Morphometric variability between populations of *Xiphinema diversicaudatum* (Nematoda : Dorylaimoidea)

Derek J. F. Brown and Pauline B. Topham
Scottish Crop Research Institute, Invergowrie, Dundee, DD2 5DA, Scotland

Summary

The morphometrics of population of *Xiphinema diversicaudatum* from 26 biotopes from twelve European countries, the United States of America and New Zealand were examined. Significant differences occurred between populations and the variability was greater than has previously been reported. Moreover, it was greater than has been reported to be caused by employing different methods to process specimens for examination by optical microscopy. Although several groups of populations of *X. diversicaudatum* with generally similar morphometrics (= morpho-groups) were established using canonical variate analysis all populations formed a homogenous group at the 80 % level of similarity. Geographical origin of the populations of *X. diversicaudatum* did not determine the composition of the morpho-groups and morphometric clines were not apparent. The variability present between the morphometrics of populations of *X. diversicaudatum* probably reflects the nematode's ability to adapt to different biotopes. Thus the species may pose a threat to many temperate areas to which it may be inadvertently introduced.

Résumé

Variabilité morphométrique entre populations de Xiphinema diversicaudatum *(Nematoda : Dorylaimoidea)*

Les auteurs étudient la morphométrie des populations de *Xiphinema diversicaudatum* provenant de 26 biotopes d'Europe, des U.S.A. et de Nouvelle-Zélande. Des différences significatives existent entre populations et la variabilité apparaît plus grande qu'il n'avait été rapporté antérieurement. De plus cette variabilité est supérieure à celle signalée pour être causée par l'emploi de méthodes différentes de préparation des spécimens en vue de l'examen en microscopie optique. Bien qu'il ait pu être défini, en utilisant l'analyse factorielle discriminante, plusieurs groupes de populations ayant chacun une morphométrie proche (« morpho-groupes »), l'ensemble des populations forme un groupe homogène avec un coefficient de similarité de 80 %. L'origine géographique des populations de *X. diversicaudatum* n'intervient pas dans la composition des morpho-groupes et aucune dérive morphométrique n'est apparente. La variabilité morphométrique entre populations de *X. diversicaudatum* reflète probablement l'aptitude des nématodes à s'adapter à des biotopes différents. Cette espèce peut donc constituer une menace pour de nombreux pays tempérés où elle serait introduite par inadvertance.

Morphometric differences occurring between populations of a nematode species or between specimens within a population have been reported by many research workers. The differences have been reported to be the result of geographical distribution, ecophenotypic effects and different hosts (Goodey, 1952; Rhode & Jenkins, 1957; Bird & Mai, 1965; Fisher, 1965; De Grisse & Loof, 1970; Tarte & Mai, 1976; Azmi & Jairajpuri, 1978; Evans & Franco, 1977; Tarjan & Frederick, 1978). Much variability is evident in the published data of morphometrics of different populations of *X. diversicaudatum* (Micoletzky, 1927), Thorne, 1939 (Goodey, Peacock & Pitcher, 1960; Martelli & Lamberti, 1967; Terlidou, 1967; Szczygiel, 1974; Teploukhova, 1974; Erbenova, 1975; Hrzic, 1978). The possibility that this variability might, in part, be the result of operator and measuring error (Brown, 1981) and the effects of different methods of killing, fixing and mounting specimens from the different populations was discussed by Brown and Topham (1984). Alternatively, the morphometric differences between populations of *X. diversicaudatum* may reflect natural variation resulting from population's adaptation to survive in different biotopes or genetic drift and this aspect is explored in the present study.

Cultures of *X. diversicaudatum* from biotopes from different countries and continents were sent to the Scottish Crop Research Institute. A standard method was adopted for killing, fixing, mounting and measuring specimens from each culture in order to assess morphometric variability due to biotopic influence.

Materials and methods

Populations of *X. diversicaudatum*

Cultures of *X. diversicaudatum* populations were sent in small quantities of soil (c. 1 kg) from 26 biotopes from twelve European countries, the United States of Ame-

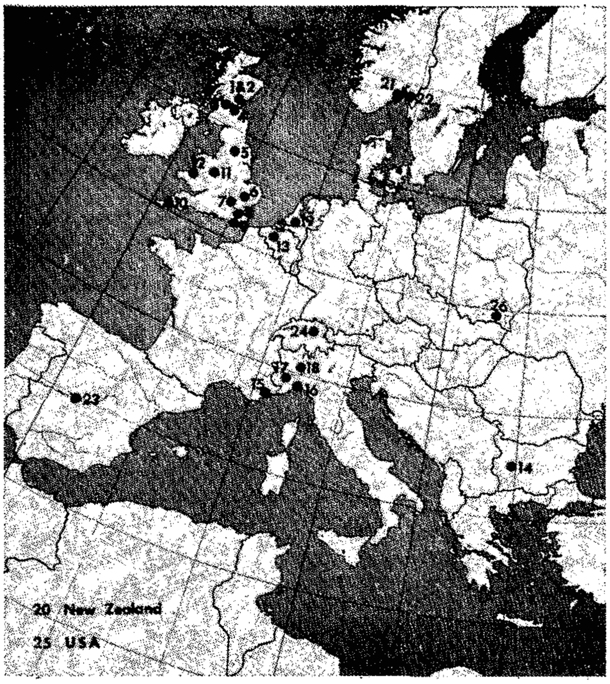

Fig. 1. Geographical locations of populations of *X. diversicaudatum* : 1, Dundee (field), Scotland; 2, Dundee (glasshouse), Scotland; 3, Cupar, Scotland; 4, Kilsyth, Scotland; 5, Ilkley, England; 6, Bury St. Edmunds, England; 7, Harpenden, England; 8, Aylesford, England; 9, High Halstow, England; 10, Treswithian, England; 11, Wrekin, Wales; 12, Nevern, Wales; 13, Saint-Katherina-Lombeek, Belgium; 14, Kostinbrod, Bulgaria; 15, Les Adrets, France; 16, Liguria region, Italy; 17, Lombardi region, Italy; 18, Piemonte region, Italy; 19, Wageningen, Netherlands; 20, Alexandra, New Zealand; 21, Sandefjord, Norway; 22, Rygge, Norway; 23, Cazalegas, Spain; 24, Holzieken, Switzerland; 25, San Diego, U.S.A.; 26, Nowy Sacz, Poland.

rica and New Zealand (Table 1; Figure 1). All cultures came from field populations except those from Dundee, Les Adrets and Wageningen which came from glasshouse populations.

Upon receipt of each culture at the S.C.R.I. ten female and five male specimens were extracted using the method of McElroy, Brown and Boag (1977) and used for morphological and morphometrical studies. The remaining soil with nematodes was put in a series of

Table 1

Populations of *X. diversicaudatum* collected and kept at the S.C.R.I.

Country	*Location*	*Host Plant*	*Population number*
Scotland	Dundee (field)	*Sambucus nigra*	1
Scotland	Dundee (glasshouse)	*Rosa* sp.	2
Scotland	Cupar	*Fragaria* × *ananassa*	3
Scotland	Kilsyth	Deciduous woodland	4
England	Ilkley	*Lolium perenne*	5
England	Bury St. Edmunds	Deciduous woodland	6
England	Harpenden	*Lolium perenne*	7
England	Aylesford	Scrubland	8
England	High Halstow	Deciduous woodland	9
England	Treswithian	*Lolium perenne*	10
Wales	Wrekin	*Lolium perenne*	11
Wales	Nevern	*Rosa* sp.	12
Belgium	Saint-Katherina-Lombeek	*Fragaria* × *ananassa*	13
Bulgaria	Kostinbrod	*Ribes nigrum*	14
France	Les Adrets	*Rosa* sp.	15
Italy	Liguria region	*Vitis vinifera*	16
Italy	Lombardi region	*Rubus idaeus*	17

Table 1 (contd.)

Country	*Location*	*Host Plant*	*Population number*
Italy	Piemonte region	*Prunus persica*	18
Netherlands	Wageningen	*Rosa* sp.	19
New Zealand	Alexandra	*Prunus armeniaca*	20
Norway	Sandefjord	*Fragaria* × *ananassa*	21
Norway	Rygge	*Fragaria* × *ananassa*	22
Spain	Cazalegas	*Vitis vinifera*	23
Switzerland	Holzieken	*Triticum spelta*	24
U.S.A.	San Diego	*Prunus persica*	25
Poland	Nowy Sacz	*Fragaria* × *ananassa*	26

Table 2

Structures and ratios measured in *X. diversicaudatum* specimens

Structure		*Abbreviation used in text*
Length of body	mm	L
Length of anterior end to the anus	mm	L′
Length of anterior end to the vulva *	mm	anterior to vulva
Length of anterior end to the œsophageal-intestinal junction	µm	anterior to œsoph-intest junction
Length of body occupied by the anterior gonad*	µm	anterior gonad
Length of body occupied by the posterior gonad*	µm	posterior gonad
Length of tail	µm	tail length
Length of odontostyle	µm	odontostyle
Length of odontophore	µm	odontophore
Length of odontostyle plus odontophore	µm	spear
Body width at the spear base	µm	width at spear base
Greatest body width	µm	greatest width
Body width at the anus	µm	width at anus
Spicula +	µm	spicula
Length of body occupied by the testes +	mm	testes
L / greatest width		a
L / anterior to œsoph-intest junction		b
L / tail length		c
Tail length / width at anus		c′
Anterior to vulva × 100 / L*		V
Anterior to vulva × 100 / L′*		V′
Spear / width at spear base		S
Testes × 100 / L +		T

*, Female specimens only.
+, Male specimens only.

30 cm diam. plastic pots each with a plant of *Rubus idaeus* L. cv. Malling Jewel, *Fragaria* × *ananassa* Duch. cv. Cambridge Favourite and *Rosa* L. sp. and maintained in a heated glasshouse (18°) with natural daylight.

MORPHOLOGY AND MORPHOMETRICS

The ten female and five male specimens from each population were heat killed and fixed with triethanolamine/formalin (Courtney, Polley & Miller, 1955) using the method of Seinhorst (1966) and processed to glycerol using a slow replacement method.

A Reichert Diapan microscope, with drawing arm attached, and with 6.3 fold eyepieces, 2.5, 4, 10, 63 and 100 fold objectives, was used to examine and obtain measurements of the specimens. The measurements and ratios obtained for each specimen and their abbreviations used in the text are listed in Table 2.

Table 3

Percentage differences from grand means in morphometric means of *X. diversicaduatum* females (n = 10) from different populations.

*Populations**	*L*	*Anterior* o/i junc	*Anterior* vulva	*Gonads* ant.	*Gonads* post.	*Tail*	*Odonto-* style	*Odonto-* phore	*Spear*
Grand Means	4.68	504	1.98	767	819	48.5	131.7	79.6	211.3
1	11.6	0.1	16.3	17.3	14.5	− 2	3.4	− 0.7	1.9
2	− 1.7	2	1.3	1	− 3.8	5	− 0.6	− 2.3	− 2.3
3	5.7	− 0.1	2.3	9.1	5.4	− 8.6	0.4	1.6	0.9
4	11.3	5.8	11.9	18.9	18.3	2.5	3.4	8.6	5.4
5	6.3	14.8	10	1.8	− 2.3	15.5	13.9	12.6	13.5
6	− 2.3	− 1.9	− 4.6	1	− 6.9	− 8.6	− 3.4	− 3.2	− 3.3
7	− 4.6	2.6	− 5.2	4.3	9.9	2.1	1.2	4	2.2
8	− 11.2	3.3	− 12.2	− 5.5	− 13	− 6.4	− 2	− 0.4	− 1.4
9	11.4	8.1	9.9	5.9	13	2.1	4.6	7.2	5.6
10	2.5	4.7	4.9	15.7	8.4	0.7	1.9	0	1.2
11	3.4	4.7	2.2	5.9	− 0.7	− 2.2	1.7	3.5	2.4
12	7.6	6.3	13	− 0.7	6.9	6.6	4.9	6.6	5.5
13	8.7	3.8	7.4	5.9	− 2.3	5	4.1	4.4	4.2
14	− 8.2	− 7.3	− 5.9	− 23.4	− 14.5	9.7	− 8.5	− 5.9	− 7.6
15	− 8.1	− 9	− 7	− 15.3	− 6.9	5	− 5.7	− 5.8	− 5.7
16	− 12.4	− 9	− 11.8	− 7.1	− 3.8	− 11.7	− 3.6	− 4.8	− 4.1
17	− 9.5	− 6.9	− 7.7	− 2.3	− 3.8	− 8	− 4.8	− 6.6	− 5.5
18	− 11.6	− 9	− 12.8	− 0.6	− 16	− 10.3	− 6.6	− 4.2	− 5.7
19	− 9.2	− 7.8	− 10.3	− 15.3	− 2.7	1.3	− 8.5	− 5.7	− 7.5
20	− 3.3	− 0.3	− 1.4	5.9	− 6.9	1.7	− 1.6	− 2.2	− 1.8
21	0.4	− 3.4	− 4	12.4	6.9	− 0.6	− 1.8	− 2.4	− 2
22	− 3.9	− 1.9	− 7.8	9.1	20.6	− 2	− 2.8	− 4.4	− 3.4
23	6	− 7.6	− 10.5	− 32.2	− 28.2	− 12.5	− 5.9	− 10.1	− 7.5
24	6	2.9	4.8	1	9.9	1.3	3.4	4.4	2.8
25	− 2.2	− 7.8	− 7.1	− 8.8	− 3.8	− 0.1	− 4.4	− 1	− 3.2
26	2.7	12.9	3.4	− 3.1	− 8.2	15.3	17.2	− 9.5	14.3
L.S.D. **									
P 5 % ±	6.5	4.4	6.9	12.5	13.2	7.1	3	3.7	2
P 1 % ±	8.6	5.8	9.1	16.4	17.3	9.4	3.9	4.9	2.7
P 0.1 % ±	11	7.4	11.7	21	22.2	12	5	6.3	3.4
C.V. % ***	7.4	5	7.9	14.2	14.9	8.1	3.4	4.2	2.8

* For explanation of codes see Table 1.
** Least significant differences as percentages of the Grand Means.
*** Coefficient of variation percentages.

ANALYSIS OF DATA

The results were analysed statistically using the GENSTAT computer package (Alvey, Galway & Lane, 1982). Canonical variate analysis (C.V.A.), was used to make an objective assessment of the relative similarity of populations, based on five selected morphometric features, L, V, c', odontostyle and odontophore lengths. Single-linkage cluster analysis was used to compile a dendrogram showing the clustering of populations at different levels on a scale of similarity. The similarity values, S, between each pair of populations were calculated as S = (1 — D/10) × 100, where D was the Mahalanobis' distances calculated in the C.V.A.

Results

(See Table 2 for abbreviations of structures used in text)

MORPHOMETRIC DIFFERENCES BETWEEN POPULATIONS OF *X. diversicaudatum*

The populations of « *X. diversicaudatum* » received at the S.C.R.I. belonged to the group of *Xiphinema* species in which the females have two genital branches

Table 3 (contd.)

*Populations**	*Body widths*			*Ratios*					
	s/base	*great*	*anus*	*a*	*b*	*c*	*c'*	*S*	*V*
Grand Means	45.8	59.6	44.1	79	9.3	97.3	1.11	4.63	42.3
1	2.6	4	6.1	6.9	11.8	13.2	— 8.1	— 1	4.1
2	— 1.9	— 4	— 2.5	1.9	— 3.9	— 6.4	7.5	0.5	3.1
3	4.8	3.2	3.4	2	6.2	15.5	— 11.9	— 4	— 3.3
4	5.3	5.2	10.4	7	6.5	9.6	— 7.7	— 0.2	— 1
5	27.8	33.6	32.4	— 20.5	— 0.5	— 7.8	— 12.9	— 10.8	3.5
6	0.5	0.7	— 2.4	— 3.4	— 7.3	6.6	— 11.2	— 4.1	— 2.1
7	— 0.2	0.2	— 4.1	— 5.3	— 7.3	— 7.2	5.9	2.2	— 0.6
8	— 1.3	— 1.8	5.2	— 9.8	— 14.1	— 5.6	— 11.3	— 0.3	— 1.1
9	2.4	6.4	6.1	6	4.8	10.8	— 4.2	2.8	— 3.2
10	4.4	3.2	2.9	— 1.2	— 2.3	2.2	— 2.7	— 3.3	2.1
11	0.9	2.4	— 1.7	0.6	— 1.3	5.2	— 1.2	1.2	— 1
12	1.1	1.7	2.2	5.3	0.9	0.5	3.9	— 4.3	5.2
13	— 1.3	2.9	0.9	5	4.5	3	3.4	5.4	— 0.9
14	— 5.2	— 6.9	— 6.8	— 1.8	— 1.2	— 16.4	16.9	— 2.8	2.2
15	— 8.1	— 9.2	— 12.5	0.6	0.8	— 13	19.3	2.2	1.3
16	— 8.1	— 8.7	— 5.3	— 4.6	— 4	— 1.4	— 7.6	4.1	0.5
17	— 6.1	— 5.5	— 5.3	— 4.7	— 2.9	— 2.4	— 3.6	0.4	2
18	— 8.3	— 7.7	— 3.4	— 4.7	— 3	— 1.2	— 7.7	2.5	— 1.3
19	— 2.2	— 1.2	— 4.8	— 7.6	— 0.5	— 9.5	— 5.8	— 5.7	— 2.3
20	— 4.8	— 11.9	— 10.7	9.1	— 3.3	— 5.4	13.3	2.1	2.1
21	— 3	— 5.7	— 3.2	6	4.1	0.4	2.2	0.7	— 4.4
22	— 2.2	— 4.9	— 2.1	0.8	— 2.1	— 2.6	— 0.6	— 1.5	— 4.1
23	— 12.6	— 13.7	— 17.5	22.3	14.6	20.5	5.3	5.6	4.4
24	6.4	8.9	4	— 3.1	2.8	4.2	— 3.2	— 3.5	— 1
25	— 6.7	— 7.4	— 9.6	4.9	5.9	— 1.4	9.3	3.6	— 4.9
26	15.7	16.3	13.6	— 11.5	— 9.3	— 11.4	1.1	— 1.3	0.8
L.S.D.**									
P 5 % ±	4	5	5	4.7	5.7	6.5	6.1	3.1	4.3
P 1 % ±	5.2	6.6	6.6	6.1	7.5	8.6	8	4.1	5.6
P 0.1 % ±	6.7	8.5	8.5	7.9	9.7	11	10.3	5.3	7.2
C.V. %***	4.5	5.7	5.7	6.3	8	9.2	8.4	4.3	4.8

* For explanation of codes see Table 1.
** Least significant differences as percentages of the Grand Means.
*** Coefficient of variation percentages.

of similar length and structure and which contain a pseudo Z differentiation. Furthermore, most individuals had rounded, digitate tails and the apophyses present in the pseudo Z differentiations in the female genital tracts were invariably globular, comprised of a central, spherical, refringent portion surrounded by a less refringent part, usually lobed. Males were relatively common in each population. Some of the more important morphometric characteristics of the populations studied were :

Pops. 1 and 2, *Dundee, Scotland.* Population 1 was the most northerly situated population of *X. diversicaudatum* in Britain and the biotope probably represents the northern boundary for the survival of the species in the British Isles. Mean body length for females was larger and mean spear length was smaller for the Dundee specimens than the measurements given by Goodey, Peacock and Pitcher (1960) for their British specimens (5.2 vs 4.9 mm, mean body lengths; 215 vs 228 µm, mean spear lengths). The morphometrics of specimens from pop. 2, which was originally from the field site of pop. 1, but which had been maintained for four years as a culture in a heated glasshouse, were significantly smaller than the morphometrics of specimens from pop. 1 (Tables 3 and 4).

Table 4

Percentage differences from grand means in morphometric means of *X. diversicaudatum* males (n = 5) from different populations.

Populations *	*L*	*Ant o/i*	*Testes*	*Tail*	*Spicula*	*Odonto- style*	*Odonto- phore*	*Spear*
Grand Means	4.58	498	2.68	49.8	68.8	130.3	78.8	209.1
1	20.5	6.8	11.5	−4.5	16	5.9	4.9	5.5
2	−4.7	−0.7	−12.9	0.7	−0.6	−1.9	1.1	−0.8
3	2.5	4.9	1.2	−0.1	6.4	0.5	4.1	1.9
4	19.3	8.1	21.7	0.3	6.4	7	2.8	5.4
5	11.7	14.1	21.3	18.8	10.4	18.3	14.5	16.9
6	5.1	4	5.8	−3.9	1.7	4.3	1.3	3.2
7	−9.1	1.1	−5.4	−9.3	−5.3	−1.5	−0.7	−1.2
8	−15.3	2.1	−12.8	−10.5	4	−1	−2	−1.4
9	13.9	9	16.5	3.9	6.4	5.6	7.7	6.4
10	6.2	1.1	9.6	−5.7	1.7	−0.3	−1.5	−0.7
11	−6.2	3.1	−10.9	−9.8	−5.3	0.5	1.1	0.7
12	11.7	4	0.3	1.1	4	4.5	5.6	4.9
13	11.7	4.4	14.2	−1.3	4	5	−0.2	3
14	−9.5	−9	−7.1	5.5	−7.6	−12.7	−9.1	−11.3
15	−6.9	−6.6	−1.8	7.5	−2.9	−5	−5.8	−5.3
16	−6.8	−7.6	−1.6	−2.1	−2.9	−4.6	−2.2	3.7
17	−18.7	−9.9	−20.3	−6.1	−7.6	−5.8	−7.6	−6.5
18	−10.6	−7.6	−18.5	3.9	−9.9	−6.4	−4.8	−5.8
19	−13.4	−9.9	−7.1	1.1	−9.9	−11.3	−7.1	−9.7
20	5.1	4	4.9	1.9	−2.9	0	2.3	−0.9
21	−11.3	−8.1	−7.2	−3.3	1.7	−5.5	−4.5	−5.1
22	−8.4	−10.4	−12.7	2.7	−9.9	−4.9	−5.5	−5.1
23	13.9	−11.3	11.5	−9.7	−12.2	−2.4	−8.6	−4.7
24	1.2	3.5	−5.3	−2.1	2.9	1.6	5.9	3.2
25	−0.8	−3.8	2.1	0.7	4	−5	−2.5	−4.1
26	−1.4	15	3	12	7.5	15.1	11	13.5
L.S.D.**								
P 5 % ±	9.3	7.2	14.5	9.1	8.7	4.3	5.4	2.1
P 1 % ±	12.3	9.5	19	11.9	11.4	5.6	7.2	2.7
P 0.1 % ±	15.9	12.3	24.6	15.4	14.8	7.3	9.2	3.5
C.V. % ***	7.4	5.8	11.6	7.2	6.9	3.4	4.3	2.8

* For explanation of codes see Table 1.
** Least significant differences as percentages of the Grand Means.
*** Coefficient of variation percentages.

Table 4 (contd.)

Populations *	*Widths*			*Ratios*					
	spear base	*great*	*anus*	*a*	*b*	*c*	*c'*	*S*	*T*
Grand Means	44.7	54	43.5	85.4	9.21	92.4	1.15	4.7	58.6
1	3.4	9.6	6.1	9	13	25.4	— 10.6	1.6	— 7.5
2	— 2.9	— 11.1	— 0.3	6.5	— 4.2	— 5.5	0.6	1.9	— 8.8
3	3.8	2.2	2.4	— 0.4	— 2.3	2	— 3.1	— 2.2	— 1.4
4	2.5	2.6	7	15.4	9.9	18.7	— 6.8	2.4	2.3
5	37.8	48.8	38.3	— 25.4	— 2.2	— 6.1	— 14.5	— 15.2	8.4
6	3.4	6.3	6.6	— 1.7	0.9	0.7	— 3.2	— 0.5	0.1
7	— 5.6	— 6.3	— 7.2	— 3.7	— 10.4	0	— 2.8	4.4	4
8	— 2.9	0	6.6	— 16.5	— 17.6	— 6.3	— 16.6	1.2	2
9	3.4	4.4	4.3	8.1	4.3	9.8	— 0.6	2.5	2.1
10	5.2	4.4	3.4	1.2	4.7	12.4	— 9.3	— 5.9	3.2
11	— 2	6	— 5.8	— 0.9	— 9.2	3.2	— 4.7	2.4	— 4.9
12	2.5	7.7	7	2.9	7.4	9.6	— 6	2	— 10.4
13	5.2	5.1	— 1.2	5.3	7	12.8	0.7	— 2.1	1.7
14	— 6.5	— 6.7	— 4.9	— 3.9	— 0.9	— 13.8	10.5	— 5.6	2.7
15	— 8.3	— 9.3	— 8.1	1.9	— 0.4	— 13.7	16.4	2.8	5.3
16	— 9.2	— 9.7	— 8.1	2.3	0.4	— 5.4	6.1	5.7	5.7
17	— 8.7	— 11.1	— 10.9	— 8.8	— 9.4	— 13.4	4.7	2.1	— 2.2
18	— 8.7	— 6.7	— 2.6	— 5.1	— 3.5	— 14.7	6.2	3.2	— 8.9
19	— 5.6	— 8.6	— 9	— 9.7	— 4	— 13.9	10.4	— 4.7	7.2
20	1.6	— 7.4	— 3.5	12.8	0.9	3.2	5.2	— 1	— 0.5
21	— 10	— 11.5	— 7.7	— 0.5	— 2.5	— 7.8	3.9	— 5	4.9
22	— 5.1	— 6.7	— 5.8	— 2.7	2.2	— 11.3	8.5	— 0.3	— 4.6
23	— 8.7	— 14.1	— 13.6	31.4	29.4	25.5	4	3.9	— 1.8
24	3.4	4.4	1.5	— 3.9	— 2.4	— 2.7	— 4	— 0.4	— 6.1
25	— 1.2	— 6.3	— 4.5	5.1	3.4	— 1.8	4.8	— 3.3	2.6
26	13.2	25.9	10.2	— 22.2	— 14.5	— 2.3	1.7	0.1	4.7
L.S.D.**									
P 5 % ±	5.5	7.5	5.6	4.3	5.8	6.9	5.9	3.1	10.7
P 1 % ±	7.3	9.9	7.3	5.7	7.6	9	7.7	4	14.1
P 0.1 % ±	9.4	12.7	9.5	7.3	9.8	11.6	9.9	5.2	18.3
C.V. %***	4.4	6	4.4	6.3	8	9.2	8.4	4.3	8.6

* For explanation of codes see Table 1.
** Least significant differences as percentages of the Grand Means.
*** Coefficient of variation percentages.

Pops. 3 and 4, *Cupar and Kilsyth, Scotland.* The specimens from pop. 3, were generally smaller than the specimens from pop. 4, and the mean body length for pop. 4 was most similar to that of pop. 9. Also, in most other respects pop. 4 was most similar to that of pop. 9 than to other, geographically more closely related populations.

Pops. 5, 6, 7, 8, 9 and 10, *various locations throughout England.* Much morphometric variation was apparent between these populations. Pop. 5 had mean values for odontostyle, odontophore, spear and tail lengths most similar to pop. 26 from Poland. These values were the largest recorded for these structures during the study. Therefore, pop. 5 was quite unlike any of the other populations from Britain due to its large morphometric means for the aforementioned structures. The British populations described by Goodey, Peacock and Pitcher (1960) were from Kent and Somerset in southeast and southwest England respectively. Pops. 8 and 10 were from southeast and southwest England respectively. However, pops. 8 and 10 and pops. 6 and 7 all had smaller morphometric means for L, odontostyle, odontophore, spear and tail than the values given by Goodey, Peacock and Pitcher (1960).

Pops. 11 and 12, *Wrekin and Nevern, Wales.* Pop. 12 generally had larger morphometric means than pop. 11. Also, these populations in common with all the other British populations had smaller morphometric means for odontostyle, odontophore, spear and tail length than those given by Goodey, Peacock and Pitcher (1960).

Pops. 13 and 24, *Saint-Katherina-Lombeek, Belgium and Holzieken, Switzerland.* The morphometrics of specimens from these two populations were similar (Tab. 3 and 4) and they, together with pops. 10 and 11, constitute a subgroup of populations (Fig. 2, 3, 4 and 5).

Pop. 14, *Kostinbrod, Bulgaria.* This population could be placed in a group comprising pops. 15, 18, 19 and 23 in which the morphometric means for L and spear length were less than 4.5 mm and less than 200 µm respectively. Pops. 14 and 19 had the smallest mean lengths for odontostyle (120 µm) recorded in the study.

Pop. 15, *Les Adrets, France. X. diversicaudatum* is found in field soils in the Camargue and around Montpellier in southern France. To the east of Montpellier, *X. diversicaudatum* was found only in soils in

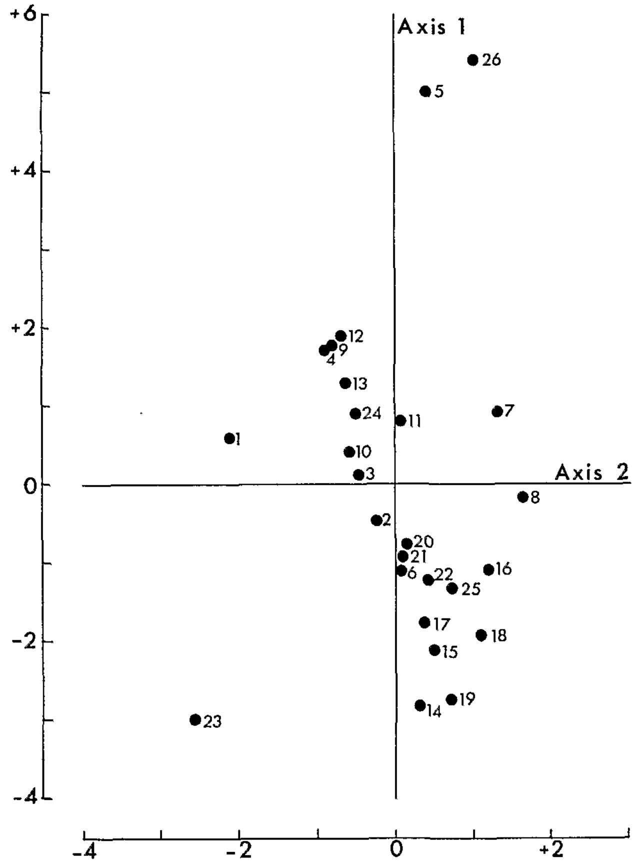

Fig. 2. Distribution of 26 populations of *X. diversicaudatum* relative to axes 1 and 2 of a C.V.A. using the characters L, V, c′, odontostyle and odontophore lengths. The 95 % confidence radius for each population is 0.774.
See Table 1 for key to population number code.

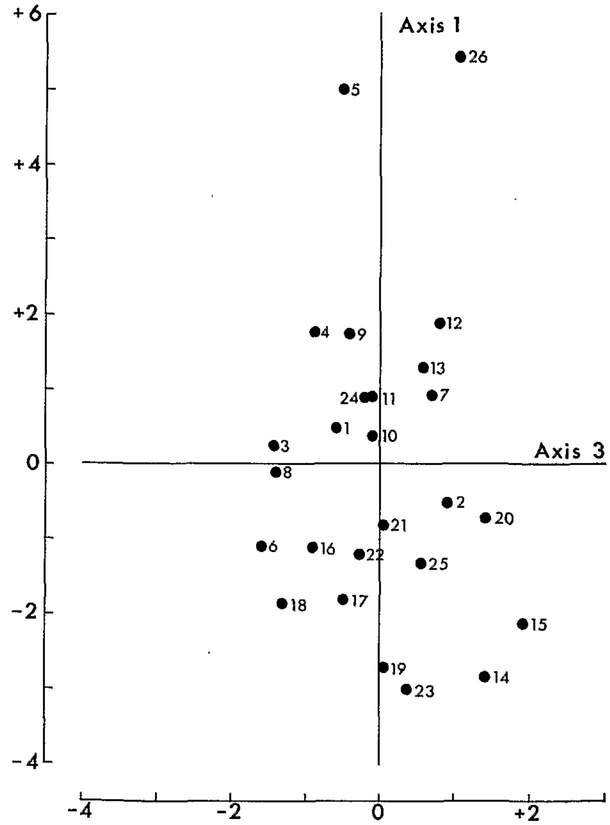

Fig. 3. As for Figure 2 but with axes 1 and 3.

glasshouses and not in the field. Therefore, pop. 15 was probably introduced to Les Adrets and its origins are unknown. The mean value for ratio c′ for pops. 14, 15 and 20 was 1.3, the largest value recorded in the present study for this ratio.

Pops. 16, 17 and 18, *Liguria, Lombardi and Piemonte in northern Italy.* Similar morphometric means were recorded for all three populations. The mean L value for pops. 16 and 18 was 4.1 mm which was the lowest mean L value recorded in the study. Generally, the morphometrics from these three populations were similar to the morphometrics of an Italian population (Martelli & Lamberti, 1967). However, the mean values for odontostyle, odontophore and spear lengths of pops. 16, 17 and 18 were somewhat smaller than those previously reported for the Italian population.

Pop. 19, *Wageningen, The Netherlands.* As with pop. 15, this population was obtained from soil from a heated glasshouse and its origin in unknown although it is believed to be from field soil in the locality (J. W. Seinhorst, pers. comm.). This population had the smallest mean values for odontostyle and spear lengths recorded during the study (120 µm and 195 µm).

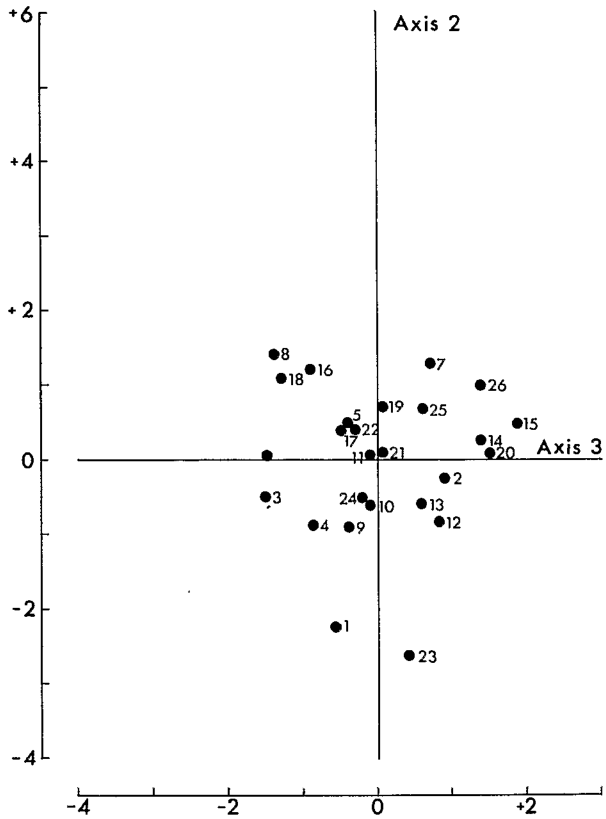

Fig. 4. As for Figure 2 but with axes 2 and 3.

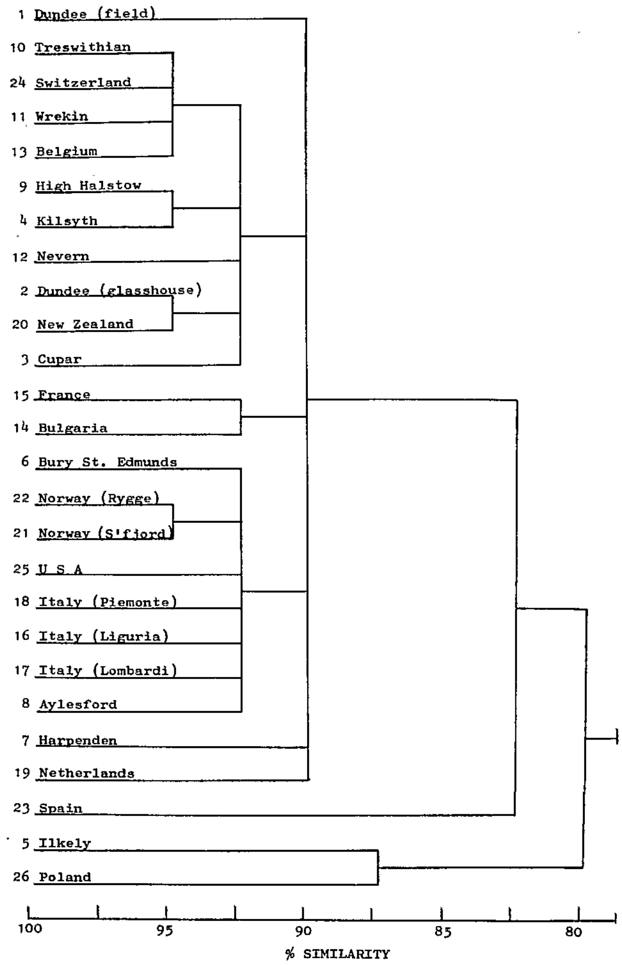

Fig. 5. Dendrogram showing the clustering of 26 populations of *X. diversicaudatum* at different levels of similarity as computed by canonical variate analysis of five morphometric characters. On the scale of similarity 100 = perfect similarity. For exaplanation of population code numbers see Table 1.

Pop. 20, *Alexandra, New Zealand. X. diversicaudatum* appears to have an exclusively European natural distribution but is also present in New Zealand and the U.S.A. Therefore, pop. 20 represents the most geographically distant population from the specie's natural distribution area. However, apart from a somewhat large mean c′ value, similar to pops. 14 and 15, pop. 20 is generally morphometrically similar to many of the other populations studied and was most similar in L, odontostyle, odontophore, spear and tail lengths to pop. 2.

Pops. 21 and 22, *Sandefjord and Rygge, Norway.* These were obtained from the most northern biotopes in Europe at which *X. diversicaudatum* exists. The two populations were morphometrically similar to each other and pop. 21 had the smallest mean value recorded, for V, 40 %, similar to pop. 25.

Pop. 23, *Cazalegas, Spain.* This population was obtained from the most westerly European biotope examined in the study. The nematodes, although similar to specimens from other populations, had the smallest mean values recorded in the study for odontophore length (72 µm) and for tail length (42 µm) and the largest mean values for ratios a (97) and c (117). Pop. 23 could be distinguished from other populations of *X. diversicaudatum* examined in the study by its having small mean values for odontostyle (124 µm), odontophore (72 µm), spear (196 µm) and tail length (42 µm) and a relatively large mean value for body length (5.00 mm).

Pop. 25, *San Diego, U.S.A.* This population is probably a representative of the species having been introduced and surviving outwith its natural European distribution, similar to pop. 20. The morphometric means recorded for this population were similar to those for several other European populations of *X. diversicaudatum* and were most similar to those recorded for pop. 6. Morphometric means given for specimens of *X. diversicaudatum* from the U.S.A. by Goodey, Peacock and Pitcher (1960) differ from the mean values recorded from specimens examined in the present study. For example, the mean values given by these authors are smaller than the values obtained in the present study for L (4.2*vs* 4.6 mm), a (68 *vs* 83), c (90 *vs* 96) and c′ (1.1 *vs* 1.2). Conversely, larger values were given by *ibid.* for lengths of odontostyle (131 *vs* 126 μm), odontophore (86 *vs* 79 μm), spear (217 *vs* 206 μm), tail (50 *vs* 48 μm) and ratio V (45 *vs* 40 %).

Pop. 26, *Nowy Sacz, Poland.* This population had the largest mean length for odontostyle (154 μm), spear (241 μm) and tail (56 μm) recorded in the study and was most similar to pop. 5. The morphometric means given by Szczygiel (1974) for specimens of *X. diversicaudatum* from Poland were all smaller than the values recorded for pop. 26 in the present study.

As all the populations studied were deemed to belong to *X. diversicaudatum* the grand mean for each morphometric was compared with the morphometric means obtained for each population. For structures measured in both males and females the grand means were similar for both sexes. The percentage differences between the morphometric means, obtained from groups of ten females and five males from the different populations studied, and the grand means for the morphometric characters studied are given in Tables 3 and 4. For all but one of the morphometric characters at least one of the populations was statistically significantly different from the grand mean. An exception was T in the males for which no significant differences occurred between the population means and the grand mean.

With females the differences between the smallest and largest morphometric means, expressed as a percentage of the grand means ranged from 10 % for V to 57 % for posterior gonad. Similarly, for males the percentage differences ranged from 21 % for S to 63 % for greatest width. Odontostyle, odontophore, spear, tail and L had averages of 26 % and 30 % differences between the smallest and largest morphometric means for females and males respectively.

The percent coefficient of variation (CV), obtained for the different morphometric structures, measures variation within the populations studied. It was found to be similar for male and female specimens. Spear, odontostyle, odontophore and S CV's were the smallest values obtained and c, c′ and the length of body occupied by the male and female genital tracts had the largest CV values recorded (Tables 3 and 4).

With females, populations 2 and 11 had morphometric means most similar to the grand means, each having only two values significantly different from the corresponding grand means. Populations 5, 23 and 26 had most means significantly different from the grand means. Also, males in populations 5 and 23 had most significantly different mean values when compared with the grand mean values but population 3 had no significant differences between its morphometric means and those of the grand means (Tables 3 and 4).

Table 5

" Importance values "* for five variates used in canonical variate analysis of 26 populations of *X. diversicaudatum.*

Canonical variate	*Axis* 1	2	3
L	− 0.2173	− 1.2142	− 0.0648
V	0.0218	− 0.2739	0.0788
c′	− 0.0817	0.0662	0.9903
Odontostyle	1.4930	0.1555	0.5084
Odontophore	0.7714	0.6490	− 0.1011

* " Importance value " = C.V.A. loading X SD of variate.

MORPHOMETRIC SIMILARITY BETWEEN POPULATIONS OF *X. DIVERSICAUDATUM*

Five morphometric characters, L, V, c′, odontostyle and the odontophore were chosen for use because they had been used by Luc and Southey (1980) and thus a comparison could be made with their results. It is possible that more discrimination between populations could have been obtained using other characters, but the characters used here have value in distinguishuing taxa at the specific level (Luc & Dalmasso, 1976). Figure 2 shows the two-dimensional placings of the 26 populations studied relative to the first two axes of the C.V.A. based on population female means for the five variates. Figures 3 and 4 show similar plots for axis 1 and 3 and 2 and 3 respectively. Although five axes were available 78.4 % of the variance was accounted for by axis 1 and 2 and 91.8 % by axis 1, 2 and 3. Thus, as almost 92 % of the variation between population means were present in the first three axes the final two axes were not plotted.

Although some populations from the same geographical areas e.g. pops. 21 and 22; 15, 16, 17 and 18, were found to cluster together i.e. form morpho-groups, geographic differentiation and morphological differentiation were not correlated. The populations tended to form a homogenous group with some notable outliers e.g. populations 5 and 26 and 23. Table 5 gives " importance values " for each of the five characters used for the analysis; the values were calculated by multiplying the appropriate loading used in the analysis by the standard deviation of the population female means for each character. Odontostyle and odontophore lengths contributed most to the separation of populations on axis 1, L and odontophore lengths on axis 2 and c′ and odontostyle length on axis 3.

The results of a single-linkage cluster analysis are presented in Figures 2, 3 and 4 and as a dendrogram (Fig. 5). Ten populations clustered to form four groups at the 95 % level of similarity; 20 populations formed three groups at 92.5 %; pops. 1, 6 and 18 clustered with these other populations to form groups at 90 %; all of these populations formed a single group and were joined by pop. 23 as a separate outlier, at 82.5 %; pops. 5 and 26 formed a group at 87.5 % but these populations did not cluster with the others until 80 %. Therefore, all of the populations examined in the study formed a single homogenous group at the 80 % level of similarity (Figs. 2, 3, 4 and 5).

Discussion

Much variability between populations is apparent in published morphometrics of *X. diversicaudatum.* By using a standard preparation method the results from the present study suggest that some of the different values reported by the various authors may result from differences between populations of *X. diversicaudatum* and not be entirely caused by fixation artifacts or measurement error (Brown, 1981; Brown & Topham, 1984).

The morphometric variability between populations of *X. diversicaudatum* in the present study was found to be somewhat larger than had previously been reported. For example, the percentage differences between the largest and smallest mean values for tail and spear lengths in the present study were 28 % and 24 % respectively but in published morphometrics of *X. diversicaudatum* the values were only 24 % and 10 % respectively (Brown & Topham, 1984).

Techniques similar to those used to examine the taxonomic status of *X. insigne* and *X. elongatum* by Luc and Southey (1980) were used to establish whether morpho-groups exist among *X. diversicaudatum* populations. Luc and Southey (1980) reported that populations of *X. insigne, X. elongatum* and *X. savanicola* clustered (i.e. formed a morpho-group) at the 75 % level of similarity. Also, they reported that populations of *X. insigne* and *X. elongatum* formed into clusters at the 80 % and higher levels of similarity. In the present study populations of *X. diversicaudatum* clustered at 95, 92.5, 90 and 87.5 % levels of similarity and the morphometrically most different population, pop. 23, from the other populations clustered at the 82.5 % level.

Specimens from all the populations used in the present study appeared to be anatomically similar and differed only in their morphometrics. Therefore, it was concluded that all of the populations belonged to the one species, *X. diversicaudatum.* The morpho-groups of populations established in the present study were therefore considered to be intraspecific groups of *X. diversicaudatum.*

The geographical origin of each population in general did not appear to influence the arrangement of populations into morpho-groups. For instance, although two populations from Norway were grouped together, three populations from Italy were grouped with populations from England and the U.S.A. The morpho-groups of populations of *X. diversicaudatum,* therefore, appeared to be somewhat arbitary and clustered in a way similar to populations of *X. insigne* and *X. elongatum* (Luc & Southey, 1980) i.e. they did not always cluster according to their geographical origin.

The populations did not appear to form any morphometric clines. Populations with generally small morphometric means were recorded from biotopes in relatively close proximity to biotopes with populations with generally large morphometric means. For example, a population from Aylesford, England was morphometrically similar to populations from Italy and France which all had generally small morphometric means. But, a population from High Halstow, England, which is situated about 15 km south west of Aylesford was morphometrically similar to a population from Kilsyth, Scotland and these populations generally had relatively large morphometric means somewhat similar to other British populations. The morphometric differences between the populations from Aylesford and High Halstow may account for the report by Weischer (1964) of « large » and « small » forms of *X. diversicaudatum* from England. Also, it may be speculated that the Aylesford population of *X. diversicaudatum* may be an introduction from elsewhere in Europe as is believed to be the case with *X. pachtaicum* which was identified from nearby orchard soils (Taylor & Brown, 1976).

The results suggest that geographical location *per se* is not likely to be the only factor which determines the final morphometrics of a population of *X. diversicaudatum.* This is demonstrated by the morphometric changes which occurred when specimens from the Dundee (field) population were cultured in a glasshouse. After four years the morphometrics of the population in the glasshouse were significantly smaller than those of the field population. Therefore, it is concluded that biotopic changes e.g. changes in geographical location, plant, host, soil type, climate, etc. can influence significantly the morphometrics of *X. diversicaudatum.*

Plant nematology relies on the « morpho-species » concept in systematics and morphometrics are used as a convenient way of describing mathematically specific structures. Where the morphometric (hence morphological) differences between populations are large and distinct the morphometrically most different populations may be proposed as new « morpho-species ». Many morphometrics used in the taxonomy of the Longidoridae were altered significantly in specimens of *X. diversicaudatum* prepared by different methods for examination by optical microscopy (Brown, 1981; Brown & Topham, 1984). However, in the study examining preparation methods (Brown & Topham, 1984) the ranges of values frequently overlapped between the treatments with the largest and smallest morphometric means. But, in the present study the ranges of values in the populations with the largest and smallest morphometric means for a particular structure often were discontinuous between the two populations. The use of these discontinuities to refer groups of populations to separate specific rank would be inappropriate as females from several of the populations have been successfully cross-bred with males from a Scottish population (Brown, unpubl. results). Thus these populations belong to the one classical biological species. Therefore, with *X. diversicaudatum*, which is an amphimictic species unlike many other species in the Longidoridae which are thelytokous, it is possible to apply the objective biological species concept rather than to rely on the subjective morphological species concept.

ACKNOWLEDGEMENTS

We thank Drs. M. Arias, Spain, C. J. Barber, New Zealand, B. Choleva, Bulgaria, W. A. Coolen, Belgium, J. Cotten, England, A. Dalmasso, France, J. Klingler, Switzerland, D. G. McNamara, England, F. Roca, Italy, J. W. Seinhorst, Netherlands, K. F. Sims, U.S.A., M. Støen, Norway and A. Szczygiel, Poland for supplying cultures of *X. diversicaudatum* and R. J. Clark for help with computing.

REFERENCES

ALVEY, N., GALWEY, N. & LANE, P. (1982). *An Introduction to GENSTAT.* London, Academic Press, 152 pp.

AZMI, M. I. & JAIRAJPURI, M. S. (1978). Morphometric and allometric variations in the adults and juveniles of *Helicotylenchus indicus* Siddiqi, 1962. *Ind. J. Nematol.*, 6 (1976) : 13-22.

BIRD, G. W. & MAI, W. F. (1965). Morphometric and allometric variations of *Trichodorus christiei. Nematologica*, 13 · 617-632.

BROWN, D. J. F. (1981). The effect of operator and measuring system error on the morphometrical variability of one nematode specimen. *Revue Nématol.*, 4 : 169-171.

BROWN, D. J. F. & TOPHAM, P. B. (1984). A comparison of the reported variation in the morphometrics of *Xiphinema diversicaudatum* (Nematoda : Dorylaimida) and the effect of preparing specimens for examination by optical microscopy. *Nematol. medit.*, 12 : 169-186.

COURTNEY, W. D., POLLEY, D. & MILLER, V. L. (1955). T.A.F., an improved fixative in nematode technique. *Pl. Dis. Reptr*, 39 : 570-571.

DE GRISSE, A. T. & LOOF, P. A. A. (1970). Intraspecific variation in some Criconematidae (Nematoda). *Meded. Fak. LandWetens. Gent*, 35 : 41-63.

ERBENOVA, M. (1975). [Ectoparasitic eelworms of the genus *Xiphinema* Cobb in the orchards of the C.S.R.]. *Sbornik U.V.T.I.-Zah-radnictvi (Praha)*, 2 : 79-86.

EVANS, K. & FRANCO, J. (1977). Morphological variation in some populations of potato cyst-nematodes from Europe and South America. *Nematologica*, 23 : 417-430.

FISHER, J. M. (1965). Studies in *Paratylenchus nanus I.* Effects of variation in environment on several morphometric characters of adults. *Nematologica*, 11 : 269-279.

GOODEY, J. B. (1952). The influence of the host on the dimensions of the plant parasitic-nematode *Ditylenchus destructor. Ann. appl. Biol.*, 39 : 468-474.

GOODEY, J. B., PEACOCK, F. C. & PITCHER, R. S. (1960). A redescription of *Xiphinema diversicaudatum* (Micoletzky, 1923 & 1927) Thorne, 1939 and observations on its larval stages. *Nematologica*, 5 : 127-135.

HRZIC, A. (1978). Prispevek k poznavanju nematofaune vinogradniske zemlje Slovenije (*Xiphinema* spp.). *Zast. Bilja*, 29 : 387-396.

LUC, M. & DALMASSO, A. (1976). Considerations on the genus *Xiphinema* Cobb, 1913 (Nematoda : Longidoridae) and a « lattice » for the identification of species. *Cah. O.R.S.T.O.M., Sér. Biol.*, 10 (1975) : 303-327.

LUC, MM. & SOUTHEY, J. F. (1980). Study of biometrical variability in *Xiphinema insigne* Lous, 1949 & *X. elongatum* Schuurmans Stekhoven & Teunissen, 1938; description of *X. savanicola* n. sp. (Nematoda : Longidoridae) and comments on thelytokous species. *Revue Nématol.*, 3 : 243-269.

MARTELLI, G. & LAMBERTI, F. (1967). Le specie di *Xiphinema* Cobb, 1913 trovate in Italie e commenti sulla presenza di *Xiphinema americanum* Cobb (Nematoda : Dorylaimoidea). *Phytopath. medit.*, 6 : 65-85.

McELROY, F. D., BROWN, D. J. F. & BOAG, B. (1977). The virus-vector and damage potential, morphometrics and distribution of *Paralongidorus maximus. J. Nematol.*, 9 : 122-130.

ROHDE, R. A. & JENKINS, W. R. (1957). Effect of temperature on the life cycle of stubby-root nematodes. *Phytopathology*, 47 : 29.

SEINHORST, J. W. (1966). Killing nematodes for taxonomic study with hot F.A. 4 : 1. *Nematologica*, 12 : 178.

SZCZYGIEL, A. (1974). Plant parasitic nematodes associated with strawberry plantations in Poland. *Zesz. Probl. Postep. Nauk. Roln.*, 154 : 1-132.

TARJAN, A. C. & FREDERICK, J. J. (1978). Intraspecific morphological variation among populations of *Pratylenchus brachyurus* and *P. coffeae. J. Nematol.*, 10 : 152-160.

TARTE, R. & MAI, W. F. (1976). Morphological variation in *Pratylenchus penetrans. J. Nematol.*, 18 : 185-195.

TAYLOR, C. E. & BROWN, D. J. F. (1976). The geographical distribution of *Xiphinema* and *Longidorus* nematodes in the British Isles and Ireland. *Ann. appl. Biol.*, 84 : 383-402.

TEPLOUKHOVA, T. N. (1974). [Some data on the nematode vectors of phytopathogenic viruses in the U.S.S.R.]. *Zashch. Rast.*, 41 : 40-45.

TERLIDOU, M. C. (1967). [Nematodes attacking grapevines and their control]. *Vine Inst. Lykovryssi. Kiffisicas, Greece*, 106 p.

WEISCHER, B. (1964). International Symposium on *Xiphinema. Nematol. News*, 6 : 1-6.

Accepté pour publication le 1er octobre 1984.