Journal of Nematology 20(1):47–57. 1988.

Morphological Variation in *Xiphinema* spp. from New York Orchards[1]

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Abstract: *Xiphinema* specimens were collected from orchards in southeastern, northeastern, and western New York. Total length, distance of vulva from anterior end, spear length (odontostyle plus odontophore), body diameter at vulva, tail length, anal body diameter, and length and diameter of hyaline tail tip were measured on fixed, glycerol-infiltrated adult females. Most specimens were identified as *X. americanum* or *X. rivesi*, but one western New York population was identified as *X. californicum* (a new record for New York). Multivariate analyses indicated that, with one exception, western New York populations of both *X. americanum* and *X. rivesi* were smaller and slimmer than their eastern counterparts. Regional differences were generally larger than differences attributed to host species.
Key words: Xiphinema americanum, X. californicum, X. rivesi, Malus pumila, Prunus avium, P. persica, morphology.

Tomato ringspot virus (TmRSV) causes disease in certain apple scion–rootstock combinations (13). Disease prevalence is higher in the Hudson Valley than elsewhere in New York state (12), although susceptible trees are common in all areas. TmRSV is transmitted by *Xiphinema americanum* and *X. rivesi* (1), which have been collected from various sites in the northeastern United States and southeastern Canada (3,4,12), and by *X. californicum* (7,8). There is no key to the 26 species in the complex to which these three species belong (3,9). The species are based on morphological comparisons of preserved specimens from around the world.

Information on environmental influences on morphology is lacking. Environmental factors, notably host species, have been shown to affect the morphology of other plant-parasitic nematodes. Alterations in body length and width are common and occasionally substantial. For example, *Pratylenchus penetrans* specimens from beet were 15% shorter and specimens from pea were 20% stouter than specimens from alfalfa callus cultures (14). Since nematode species are described and identified chiefly on morphological grounds, biologically sound classification schemes must take phenotypic plasticity into account. The present study was undertaken to investigate morphological variation in *Xiphinema americanum* and related species and to determine whether variation in these vector species was correlated with regional differences in the prevalence of TmRSV-incited disease in New York apple trees.

MATERIALS AND METHODS

Sources, preparation, and measurement of specimens: Soil samples were obtained between October 1981 and September 1982 from apple orchards in the three major New York apple-growing regions: the Hudson Valley, the Champlain Valley, and western New York south of Lake Ontario. Thirteen orchards (designated by letters A through M) were included in the initial survey (Table 1, Fig. 1). *Xiphinema* populations generally exceeded 40/100 cm^3 soil. Nematodes were extracted from soil by sugar flotation–centrifugation, heat-killed, fixed in formalin-acetic acid-alcohol (6) or formalin, and slowly infiltrated with glycerol for light microscopy. Total length (L), distance of vulva from anterior end (AV), spear length (S = odontostyle + odonto-

Received for publication 22 January 1987.
[1] Part of a Ph.D. dissertation submitted to Cornell University, Ithaca, NY 14853.
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The author was a National Science Foundation Graduate Fellow during part of this study. She thanks Drs. D. A. Rosenberger and D. Gonsalves for sharing material from their orchard surveys and Drs. C. McCulloch and P. Dixon for advice on statistical analysis. Dr. A. Morgan Golden, United States Department of Agriculture, Beltsville, Maryland; Dr. B. A. Ebsary, Biosystematics Research Institute, Ottawa, Ontario; and Ms. E. Mae Noffsinger, University of California, Davis, California, were consulted concerning the identification of some of the *Xiphinema* populations.

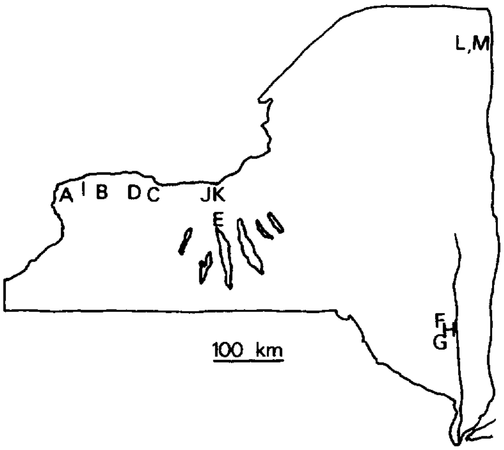

FIG. 1. Location of New York orchards sampled for *Xiphinema* spp.

phore), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), length of hyaline tail tip (JL) and diameter of hyaline tail tip (JD) were measured on 10–25 specimens from each orchard.

Orchards E, F, and C were sampled again in September and October 1984 to investigate the contribution of host plant to morphological variation. Samples were taken from the root zone of apple trees in all three orchards and from the available *Prunus* species (either sweet cherry or peach) in each orchard. All plantings were at least 8 years old. Apple trees were on MM106 rootstocks; peaches were on Halford seedling; and cherries were either definitely (in orchard C) or probably (in orchard E) on Mazzard rootstocks. Samples were taken in herbicide-treated strips or cultivated areas or at depths below the densest root zone under sod and were processed within 3 days of collection. Specimens were fixed in triethanolamine-formalin (6) but otherwise were handled as before. Eighteen females were measured from each host species in all three orchards.

Multivariate analysis: Canonical discriminant analysis (CDA) and principal components analysis (PCA) were performed on log-transformed data. Both analyses generate a series of new variables that are linear combinations of the input variables. Because the analyses were performed on log-transformed data, the generated variables represent ratios of the original untransformed measurements: sums and differences in logarithms are equivalent to products and quotients. The data were transformed solely to exploit this feature of the analysis. CDA was used to generate variables that maximally separated the 13

TABLE 1. Location of New York apple orchards sampled for *Xiphinema* spp., sampling and processing dates, and species recovered.

Orchard	Region†	Sampled	Extracted	Fixative	Species	CU collection number
A	WNY	19 Jul 82	12 Oct 82	FAA	*americanum*	2974
B	WNY	14 Jul 82	13 Aug 82	FAA	*americanum*	2970
C	WNY	29 Jun 82	27 Aug 82	FAA	*californicum*	2963b
D	WNY	13 Jul 82	12 Oct 82	FAA	*americanum*	2973
E	WNY	30 Jun 82	13 Aug 82	FAA	*rivesi*	2969
F	HUD	30 Aug 82	15 Sep 82	FAA	*americanum*	2976
G	HUD	30 Aug 82	22 Sep 82	FAA	mixed ‡	2975
H	HUD	30 Aug 82	10 Sep 82	FAA	mixed‡	2977
I	WNY	21 Jul 82	20 Aug 82	FAA	*rivesi*	2971
J	WNY	8 Jun 82	12 Jun 82	formalin	*americanum*	2961
K	WNY	19 Oct 81	20 Oct 81	formalin	mixed‡	2962
L	CMP	21 Jul 82	30 Jul 82	formalin	*americanum*	2967
M	CMP	21 Jul 82	30 Jul 82	formalin	*rivesi*	2965

Specimens collected from orchards E, F, G, J, and K in 1983 were sent to E. Mae Noffsinger, University of California, Davis. She identified the collections from orchards F and K as mixtures of *X. americanum* and *X. intermedium*, and the collection from orchard J as a mixture of *X. americanum* and *X. rivesi*, but confirmed the author's diagnosis for the collections from orchards E and G (pers. comm.).

† Regions sampled were western NY (WNY), the Hudson Valley (HUD), and the Champlain Valley (CMP).

‡ *X. americanum* and *X. rivesi*.

TABLE 2. Means and standard deviations of measurements of adult female *Xiphinema* spp. from 13 New York apple orchards.

Orchard	n	L (mm)	AV (mm)	S (μm)	DV (μm)	TL (μm)	TD (μm)	JL (μm)	JD (μm)
A	25	1.73	0.90	130	37	33	20	8.8	8.1
		0.09	0.04	3	4	2	1	0.9	0.6
B	25	1.67	0.86	127	35	35	18	8.2	7.2
		0.08	0.05	6	3	2	1	0.8	0.6
C	25	1.89	0.98	140	38	33	20	9.9	8.6
		0.08	0.04	4	2	2	1	0.9	0.9
D	25	1.66	0.87	124	35	35	19	8.3	7.4
		0.07	0.03	3	2	2	1	1.0	0.7
E	25	1.93	1.01	138	40	32	23	8.0	9.9
		0.12	0.06	4	4	3	2	1.0	1.4
F	25	1.74	0.88	118	40	33	21	9.8	8.7
		0.09	0.05	4	3	2	1	1.2	1.1
G	25	1.79	0.93	134	42	33	24	8.2	11.4
		0.15	0.10	12	4	2	3	0.9	2.0
H	10	1.88	0.97	134	41	35	22	8.0	10.1
		0.22	0.12	11	6	2	4	1.1	2.7
I	20	1.94	1.03	137	39	31	21	7.0	8.7
		0.11	0.06	4	4	2	2	1.0	0.9
J	10	1.77	0.91	130	40	35	20	10.7	8.9
		0.09	0.04	6	2	3	1	1.3	1.3
K	15	1.91	0.98	132	46	34	24	8.6	10.3
		0.21	0.10	10	7	3	4	1.2	3.1
L	15	1.80	0.93	126	40	35	21	9.1	8.4
		0.12	0.06	5	4	4	4	1.1	1.9
M	15	1.92	1.02	143	50	30	26	8.7	13.7
		0.09	0.05	3	4	2	2	1.1	1.4

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

populations in the original orchard survey. Two variations of PCA were used with slightly different goals. In the 13-orchard survey, average variability within populations was summarized by PCA of the pooled, within-orchard correlation matrix. In the study of host influence on morphology, total variability was summarized

TABLE 3. Means and standard deviations of measurements of 18 adult female *Xiphinema* spp. from two deciduous tree fruit genera in three New York orchards.

	L (mm)	AV (mm)	S (μm)	DV (μm)	TL (μm)	TD (μm)	JL (μm)	JD (μm)
Orchard C								
Prunus	1.84	0.99	131	43	33	22	7.0	8.4
	0.14	0.07	10	5	2	3	1.2	1.6
Malus	1.76	0.90	125	33	34	18	7.2	6.1
	0.10	0.04	3	3	2	1	1.0	0.8
Orchard E								
Prunus	1.88	0.98	136	41	31	22	6.6	8.9
	0.15	0.08	6	4	4	2	1.1	1.1
Malus	2.00	1.06	143	40	30	22	6.9	8.8
	0.12	0.07	5	4	2	1	0.9	0.8
Orchard F								
Prunus	1.87	0.97	140	44	32	26	6.7	10.8
	0.12	0.07	4	3	2	2	0.9	1.1
Malus	1.78	0.92	117	38	34	21	8.7	7.8
	0.09	0.05	6	2	4	2	1.2	1.0

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

TABLE 4. Canonical discriminant analysis of log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards.

Canonical variable	Canonical correlation	Standardized canonical coefficients							
		L	AV	S	DV	TL	TD	JL	JD
C1	0.850	−0.9	−0.4	−0.8	1.0	0.1	0.9	−0.2	1.0
C2	0.792	−0.6	0.7	1.0	−0.4	−0.3	0.3	−0.5	0.3
C3	0.703	0.6	−1.7	1.6	0.9	0.1	−0.9	0.9	0.1
C4	0.678	−1.4	0.0	0.8	0.2	0.7	−1.0	−0.8	1.2
C5	0.384	2.9	−2.6	−0.1	−0.8	0.5	0.5	−0.2	0.4
C6	0.287	−1.1	1.6	−0.0	0.7	0.9	−0.5	−0.2	−0.0
C7	0.222	−1.5	2.0	−0.4	−1.3	0.1	0.7	0.5	0.6
C8	0.182								

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

by PCA of the overall correlation matrix. Principal components generated by this last analysis were subjected to analysis of variance, and selected contrasts and the Newman-Keuls sequential range test were used for comparison of means.

RESULTS

Specimens from the Hudson and Champlain valleys were identified as *X. americanum* (from orchards F, G, H, L) or *X. rivesi* (from orchards G, H, M). Western New York also yielded specimens of *X. rivesi* (from orchards E, I, K) and *X. americanum* (from orchards A, B, D, J, K). Western specimens of *X. americanum* tended to have longer spears than eastern specimens (Table 2). One western population (C) displayed characteristics of both species. It possessed the greater total length and longer spear of *X. rivesi* but the more acute tail and offset lip region of *X. americanum.* This population was identified as *X. californicum* (Golden, pers. comm.) or *X. floridae* (Ebsary, pers. comm.). The species was not recovered from samples collected from this orchard in 1984 (Table 3).

TABLE 5. Comparison of selected ratios with variables generated by canonical discriminant analysis and principal components analysis of log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards.

Generated variable	Ratio	Correlation
C1	$\frac{DV*TD*JD}{L*S}$	0.817
C2	S	0.887
C3	$\frac{S*DV*JL}{AV*TD}$	0.780
C4	$\frac{S*TL*JD}{L*TD*JL}$	0.742
P1	L	0.864
P2	TL*JL	0.968
P3	$\frac{TL}{JL*JD}$	0.956

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

Regional variation: All the canonical correlations except the last were significant ($P < 0.05$), but the first four canonical variables were more important than the rest (Table 4). Variables similar to these four were generated by an analysis of part of the data (from orchards A–G: results not shown). In pairwise plots of orchard means (Fig. 2), the first canonical variable separated orchards by geographical region. The mean of this variable was positive for all Hudson Valley (F, G, H) and Champlain (L, M) orchards, whereas it was positive for only one western New York orchard (K). The first canonical variable was interpreted as a ratio between the three diameter measures combined (DV, TD, JD) and body and spear lengths combined (L, S) (Table 5).

The second canonical variable discriminated between species primarily on the basis of spear length. *X. americanum* populations (from orchards A, B, D, F, J, L) had negative values, whereas *X. rivesi* populations (from orchards E, I, M) and the population from orchard C had positive values of this variable. In a scatterplot of selected populations (Fig. 3), the two species lay on separate arms of a V, with populations from eastern orchards F and M on top and populations from western orchards B, C, and E on the bottom, and with the population from orchard C at the vertex but aligned with the *X. americanum* arm. Tail measurements were an important component of both the third and fourth canonical variables (Tables 3, 4), but neither shed further light on interspecific or interregional variation (Fig. 2b).

In PCA, the first principal component had by far the largest eigenvalue, and the first three principal components together accounted for about 82% of the trace of the correlation matrix (Table 6). As in CDA, principal components similar to these three were generated by interim analyses on data from orchards A–F and A–G (results not shown).

Because all elements in the first component's eigenvector were positive, the variable was interpreted as a general measure of size. When orchard means of the first principal component were plotted (Fig. 4a), the species separated according to their sizes. *X. rivesi* (from orchards E, I, M) was larger than *X. americanum* (from orchards A, B, D, F, J, L). The population from orchard C fell between *X. americanum* and *X. rivesi.* Eastern New York populations of both *X. americanum* and *X. rivesi* tended to be larger than their western counterparts. Scatter about means of the first two principal components is shown for selected populations (Fig. 5). The second and third principal components were interpreted as measures of tail size and shape, respectively (Table 5). The species also separated in a plot of these two variables (Fig. 4b). *X. rivesi* (from orchards E, I, M) was nearest the origin, followed by the mixed-species populations (from orchards G, H, K); *X. americanum* (from orchards A, B, D, F, J, L) and

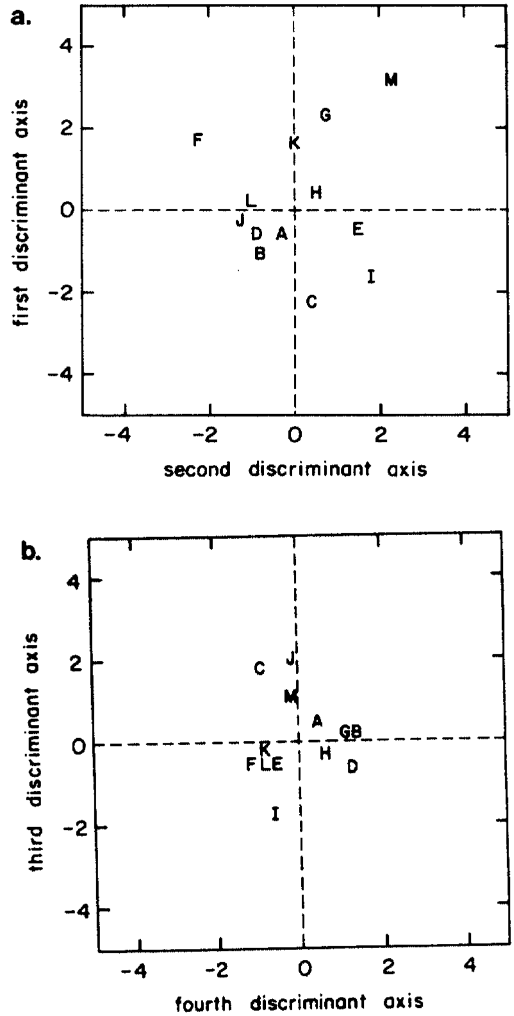

FIG. 2. Canonical discriminant analysis of log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards: pairwise plots of orchard means of canonical variables one through four. See Table 1 and Figure 1 for orchard locations. a) First and second discriminant axes. b) Third and fourth discriminant axes.

the population from orchard C were farthest from the origin.

Host influences on morphology: In 1984, *X. americanum* was recovered from apple in orchards C and F, *X. rivesi* was recovered from peach in orchard F and from both cherry and apple in orchard E, and both species were recovered from cherry in orchard C (Table 3). Pure populations of the same species were recovered from both hosts only in orchard E (*X. rivesi*). The magnitude of the difference in morphology due

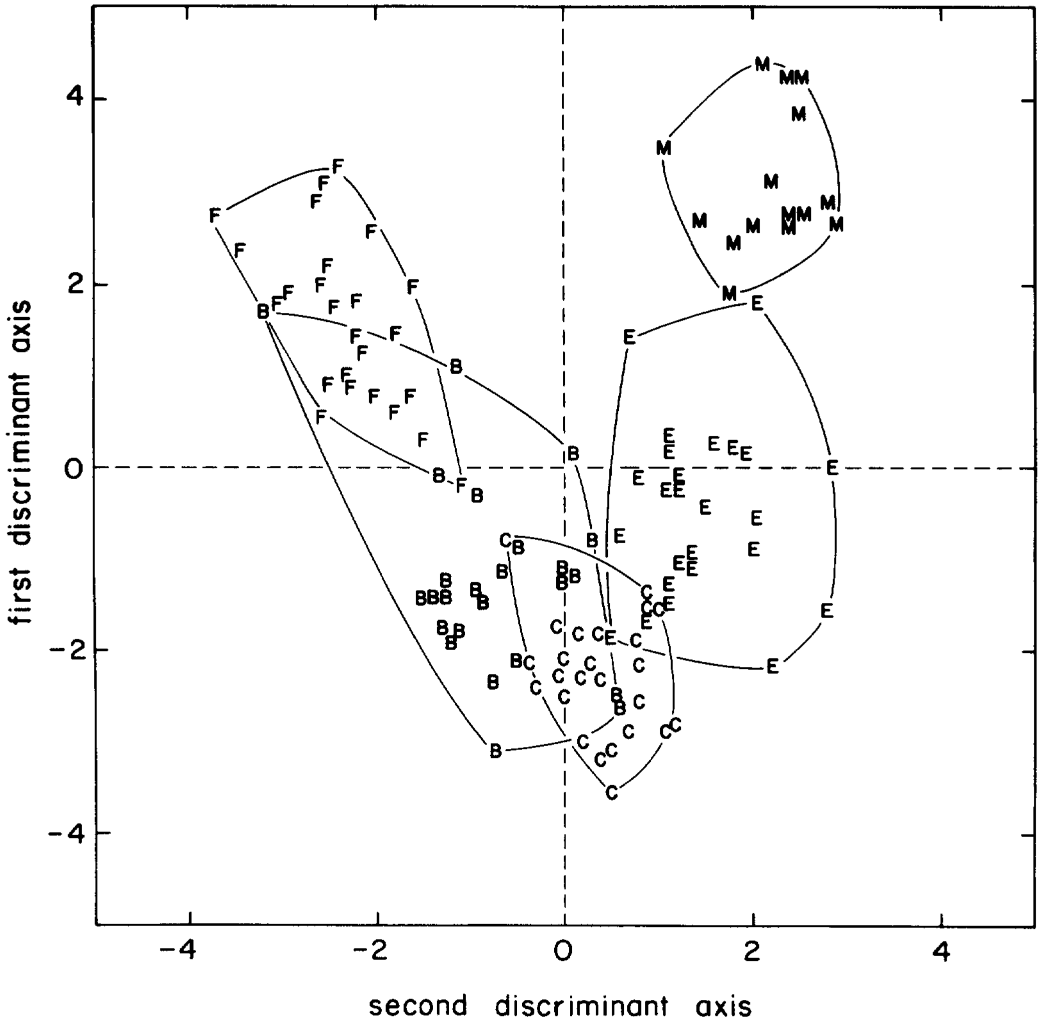

FIG. 3. Canonical discriminant analysis of log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards: scatterplot of the first two canonical variables for five populations. See Table 1 and Figure 1 for orchard locations.

TABLE 6. Principal components analysis of the pooled within-orchard correlation matrix for log-transformed measurements of adult female *Xiphinema* spp. from thirteen New York apple orchards.

Principal component	Eigenvalue	Eigenvectors							
		L	AV	S	DV	TL	TD	JL	JD
P1	4.277	0.4	0.4	0.4	0.4	0.0	0.4	0.0	0.4
P2	1.160	−0.0	−0.0	−0.0	−0.1	0.6	0.1	0.8	0.1
P3	1.087	0.1	0.1	0.1	0.0	0.7	0.1	−0.5	−0.5
P4	0.527	0.2	0.2	−0.6	0.6	0.0	−0.2	0.2	−0.2
P5	0.423	0.3	0.4	0.3	−0.3	−0.1	−0.6	0.2	−0.4
P6	0.300	−0.3	−0.2	0.5	0.5	−0.2	0.1	0.3	−0.5
P7	0.167								
P8	0.059								

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

to host (*X. rivesi* in orchard E) was compared to the difference between species on different hosts (in orchard F) and to the differences within a species from different regions (*X. americanum* on apple in orchards C, F, and *X. rivesi* on *Prunus* spp. in orchards E, F).

A substantial portion of the total variation in adult measurements was represented by the first three principal components (Table 7). The first principal component was a measure of body size relative to tail size or shape; the second, a measure of tail size; and the third, a measure of length relative to diameter. There were significant differences ($P < 0.05$) between populations of *X. rivesi* from different hosts in orchard E in both the first and third principal components (Table 8). For the third principal component, the difference due to host was larger than the interregional differences between *X. americanum* populations on apple (orchards C, F) or *X. rivesi* populations on *Prunus* spp. (orchards E, F). In neither case was the difference between populations of the same species on different hosts greater than the difference between species on different hosts (orchard F).

Discussion

This study confirms and extends an earlier report of *X. americanum* and *X. rivesi* from the Hudson Valley (12). The two species were again recovered from several of the orchards mentioned in that report. Both species were also found in orchards in western and northeastern New York. Western New York populations of *X. americanum* possessed somewhat longer spears than the topotypes (9). In this respect they resembled a Canadian population, probably from Ontario (3), studied by Lamberti and Bleve-Zacheo (9). Authorities disagreed on the identity of population C, but Golden's diagnosis of *X. californicum* was preferred because topotypes of both *X. californicum* and *X. floridae* were available to him for comparison. *X. californicum* is also a known vector of TmRSV (7,8). Neither

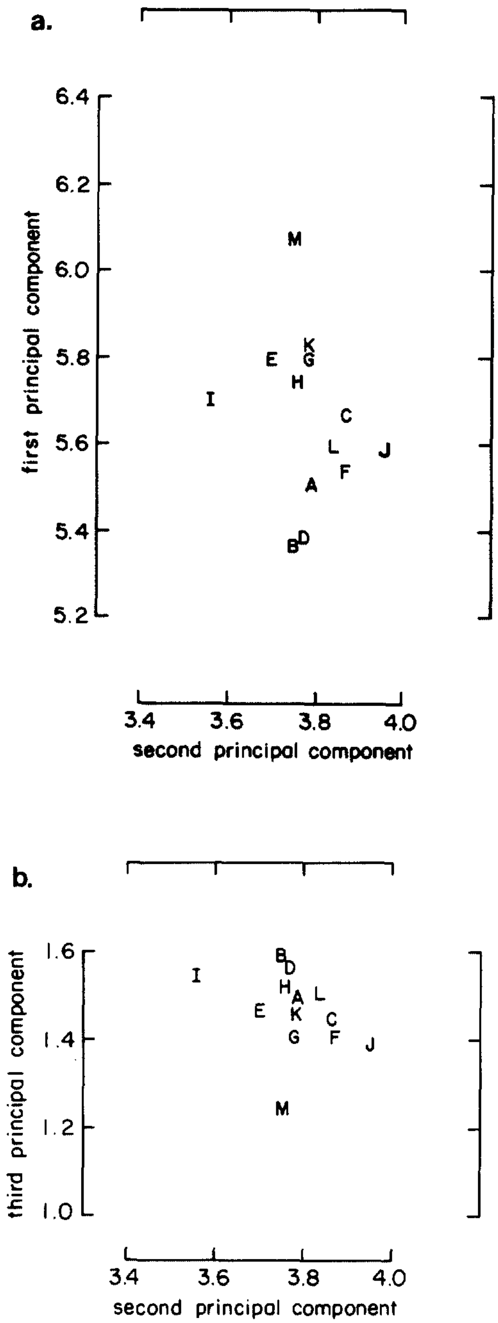

FIG. 4. Principal components analysis of the pooled within-orchard correlation matrix for log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards: pairwise plots of orchard means of principal components one through three. See Table 1 and Figure 1 for orchard locations. a) First and second principal components. b) Second and third principal components.

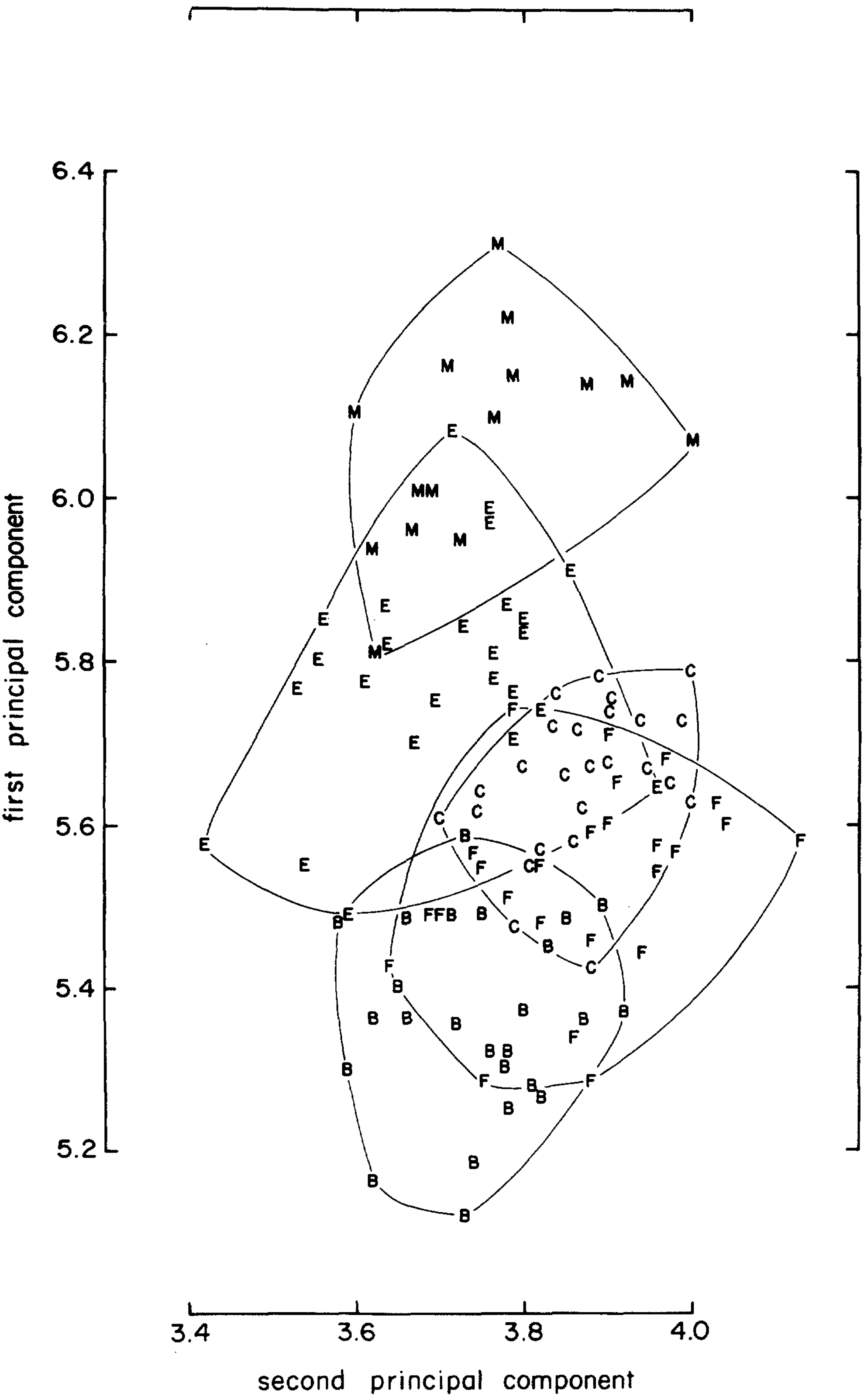
6.4
6.2
6.0
5.8
5.6
5.4
5.2
first principal component
3.4
3.6
3.8
4.0
second principal component

TABLE 7. Principal components analysis of log-transformed measurements of adult female *Xiphinema* spp. from two deciduous tree fruit genera in three New York orchards.

Principal component	Eigen-value	Eigenvectors							
		L	AV	S	DV	TL	TD	JL	JD
1	4.250	0.4	0.4	0.4	0.4	−0.1	0.4	−0.2	0.4
2	1.367	0.0	−0.0	−0.2	0.2	0.6	0.3	0.6	0.3
3	0.983	0.5	0.5	0.0	−0.1	0.4	−0.3	0.1	−0.5
4	0.697	0.1	0.2	0.0	−0.0	−0.6	−0.3	0.7	0.2
5	0.449	−0.1	−0.1	0.7	−0.6	0.2	0.0	0.1	0.2
6	0.151	−0.3	−0.1	0.5	0.6	0.1	−0.2	0.2	−0.4
7	0.070								
8	0.033								

Total length (L), distance of vulva from anterior end (AV), spear length (S), body diameter at vulva (DV), tail length (TL), anal body diameter (TD), and length (JL) and diameter (JD) of hyaline tail tip.

X. californicum nor *X. floridae* has been reported previously from New York.

One objective of this research was to determine whether morphological or specific differences existed between *Xiphinema* spp. populations from apple orchards in the Hudson Valley, where TmRSV-incited disease in apple is serious, and those from more northern orchards near Lake Ontario and Lake Champlain, where TmRSV has caused less damage. Although regional differences were detected, the distinction was between east and west rather than between north and south. The one western New York population that resembled eastern New York populations came from orchard K, where TmRSV-incited disease had been diagnosed. Apart from this orchard, the correlation between the geographical distribution of morphological types (east versus west) and diseased trees (south versus north) was poor. Orchard selection was biased in favor of those with high populations of *Xiphinema* spp. Since viruses can be transmitted experimentally by individual vectors, this selection may have excluded epidemiologically significant populations; however, even under experimental conditions, transmission is more likely with greater numbers of vectors.

TABLE 8. Morphological comparison of adult female *Xiphinema* spp. from two deciduous fruit tree genera in three New York orchards: population means and contrasts of selected principal components.

	Principal component		
	1	2	3
Means			
Orchard C			
Prunus	0.460 c	0.236 ab	0.225 bcd
Malus	−2.612 a	−0.564 a	0.733 d
Orchard E			
Prunus	0.667 cd	−0.539 a	−0.336 b
Malus	1.541 d	−0.636 a	−0.574 cd
Orchard F			
Prunus	1.678 d	0.384 b	−1.159 a
Malus	−1.733 b	1.119 c	−0.037 bc
Contrasts			
Orchard E *Malus*–orchard E *Prunus*			
$t(102)$	2.015	−0.291	3.490
P	< 0.05	ns	< 0.001
Orchard F *Prunus*–orchard E *Prunus*			
$t(102)$	2.331	2.772	−3.156
P	< 0.025	< 0.01	< 0.005
Orchard F *Malus*–orchard C *Malus*			
$t(102)$	2.027	5.054	−2.953
P	< 0.05	< 0.001	< 0.005

Means in the same column followed by the same letter are not significantly different ($\alpha = 0.05$) according to Newman-Keuls sequential range tests.

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FIG. 5. Principal components analysis of the pooled within-orchard correlation matrix for log-transformed measurements of adult female *Xiphinema* spp. from 13 New York apple orchards: scatterplot of the first two principal components for five populations. See Table 1 and Figure 1 for orchard locations.

In the 13-orchard survey, there was some concern that differences in dates of collection or duration of storage might have contributed to the differences observed in specimens from different localities. The original samples from western New York orchards were generally collected earlier in the season and stored longer before processing than samples from eastern New York orchards (Table 1). Interregional differences persisted, however, even when variation in collection dates and duration of storage were greatly reduced. *X. americanum* from western New York were smaller and slimmer than their eastern New York counterparts. Limited data indicated that at least the size differential was already apparent in first-stage juveniles (results not shown). This stage is less variable than adults from the same population (11).

The results of the 13-orchard survey were stable to the addition of data and were repeatable. Analyses of two separate data sets (from 1981–82 and from 1984) generated variables interpreted as measuring slimness. The third principal component in the follow-up study was roughly the reciprocal of the first canonical variable in the 13-orchard survey. This variable also showed the clearest evidence of the host's influence on morphology, but even here there was a broad area of overlap in the ranges of values for individuals from the two hosts. Differences attributable to host plant were usually smaller than interregional differences and were always smaller than interspecific differences.

The selection of characters by CDA (spear length) and PCA (size and tail measurements) for distinguishing the species of *Xiphinema* in this study reflected more traditional approaches to species identification. These dimensions were selected for their clarity and freedom from obvious artifact in addition to their importance in previous taxonomic studies. Characters with little variation within species are normally preferred, but that is not true of the characters (e.g., size and tail measurements) selected by PCA. Malik and Jairajpuri (11) also found length and tail measurements to be moderately variable. The ratio between the length and diameter of the hyaline tail tip was useful in distinguishing *X. rivesi* from the other two species. Although this ratio was not selected by CDA or PCA of all eight dimensions, it was selected over either dimension alone or their product when only these two dimensions were subjected to CDA (canonical correlation = 0.776). The sensitivity of the c′ ratio (TL/TD) to coverslip pressure has been clearly demonstrated (5). Because the hyaline tail tip is entirely cuticular, the proposed ratio (which could be designated c″) should be less prone to distortion.

Compared with other studies of interspecific and intraspecific variation in *Xiphinema* species in which similar analyses were performed (2,10), CDA failed to separate the species clearly. The monosexual species *X. elongatum, X. insigne,* and *X. savanicola* showed no overlap on a plot of the first two canonical variates for individual specimens from 30 populations (10). In contrast, my results showed a continuum from eastern (F) to western (B) populations of *X. americanum,* through *X. californicum* (C), to *X. rivesi* (E, M) when individual values of the first two canonical variables were plotted (Fig. 3). Greater divergence from the grand mean was found in a study of 26 populations of one bisexual species, *X. diversicaudatum* (2), than was obtained in my study of three monosexual species. Results of PCA should have provided the most compelling evidence of morphological differences among the New York species studied here. Several of the populations were species mixtures, so an analysis designed to separate populations (CDA) is not wholly satisfactory for comparing species. If CDA is used to separate essentially identical populations, it generates variables that magnify insignificant differences. Because the variables generated by PCA maximize within-population variation, populations that take on different values of these variables can be assumed to be genuinely different. Although there were differences in principal component means, the scatterplot from this analysis (Fig. 5) showed substantial overlap among species. Unless significant biological differences are found, the classification of species in the *X. americanum* complex should probably be reconsidered.

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