Morphometric and Serologic Comparisons of a Number of Populations of Cyst Nematodes[1]

R. D. Riggs, L. Rakes, and M. L. Hamblen[2]

Abstract: Thirty-five populations of *Heterodera glycines* and populations of 15 other *Heterodera, Globodera,* and *Punctodera species* were studied morphometrically and some were compared serologically. There was a wide range of each measurement within each nematode population. Except for one soybean cyst nematode population from Indiana, which was a tetraploid and considerably larger than the others, morphometric measurements overlapped. In a discriminant function comparison most of the populations were closely grouped but at least three were rather distinctly separated. Morphometrically *H. fici, H. cruciferae, H. schachtii,* and *H. trifolii* were closely associated with *H. glycines.* Serology indicated a close relationship between *H. glycines, H. lespedezae, H. trifolii, H. schachtii,* and the *Heterodera* sp. from Rumex, while *H. betulae* appeared to be more distantly related. *Key words: Heterodera glycines, Globodera, Punctodera,* races.

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Soybean cyst nematode (*Heterodera glycines* Ichinohe 1952) (SCN) was first reported in the United States in 1954 (14). In subsequent years its known distribution has expanded to cover most of the soybean-producing area (7,10).

Morphological comparisons between populations of SCN from different parts of the world have been limited. Miller (8,9) compared morphological characteristics of 11 geographic isolates of *H. glycines.* He measured selected characteristics of eggs, second-stage larvae, males, and females. The lowest and highest average dimensions obtained for each of the characters of the 11 isolates were significantly different ($P = 0.01$). However, the range of measurements overlapped for each character from any 2 of the 11 isolates compared. He also ran correlation coefficients to determine the degree of interrelationships between measurements of the various characters. While many were significantly correlated, only a few comparisons of pairs of morphometric characters had a high degree of correlation for all of the isolates. Therefore, he concluded that the use of ratios to characterize isolates of *H. glycines* is limited. Golden and Epps (1) also found variation in tail and tail terminus measurements in five geographics isolates of *H. glycines.*

Koliopanos and Triantaphyllou (6) studied the second-stage larval (L_2) length, tail length, and tail terminus length of populations of *H. glycines* from North Carolina, Virginia, Arkansas, and Tennessee. The body length varied, but the average body length was used to divide the species into two groups, with the Arkansas population in one group and the other three in another group. Tail length measurements had three significantly different groups with the Tennessee and Virginia populations in the same group. Tail terminus measurements were significantly different between all four groups.

Hirschmann (3) investigated the morphological difference between *H. glycines* and *H. trifolii.* The cysts were similar in measurements and in wall pattern but there were differences in measurements of second-stage larvae. *Heterodera trifolii* L_2 were longer; had longer stylets, tail, and tail termini; and had a greater distance from the stylet knobs to the dorsal gland orifice (DGO).

This study compares the morphometrics and serological reactions of several populations of SCN and of *H. glycines* with several other *Heterodera* and *Globodera* spp. The purpose was to examine similarities and differences under similar conditions for development and measurement in an attempt to find an aid in taxonomic separation within this group.

MATERIALS AND METHODS

Fifty-five populations of cyst nematodes (35 *H. glycines,* one or more populations

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[2]Respectively, Professor and Research Assistants, Department of Plant Pathology, University of Arkansas, Fayetteville, AR 72701.

from each state in which SCN infestations were known, and 20 populations of other species) were used in this study (Table 1). Each cyst population was reared under greenhouse conditions on specific hosts (Table 1).

The following measurements were made for morphological comparisons of the populations: egg numbers in female and in egg masses, cyst length and width, L_2 length and width, tail terminus length, stylet length, and distance from stylet base to DGO. Measurements were made on nematodes selected from actively developing cultures. Twenty-five cysts were selected at random from each population, and egg counts and cyst measurements were made. Four larvae were selected at random from each cyst for L_2 measurements. The measurements of the four larvae were averaged in all measurements analyzed by various statistical methods to determine the relationships. The measurements of the SCN populations were subjected to a BMDP stepwise discriminant function analysis to determine whether the different populations could be associated by measurement with recognized physiological races of *H. glycines*. The measurements of all populations of cyst nematode species were grouped in a dendrogram (5), then the groups were checked by a discriminant function analysis. Finally, all measurements for all species were subjected to an analysis of variance.

Nematodes for serological studies were obtained and immunoelectrophoresis tests were run as described previously (12).

RESULTS

An analysis of variance demonstrated significant differences between populations of SCN in each character measured (Table 2). Population SCN-12A was significantly different from other populations in most factors, but this would be expected of a tetraploid (13). Except for most characters of SCN-12A, there was overlap between populations. When the SCN populations were compared to populations of other species there was an intermingling of measurements (Table 3). There were significant differences, but the differences were not always between species.

The discriminant function analysis used five of the nine factors for the grouping of SCN populations by races. The factor used first in the step-wise separation was L_2 stylet length followed by L_2 body width, tail terminus length, stylet base to DGO, and cyst width. This analysis of 34 SCN populations revealed that no consistent grouping into races could be made based on the morphometric measurements used in this study (Table 4). However, measurements of Race 1 (2) population (Table 1, SCN 13) were distinct enough from other populations that the analysis placed all 25 individuals in Race 1 and all were a "good fit." Nineteen of the 25 Race 2 (SCN 6A) individuals were identified as Race 2 by the measurements, but only 17 were a "good fit." Measurements of Races 3 (SCN 1) and 4 (SCN 2) were not distinctive (Table 4).

The discriminant function analysis was plotted two-dimensionally to demonstrate the relative separation of the 34 SCN populations (Fig. 1) and also to show the relationship of the four races of SCN to the other cyst-forming species measured (Fig. 2). The comparison of measurements of SCN indicated that most populations were fairly closely grouped, but certain populations were more distantly removed from the mean of the group. A study of the relationship of other species with the four designated races of SCN and each other revealed a progressive separation (Fig. 1). CRCN and FCN appeared to be closely related to SCN and to each other. LECN, BCN, CCN, and BGCN were more distantly removed. LECN appeared to be about intermediate between CCN and BCN. BCN was well separated from the others, but was closer to LECN. BGCN and LECN were relatively unrelated. The populations most distantly removed from SCN were KCN, SACN, and RCN. They were not closely associated with the other species or with each other.

All populations were grouped into eight groups using SAS dendogram analysis (5) of the measurements (Table 5) and were subjected to a discriminant function analysis to test the fit within the group. Cyst width was the character selected first as a discriminating factor followed by cyst length, L_2 length, and number of eggs in body. Three populations did not fit into

Table 1. Cyst nematode (*Heterodera* spp., *Globodera* spp., and *Punctodera punctata*) populations used in this study, their geographic origin, and the hosts upon which they were maintained.

Population	Geographic origin	Host
H. glycines		
SCN-1	Arkansas	Lee Soybean
SCN-1A	Arkansas	Lee Soybean
SCN-1B	Arkansas	Lee Soybean
SCN-2	Arkansas	Pickett Soybean
SCN-2A	Arkansas	Pickett Soybean
SCN-2B	Arkansas	Pickett Soybean
SCN-2D	Arkansas	Pickett Soybean
SCN-3	Japan	Lee Soybean
SCN-3A	Japan	Pickett Soybean
SCN-3B	Japan	Pickett Soybean
SCN 4	Tennessee	Lee Soybean
SCN-4A	Tennessee	Pickett Soybean
SCN-5	Louisiana	Lee Soybean
SCN-6	Virginia	P.I. 91684 Soybean
SCN-6A	Virginia	Pickett Soybean
SCN-6B	Virginia	P.I. 91684 Soybean
SCN-6C	Virginia	P.I. 91684 Soybean
SCN-7	Kentucky	Lee Soybean
SCN-8	Florida	Lee Soybean
SCN-9	Mississippi	Lee Soybean
SCN-10	Missouri	Lee Soybean
SCN-10A	Missouri	Pickett Soybean
SCN-10B	Missouri	Pickett Soybean
SCN-11	Illinois	Lee Soybean
SCN-11A	Illinois	Pickett Soybean
SCN-11B	Illinois	Pickett Soybean
SCN-12	Indiana	Lee Soybean
SCN-12A	Indiana	Lee Soybean
SCN-13	North Carolina	Lee Soybean
SCN-13C	North Carolina	Lee Soybean
SCN-15	South Carolina	Lee Soybean
SCN-15A	South Carolina	Lee Soybean
SCN-16	Alabama	Lee Soybean
SCN-16A	Alabama	Lee Soybean
SCN-16B	Alabama	Lee Soybean
Globodera solanacearum		
OCN	Virginia	*Solanum dulcamara*
G. tabacum		
TCN	Virginia	*Nicotiana tabacum*
G. virginiae	Virginia	*Solanum carolinense*
H. betulae		
BCN-1	Arkansas	*Betula niger*
BCN-2	Arkansas	*Robinia Pseudoacacia*
H. cajani		
CACN	Egypt	*Cajanus cajan*
H. cruciferae		
CRCN	California	*Brassica oleracea* var. *capitata*
H. fici		
FCN	Virginia	*Ficus*
H. graminophila		
BGCN	Louisiana	*Echinochloa*
H. lespedezae		
LECN	North Carolina	*Lespedeza striata*

Table 1. (Continued)

Population	Geographic origin	Host
H. leuceilyma		
SACN	Florida	*Stenotaphrum secundatum*
H. schachtii		
SBCN-1	California	*Beta vulgaris*
SBCN-2	Florida	*Brassica oleracea* var. *capitata*
H. trifolii		
CCN-1	Kentucky	*Trifolium pratense*
CCN-2	Arkansas	*Trifolium repens*
H. weissi		
KCN-1	Illinois	*Polygonum pennsylvanicum*
KCN-2	Arkansas	*Polygonum pennsylvanicum*
Heterodera sp.		
RCN-1	Arkansas	*Rumex crispus*
RCN-2	Arkansas	*Rumex crispus*
Punctodera punctata		
GCN	Texas	*Poa annua*

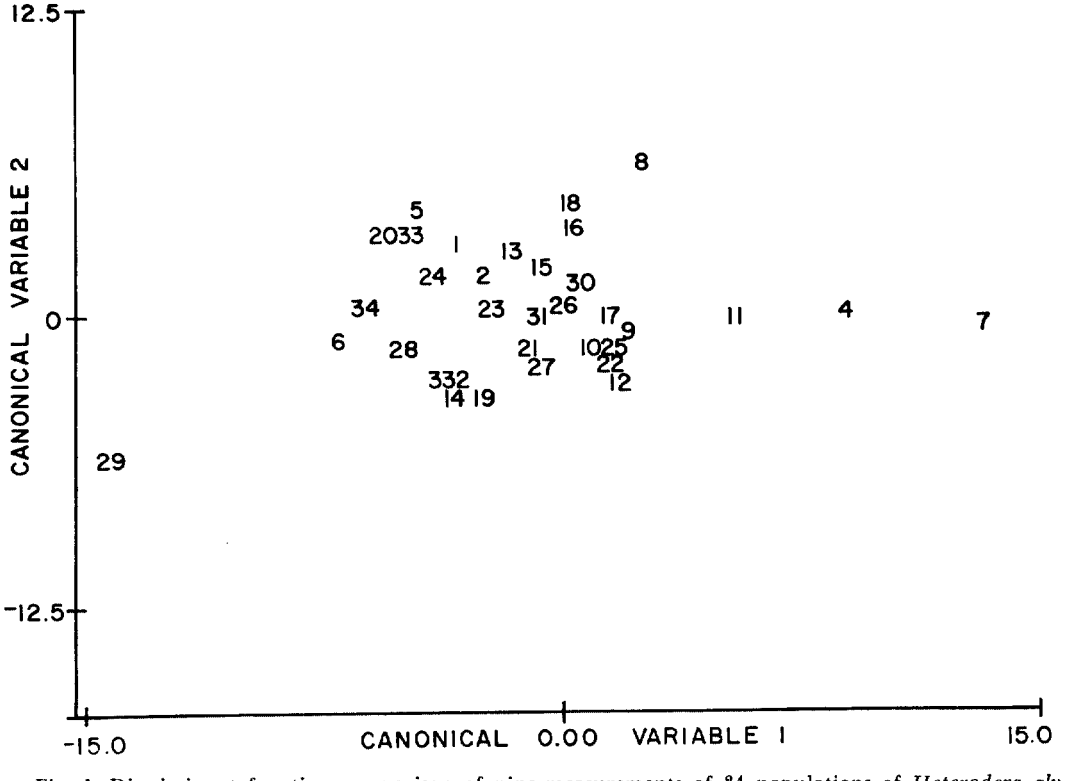

Fig. 1. Discriminant function comparison of nine measurements of 34 populations of *Heterodera glycines* from the United States and Japan. (Populations 1–34 correspond to the SCN populations in Table 4.)

Table 2. Average egg counts and cyst and larval measurements for 35 collections of *Heterodera glycines*.

Collection	Eggs*		Cyst		Larval†				
	Body	Mass	L	W	L	W	DGO	TT	Stylet
SCN-1	117	0	740	496	459	22.5	4.6	26.9	22.8
SCN-1A	77	1	623	437	402	21.3	4.2	21.8	21.6
SCN-1B	137	8	714	530	426	21.1	4.7	22.8	22.1
SCN-2	120	0	730	500	454	21.9	4.7	26.6	23.0
SCN-2A	77	1	615	413	452	21.0	4.7	27.3	23.3
SCN-2B	108	0	691	485	447	24.3	4.1	27.6	23.1
SCN-2D	172	3	805	554	460	22.7	4.7	28.5	23.7
SCN-3	135	2	689	514	431	21.1	4.6	24.8	23.5
SCN-3A	116	1	714	503	514	24.2	5.3	29.2	24.6
SCN-3B	117	39	704	511	497	22.5	5.3	27.7	24.2
SCN-4	104	2	642	448	450	22.0	4.7	26.6	23.0
SCN-4A	106	12	688	457	431	20.0	5.0	24.9	22.9
SCN-5	149	3	711	483	467	22.3	4.9	28.4	23.3
SCN-6	176	6	746	506	463	23.7	4.5	27.3	23.4
SCN-6A	125	6	744	531	447	20.8	4.8	24.9	22.9
SCN-6B	116	0	738	527	482	22.8	5.0	27.9	23.9
SCN-6C	85	1	572	391	428	21.5	4.5	21.2	23.2
SCN-7	146	12	765	544	445	20.8	4.8	26.3	23.1
SCN-8	138	12	711	485	438	23.7	4.7	24.7	22.6
SCN-9	132	5	689	499	439	20.8	4.7	27.4	23.2
SCN-10	154	3	791	548	472	21.5	4.8	28.9	23.7
SCN-10A	123	1	710	465	465	21.5	5.0	27.3	23.2
SCN-10B	146	2	686	488	440	21.5	4.5	25.7	22.5
SCN-11	140	8	776	539	472	21.3	4.6	28.8	23.5
SCN-11A	140	3	691	493	443	21.0	4.4	27.8	23.0
SCN-11B	145	2	798	519	457	21.3	4.7	28.4	23.2
SCN-12	112	7	761	521	440	20.8	4.7	25.3	22.6
SCN-12A	126	5	891	527	633	24.1	7.8	36.2	27.2
SCN-13	115	4	753	490	494	21.2	4.7	30.3	24.2
SCN-13C	86	0	679	510	469	21.3	6.1	26.7	22.1
SCN-15	192	23	746	524	464	22.0	4.5	27.2	23.3
SCN-15A	176	12	721	496	475	21.5	4.7	27.2	23.3
SCN-16	137	0	737	501	447	20.7	5.0	25.8	23.1
SCN-16A	129	8	655	438	449	21.6	4.7	24.7	22.5
SCN-16B	109	31	722	483	430	20.7	4.7	25.1	22.1
LSD .05	18.6	6.2	39.7	27.5	14.0	1.0	0.2	1.1	0.4
C.V.	26.5	190.0	9.9	10.0	5.4	8.1	8.4	7.6	3.2
S.D.	33.5	11.2	71.6	49.5	25.2	1.8	0.4	2.1	0.7

*Egg counts and cyst measurements are averages of 25 individuals. L = length, W = widest width.
†Larval measurements are averages of 4 individuals from each of 25 females. L = length, W = greatest width; DGO = distance from stylet base to dorsal gland orifice; TT = length of hyaline tail terminus.

the group in which they had been placed by dendrogram analysis (Fig. 3). According to the discriminant function, SCN-13 fit better into group 4, SCN-13C into group 3 and SCN-16A into group 1.

The populations were then placed into groups consisting of HNCN, OCN, TCN; KCN-1, KCN-2, FCN; BCN-1, BCN-2; GCN, BGCN, SACN; CCN-1, CCN-2, RCN-1, RCN-2, SBCN-1, SBCN-3, LECN; and all of the SCNs plus CACN. Number of eggs was eliminated as a character for grouping cyst nematodes because of variability and great environmental influence. Larval width was also eliminated because it did not appear to be a good taxonomic character. The discriminant function selected tail terminus length followed in order by L_2 stylet length, L_2 length, cyst width, cyst length, and stylet base to DGO as the best discriminating factor. Three populations did not fit by discriminant function analysis

Table 3. Average eggs/cyst and cyst and larval measurements for collections of 15 *Heterodera, Globodera,* and *Punctodera* spp.

Collection	Eggs*		Cyst†		Larval‡				
	Body	Mass	L	W	L	W	DGO	TT	Stylet length
BCN-1	209	0	964	776	486	22.2	6.6	22.8	25.7
BCN-2	198	0	747	549	525	23.0	4.9	24.8	25.6
BGCN	124	0	710	489	508	22.6	6.3	33.3	21.6
CCN-1	123	39	832	562	599	22.6	7.0	38.3	27.0
CCN-2A	95	0	704	432	499	21.4	5.9	31.9	24.5
CCN-2B	114	0	779	481	558	22.1	6.7	36.2	26.2
CRCN	86	3	682	438	462	23.2	5.4	28.6	24.8
FCN	66	0	655	404	436	20.8	4.8	27.0	22.4
GCN	126	0	702	454	629	22.1	6.0	52.2	24.2
HNCN	126	0	631	515	532	22.0	6.6	26.9	22.5
KCN-1	69	0	577	394	489	20.9	5.8	23.7	21.2
KCN-2	64	0	524	370	461	21.1	6.0	22.9	20.4
LECN	112	2	730	470	529	23.7	7.2	30.7	27.0
OCN	126	0	591	521	560	24.0	6.4	27.5	22.6
RCN-1	104	1	741	479	510	22.1	6.4	35.4	25.5
RCN-2	138	7	738	482	536	21.6	6.1	37.0	26.2
SACN	145	1	845	579	594	22.4	5.1	43.4	23.9
SBCN-1	83	0	724	427	471	21.7	5.4	26.7	24.7
SBCN-3	89	0	785	417	496	22.0	5.8	28.6	25.0
TCN	134	0	608	607	492	22.5	6.0	26.3	21.9
CACN	62	20	616	422	519	20.7	5.7	29.2	22.9
LSD .05	18.6	6.2	39.5	28.1	14.0	0.9	0.3	1.1	0.4
C.V.	27.3	212.0	10.0	10.3	5.2	7.6	8.8	7.2	3.1
S.D.	33.5	11.3	71.3	50.6	25.3	1.7	0.5	2.0	0.7

*Egg counts from inside the body and the eggs mass from averages of 25 females.

†L = length, W = greatest width. Average of 25 individuals.

‡Larval measurements are averages of 4 individuals from each of 25 females. L = length; W = widest width; DGO = distance from stylet base to dorsal gland orifice; TT = length of hyaline tail terminus in μ.

in the groups to which they were assigned. The FCN population was grouped with the SCNs rather than the KCNs, SCN-12A was grouped with the CCNs etc., and SCN-13C and CACN were grouped with the KCNs.

In a third grouping, all populations were placed in species groups, except that the three round cysts were grouped together, the three species from grasses were grouped together, and CACN was grouped with the SCNs (Table 6) and subjected to a discriminant function analysis. Again L_2 width and egg counts were not used. The discriminatory steps were the same as above with L_2 tail terminus length first and L_2 stylet base to DGO measurement last. The measurements of the round cysts were close enough that they all fit well in the group, as was true for the grass parasites. However, SCN-12A was again grouped with the CCNs, SCN-6C was grouped with CRCN, and CACN with the KCNs.

Antigens from BCN, CACN, CRCN, SCN, BGCN, LECN, SBCN, CCN, KCN, and RCN were reacted against antisera from BCN, SCN, SBCN, CCN, and LECN (Table 7). Antigen from BCN reacted strongly against homologous antisera and very weakly against SCN and CCN antisera. There was some variation in the reactions but separation of races by serology was not possible in these tests. SCN antigens reacted against all other antisera except BCN. Antigens from CACN, BGCN, CRCN, and KCN reacted rather weakly against most of the antisera.

Table 4. Discriminant function comparison of morphometrics* of 25 individuals each of 34 populations of *Heterodera glycines*. All populations are compared against the measurements of the four designated races.

Population	No. of individuals† classed as				Host test classification‡
	Race 1	Race 2	Race 3	Race 4	
Race 1 (SCN-13)	25 (25)	0	0	0	A
Race 2 (SCN-6A)	1 (1)	19 (17)	1 (1)	4	4
Race 3 (SCN-1)	0	1	12 (10)	12 (2)	3
Race 4 (SCN-2)	0	6 (4)	10 (9)	9 (5)	2
SCN-1A	0	3 (2)	17 (15)	5 (3)	3
SCN-1B	0	17 (14)	7 (3)	1	3
SCN-2A	4 (4)	3 (2)	6 (2)	12 (6)	2
SCN-2B	7 (7)	1 (1)	12 (10)	5	2
SCN-2D	8 (4)	9 (7)	4 (3)	4 (1)	2
SCN-3	5 (5)	12 (10)	3 (1)	5 (1)	A
SCN-3A	17 (16)	2 (2)	1	5 (2)	4
SCN-3B	12 (11)	7 (6)	3 (1)	3 (1)	B
SCN-4	1 (1)	4 (3)	12 (8)	8 (5)	3
SCN-4A	1 (1)	22 (17)	0	2 (2)	C
SCN-5	1 (1)	5 (4)	7 (6)	12 (2)	3
SCN-6	6 (5)	2 (1)	12 (10)	5 (2)	C
SCN-6B	6 (6)	7 (5)	4 (2)	8 (3)	4
SCN-6C	1 (1)	1	7 (7)	16 (14)	3
SCN-7	2 (2)	21 (18)	0	2 (1)	3
SCN-8	0	4 (4)	16 (15)	5 (1)	3
SCN-9	2 (2)	12 (12)	3 (2)	8 (4)	3
SCN-10	8 (8)	9 (8)	3 (2)	5 (2)	3
SCN-10A	0	10 (9)	5 (5)	10 (4)	2
SCN-10B	0	6 (5)	13 (10)	6 (3)	B
SCN-11	6 (6)	9 (8)	1	9 (3)	3
SCN-11A	3 (3)	9 (5)	5 (5)	8 (4)	4
SCN-11B	4 (3)	12 (9)	4 (4)	5 (1)	3
SCN-12	0	16 (14)	2 (1)	7 (3)	A
SCN-13C	0	23 (23)	2 (1)	0	A
SCN-15	5 (3)	5 (2)	4 (3)	11 (7)	3
SCN-15A	3 (2)	6 (5)	7 (5)	9 (2)	A
SCN-16	2 (2)	16 (14)	2	5 (4)	3
SCN-16A	0	2 (1)	19 (11)	4 (1)	3
SCN-16B	0	10 (9)	8 (3)	7 (5)	C
TOTAL	130 (119)	291 (241)	212 (155)	215 (94)	

*See Table 3 for measurements analyzed.

†Numbers not in parenthesis are the numbers of individuals of a total of 25, classed as a particular race; the numbers in parenthesis represent those individuals which were a "good fit" according to the calculation of the analysis.

‡The numbers are the race designations as set forth by Golden et al. (2); letters represent classifications distinguished by Riggs et al. (11) which were different than those set forth by Golden et al.

DISCUSSION

The data on SCN populations confirm earlier studies by Miller and Duke (9). They indicate that even though there were significant differences in various measurements between populations, the overlap between populations was great. The morphometric differences in the various populations of SCN indicate that several subspecies could be described (Table 2). However, the overlap of measurements of a given character between populations argues against this. The most significantly different population was SCN-12A, which has been shown to be a tetraploid (13). Hirschmann and Triantaphyllou (4) demonstrated that among parthenogenetic *Heterodera* species, where differences in ploidy exist, there was a corresponding difference in size of individuals. Although SCN-12A is amphimictic, a simi-

Table 5. Grouping of 16 species of cyst nematodes including multiple population of some species, based on a SAS dendrogram (5).

Group								
1		2	3	4	5	6	7	8
SCN-1*	SCN-8	CCN-2A	SCN-2D	SCN-3A	SCN-12A	SCN-1A	OCN	BCN-1
SCN-1B	SCN-9	SBCN-1	SCN-6	LECN	CCN-1	SCN-2A	HNCN	
SCN-2	SCN-10A	SBCN-3	SCN-10	RCN-1	SACN	SCN-4	TCN	
SCN-2B	SCN-10B	CRCN	SCN-11	RCN-2		SCN-6C		
SCN-3	SCN-11A		SCN-11B	BGCN		SCN-16A		
SCN-3B	SCN-12		SCN-15	CCN-2B		KCN-1		
SCN-4A	SCN-13		SCN-15A	GCN		KCN-2		
SCN-5	SCN-13C		BCN-2			FCN		
SCN-6A	SCN-16					CACN		
SCN-6B	SCN-16B							
SCN-7								

*See Table 1 for identification of population designations.

lar ploidy-size relationship exists. BCN-1 and BCN-2 have the same number of chromosomes but are significantly different in size. BCN-1 has larger cysts while BCN-2 has longer larvae.

Results of this study indicate that the morphometric characters used will not provide a means of separating the known races of SCN. The only population which was a good fit in a particular race was SCN-13 (Table 4, Race 1). This population was obtained from North Carolina as a subculture

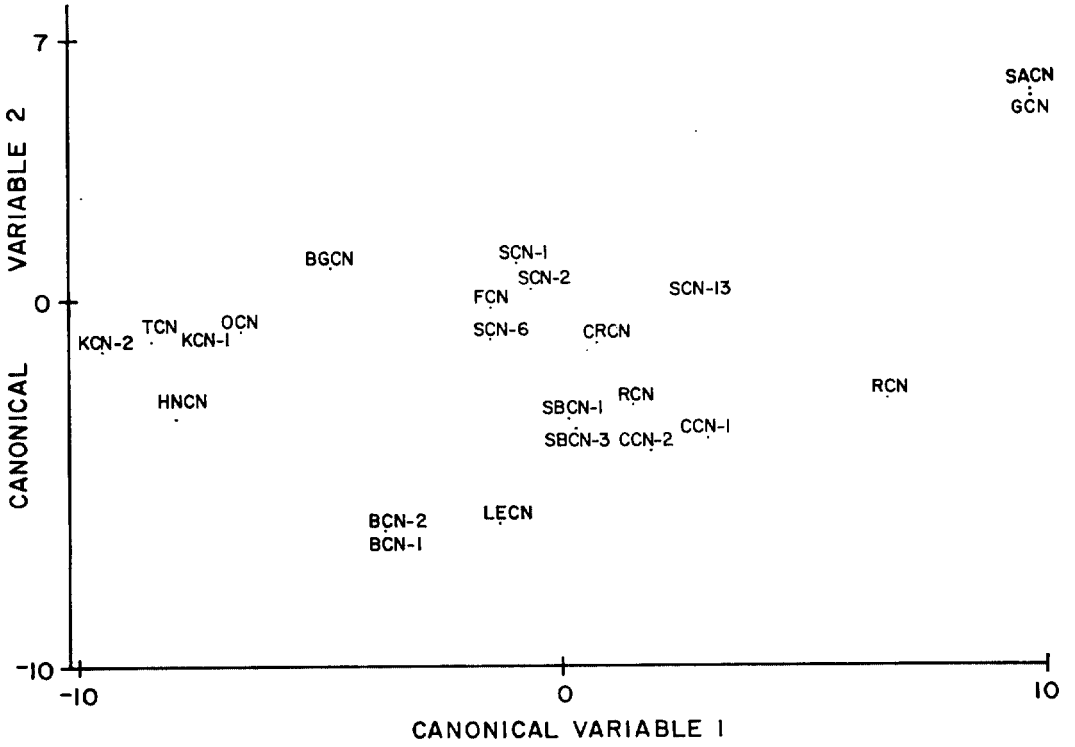

Fig. 2. Discriminant function comparison of nine measurement of 15 *Heterodera* spp., including the four races of Heterodera glycines. (See Table 1 for identification of population designations.)

Table 6. Grouping of 56 populations of cyst nematodes according to species or host relationships.

Group									
1*	2	3	4	5	6	7	8	9†	10
OCN‡	KCN-1	FCN	RCN-1	CCN-1	SBCN-1	CRCN	LECN	GCN	BCN-1
HNCN	KCN-2		RCN-2	CCN-2A	SBCN-3			BGCN	BCN-2
TCN				CCN-2B				SACN	

11		
SCN-1	SCN-5	SCN-11A
SCN-1A	SCN-6	SCN-11B
SCN-1B	SCN-6A	SCN-12
SCN-2	SCN-6B	SCN-12A
SCN-2A	SCN-6C	SCN-13
SCN-2B	SCN-7	SCN-13C
SCN-2D	SCN-8	SCN-15
SCN-3	SCN-9	SCN-15A
SCN-3A	SCN-10	SCN-16
SCN-3B	SCN-10A	SCN-16A
SCN-4	SCN-10B	SCN-16B
SCN-4A	SCN-11	CACN

*Similar hosts and shapes.
†Parasites of grasses.
‡See Table 1 for identification of population designations.

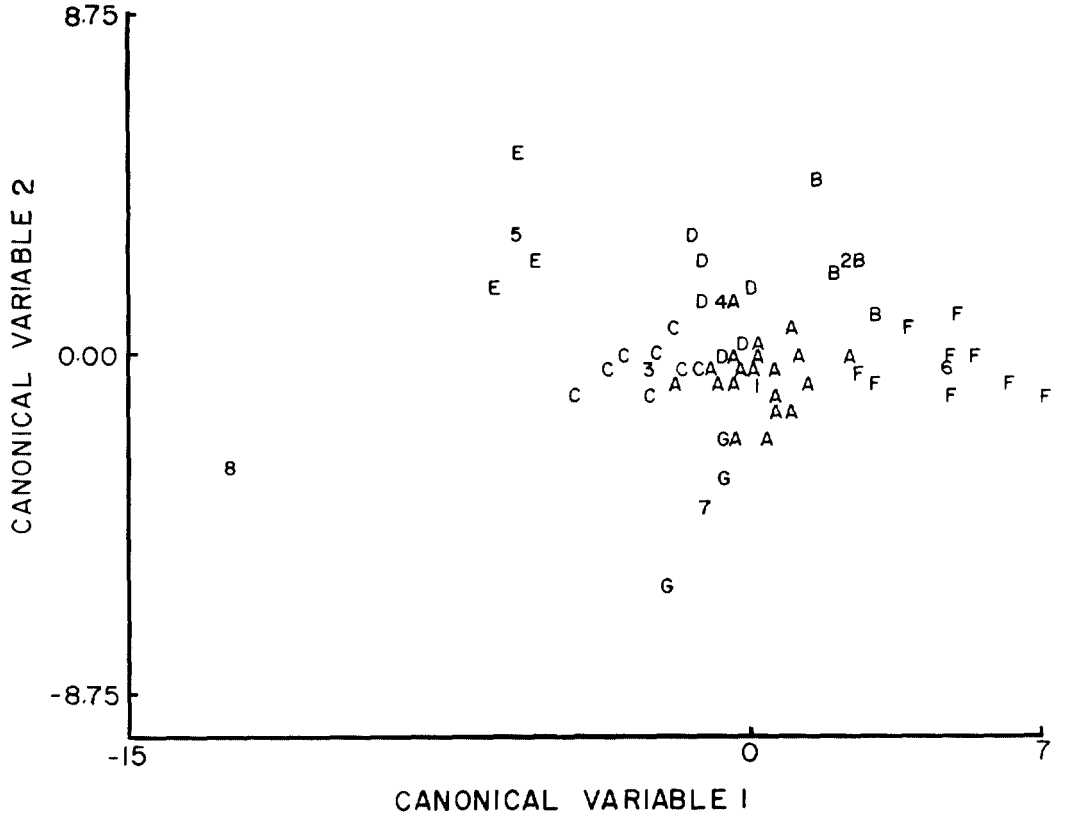

Fig. 3. Discriminant function comparison of 56 populations of 16 species of cyst nematodes grouped according to a SAS dendrogram. See Table 5 for grouping.)

Table 7. Reactions of cyst nematode antisera with homologous and heterologous antigens using gel immunoelectrophoresis.

	Antisera								
Antigens	BCN-1*	SCN-13	SCN-6A	SCN-1	SCN-2	SBCN	CCN-1	CCN-2	LECN
BCN-1	+++†	NT	–	NT	+	NT	+	NT	–
BCN-2	+++	NT	–	NT	+	NT	+	NT	?+
CACN	NT	NT	++	NT	+	NT	+	NT	++
CRCN	NT	NT	NT	++	+++	NT	+	NT	+
SCN-13	–	+++	+++	++	+++	+++	+++	++	+++
SCN-6A	–	NT	+++	+++	+++	+++	+++	+++	+++
SCN-1	–	NT	++	+++	+++	++	+++	+++	+++
SCN-2	–	+++	+++	+++	+++	++	+++	++	+++
BGCN	NT	NT	NT	NT	+	NT	?+	NT	+
LECN	–	NT	NT	+++	+++	+++	+++	NT	+++
SBCN-1	–	NT	++	+++	++	+++	++	NT	+++
SBCN-3	NT	NT	+++	NT	++	NT	++	NT	++
OCN	NT	NT	NT	NT	+	NT	+	NT	+
RCN	–	NT	+++	++	++	+++	+++	+++	+++
TCN	NT	NT	NT	NT	++	NT	+	NT	+
CCN-1	+	NT	+++	+++	++	++	+++	NT	+++
CCN-2	–	NT	+++	+++	++	++	+++	NT	+++
HNCN	NT	NT	NT	NT	+	NT	+	NT	+
KCN-2	+	NT	NT	NT	+	NT	–	NT	+

*See Table 1 for identification of population designations.
†NT, no test; –, no reaction; +, different intensities positive reaction.

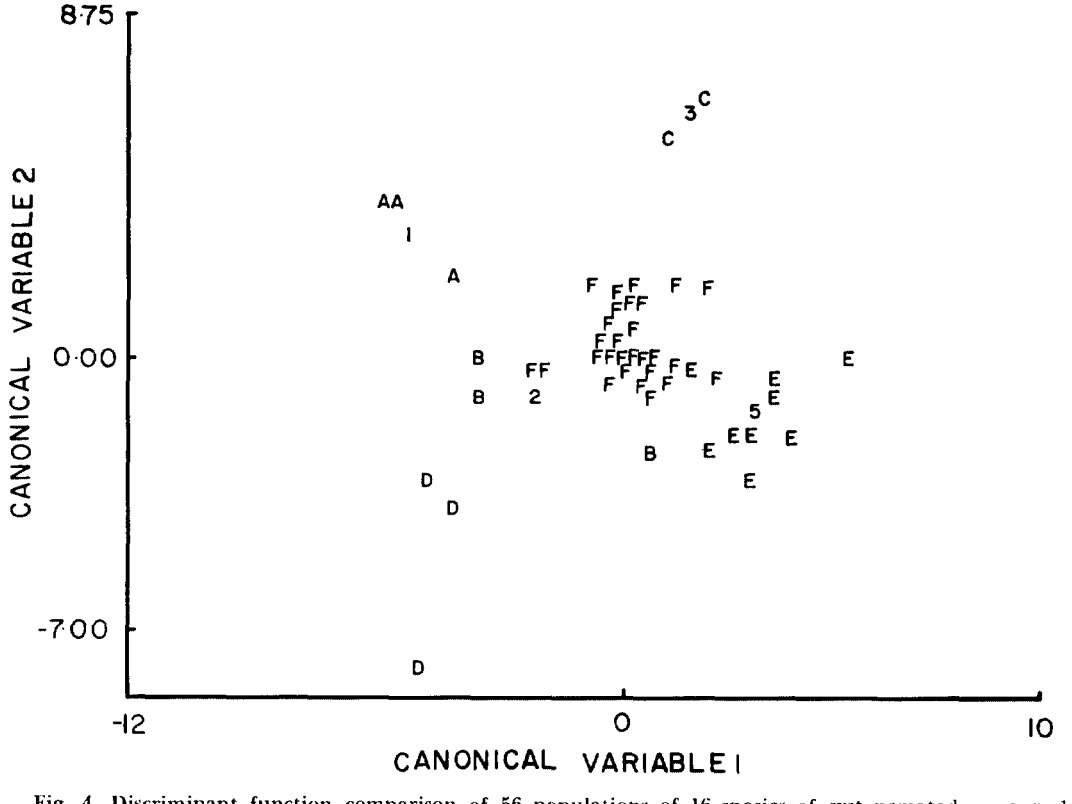

Fig. 4. Discriminant function comparison of 56 populations of 16 species of cyst nematodes grouped according to apparent host relationships. (See text, Materials and Methods, for grouping.)

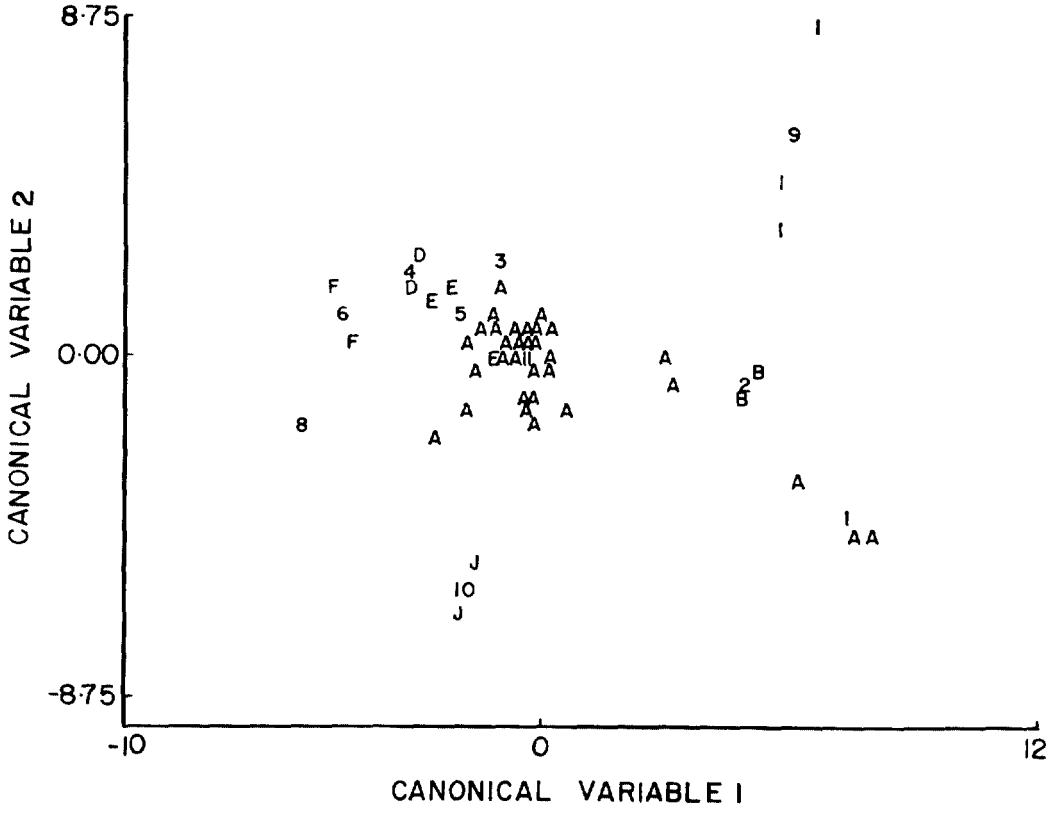

Fig. 5. Discriminant function comparison of 56 populations of 16 species of cyst nematodes grouped according to species or host relationship. (See Table 6 for grouping.)

of the population designated Race 1 (2). However, in host tests it did not give the reactions designated for Race 1 (11). For populations which fit physiologically into Races 2, 3, or 4, only in Race 2 was a majority of the individuals measured classified as that race by the discriminant function procedure.

Grouping of cyst nematodes into related groups was only partially successful. The best grouping system was one based on the species grouping (Table 6, Fig. 5). This should lend support to the validity of the species. However, in a few cases populations were not a "good fit" in the species to which they should belong. The grouping based on host compatibility (Fig. 4) was almost as good as species groupings. The host reaction may be a more convenient diagnostic character than morphometrics and it may be a better indicator of the true relationships.

In making comparisons between populations, care must be taken to insure that all populations are "healthy" and maintained under uniform conditions conducive to good growth and reproduction. For example, CCN-2A and CCN-2B (Table 3) were different, but they came from the same population on the same host. The difference appeared to be that when CCN-2A was sampled the population was in a state of decline and few individuals were available. The CCN-2B population was reproducing well and only a small portion of the available cysts were selected. The data indicate significant differences in cyst length, larval length, tail terminus, and stylet length of the two measurements. A similar situation was demonstrated for differences in host and temperatures (unpublished data).

Serology results indicated that BCN populations were more distantly related to the other populations than they were to each other. All of the species tested had some homologous antigens but some had more

than others. SCN, LECN, CCN, SBCN, and RCN appeared to be closely related to each other.

Based on both morphological and host studies, a fairly close relationship exists between the 12 *Heterodera* spp. FCN is quite different, hostwise, but very similar morphologically to SCN and other species. SACN differs significantly from other cyst species both morphologically and in host performance.

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