.

Paralongidorus maximus		Controls	
Nematode-vector group virus	Virus recovery ratio	Nematode spp.	Virus recovery ratio
Xiphinema			
GFLV	0/3	—	—
GCMV	1/16	*X. index*	0/10
SLRV	0/18	*X. diversicaudatum*	0/6
TbRSV	0/4	—	—
TomRSV	0/6	—	—
Xiphinema & *Longidorus*			
AMV	4/35	*X. diversicaudatum*	0/16
CLRV(C)	8/26	*X. diversicaudatum*	0/10
		L. elongatus	7/10
CLRV(R)	3/22	*X. diversicaudatum*	0/10
CLRV(G)	5/24	*X. diversicaudatum*	0/10
CRSV	5/11	*X. diversicaudatum*	0/6
BMV	0/6	*X. diversicaudatum*	0/10
RRV(E)	15/30	*L. elongatus*	3/6
RRV(S)	19/29	*L. elongatus*	4/6
Longidorus			
AILV	0/14	*L. elongatus*	—
PNRSV(C)	0/6	*L. elongatus*	—
PNRSV(H)	0/6	*L. elongatus*	—
TBRV(G)	2/20	*L. elongatus*	0/6
TBRV(S)	0/20	*L. elongatus*	10/11
Trichodorus			
PEBV	0/10	*L. elongatus*	—
TRV	0/10	*L. elongatus*	—

[a]Numerator is the number of groups of five nematodes containing virus; denominator is the number of groups tested. In some cases, figures are the combined totals of at least two experiments.

CRSV (9) by *X. diversicaudatum*. However we were unable to obtain transmission of either PNRSV or CRSV (9) by using *L. macrosoma*.

Although GCMV is classified as a nepovirus, the vector is unknown. *X. vuittenezi* has been found associated with spread of the disease in Hungary (13), but no tests with this species have been reported. In our tests, neither *X. vuittenezi* nor *X. index* transmitted the virus.

Several vectors have been reported for CLRV (5, 7, 8) but other workers have been unable to obtain transmission by using these species (5, 26). We were only able to obtain virus transmission with nonextracted *X. diversicaudatum*.

Relationship of nematode numbers to plant growth: The symptoms and damage caused by *P. maximus* on Scots pine in the present work were quite distinct. In one part of the forest nursery, 4-year-old Scots pines in areas 2-3 m in circumference were observed showing signs of yellowing and retarded growth, and some trees in these areas had died. In another part of the nursery, 3-year-old Scots pines in an area 40 x 40 m showed poor growth and a tendency towards yellowing which gradually merged with larger, darker, more strongly growing trees. These areas of retarded growth had been attributed to nutritional defects but subsequent examination of the soil showed them to have higher numbers of *P. maximus* than the surrounding area. Seedling heights within this area were negatively correlated with nematode numbers [$Y = 32 - 0.377 + \log_{10}$ (No. nematodes + 1); $r = -0.82^{**}$]. The roots of the affected plants were severely stunted and had fewer laterals. Fewer side rootlets were produced from these laterals and the side rootlets usually grew singly. They appeared as short, truncated, Y-shaped growths which did not exhibit the long, thin, finger-like growths usually associated with normal roots (Fig. 1-B). The

symptoms and damage described here for Scots pine are similar to those described by previous workers for other plants (11, 19, 20, 21).

Morphometrics: Measurements of the Angus population of *P. maximus* studied in this work are very similar to those described by Sturhan (21) from Germany and Heyns (11) from the other Scottish populations. Only the tail length is slightly shorter at 5.3 nm (5.1-5.7), 5.9 nm (4.0-8.4), 10.4 nm (8.6-11.2), 13.7 nm (10.1-15.4), and 14.7 nm (12.3-16.2) for larval stages 1, 2, 3, 4 and female, respectively. This difference resulted in higher C values for the Angus population. The values were 51 (46-60), 81 (69-102), 138 (120-156), 196 (176-220), and 282 (259-333) for larval stages 1, 2, 3, 4 and female, respectively. The marked degree of similarity existing between the different populations which have been measured would suggest that this species probably shows a considerable consistency throughout its geographical range.

Distribution: Paralongidorus maximus is found only in Europe (Fig. 2) where it is the only member of the genus to be recorded. The other 23 *Paralongidorus* species have been described from Africa, Australia, and India. In Great Britain, *P. maximus* has been reported from only three sites, including the site reported here. On each occasion, this species was identified from intensively cultivated ground and never from a field, mature forest, or wood. It seems probable that it has been introduced into Great Britain with planting material. Numbers were low at both the ornamental nursery site in England and in the garden site in Scotland; however, at this forest nursery site, it occurred in moderately high numbers. Its distribution in Europe would indicate that it survives best in well drained, light, highly humus, sandy soils. The soils in Great Britain in which it was found were either sandy loam or loamy sand with a pH between 5.5 and 6.7.

The vertical distribution of *P. maximus* in the forest nursery site appeared to reflect the distribution of Scots pine roots in the soil. Nematodes recovered at different depths were as follows: 0-10 cm, 11%; 10-20 cm, 48%; 20-30 cm, 26%; 30-40 cm, 14%; 40-50 cm, 1%. Highest populations occurred at 10-20 cm which is also where the majority of roots were found. This pattern differs slightly from previous work which reported *P. maximus* to depths of 70 cm with higher densities between 20 and 40 cm (21). No males were observed but rare occurrences have been recorded (21).

The information reported here indicates that *P. maximus* is not an important vector of presently known nematode-transmitted viruses. Its primary importance remains in its high direct-damage potential, especially to woody plants. The distribution of *P. maximus* in Great Britain suggests that it is rare and has likely been introduced into the country from western Europe where it is widely distributed.

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