Sex Expression and Tail Morphology of Female Progenies of Smooth-Tail and Crenate-Tail Females of Pratylenchus penetrans

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Abstract: An analysis of the offspring of single smooth- and crenate-tail females of *Pratylenchus penetrans* indicated the existence of progenies containing only males or females. Of the 80 progenies analyzed, 46 contained females with smooth and crenate tails. In general, regardless of the mother's tail type, most females possessed crenate tails, although more crenate-tail females originated from a crenate-tail female than from a smooth-tail female. Twenty-three progenies contained only females with crenate tails, most of them originating from crenate-tail females. One progeny originating from a smooth-tail female contained only females with smooth tails. No simple interpretation of the inheritance of tail type could be attempted because selection pressure favored females with crenate tails when *P. penetrans* was reared on Wando pea plants.
Key Words: Wando peas, sexual forms, genetic nature, selection pressure, adaptive capability.

The genetic nature of morphological variants rarely has been established in plant parasitic nematodes. Netscher and Pernes (1) found large differences in larval length of *Heterodera oryzae* between the offspring of two egg masses and emphasized the need to determine variability on quantitative characters in taxonomy. This need is probably more important when variable qualitative characters are concerned, especially when these characters are used to separate closely related species.

The presence of striations around the tail is one of the characters used to distinguish several related species from *Pratylenchus penetrans* (Cobb, 1917) Filip. and Schuurm.-Stekh., 1941. *Pratylenchus penetrans* was described as possessing females with a smooth tail tip (4). However, it was shown that approximately 30% of the females of the Cornell population of *P. penetrans* growing on sterile alfalfa callus tissue possessed crenate tails (5). Also, in several experiments, the proportion of females with crenate tails in relation to those with smooth tails was higher when this population was reared on Wando pea plants for several generations than when it was reared on callused alfalfa tissue. These data indicated the possibility that tail type is genetically controlled and influenced by environment. The determination of inheritance of tail type is complicated by the fact that the smooth- and crenate-tail characters occur only in females.

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The primary purpose of the research reported in this paper was to obtain information on the genetic nature of tail type by analyzing the offspring of single mature females with smooth or crenate tails.

MATERIALS AND METHODS

The nematodes utilized were obtained from a population of *P. penetrans* containing about 30% females with crenate tails and reared on alfalfa (*Medicago sativa* L. 'Ranger') callus-tissue cultures on modified White's medium (2). Adult females were mounted alive in a drop of egg white on a cover slip, placed on a deep-well slide, and observed under a microscope at 700x magnification. Egg white restricts nematode movement and facilitates observation of the type of tail terminus. Only females in which the tail terminus was easily seen when oriented in a lateral position were selected for inoculation. Unless the tail crenation could be determined with certainty, the nematodes were discarded. Because of the relatively long time required to select an individual female, up to 6 days were needed to select the number required for each experiment. During this period, the females were stored at 15 C. Uniform 2-day-old pea (*Pisum sativum* L. 'Wando') seedlings, germinated in sterile sand, were inoculated with individual adult females. Inoculated seedlings were stored at 25 C for 24 h, and then transplanted to 10-cm clay pots containing a steam sterilized sandy loam soil.

A total of 128 plants, half inoculated with a single smooth-tail female, and half inoculated with a single crenate-tail female, were maintained for 20 weeks in a growth chamber at a light intensity of 3,870 lux (360 ft-c). In a similar experiment, 40 plants were inoculated singly with one crenate-tail female, and 40 plants were inoculated singly with one smooth-tail female. The plants were maintained for 17 weeks in a greenhouse at an average light intensity of 21,520 lux (2,000 ft-c). There was a distance of about 25 cm between pots, and great care was taken when watering and handling the plants to prevent contamination from one pot to another. Plants were replanted twice during the time required for reproduction of several generations of nematodes. No fertilizer was added to any of the plants.

Nematodes were extracted from the roots of each plant at the end of the experiment, as previously reported (5). They were counted and killed in hot water at 65 C for 2 min. Females from each progeny were mounted on slides in 2.5% formalin for microscopic observation.

RESULTS

Similar results were obtained in growth chamber experiments with low light intensity of 3,870 lux (360 ft-c) and under greenhouse conditions at a higher light intensity [approximately 21,520 lux (2,000 ft-c)].

The number of nematodes in each progeny varied from 1 to 126. If only one female was recovered, it was not considered in the analysis because of the possibility that it was the initial female.

Fifty-two progenies from the growth chamber and 28 from the greenhouse were studied (Table 1). They were tabulated according to the tail type of the parent female. Most of the progenies contained both males and females. It was observed, however, that in 34.6 and 28.6% of the progenies in the growth chamber and greenhouse, respectively, no male was present. Also, females were absent in 19.2% of the progenies in the growth chamber, but all greenhouse progenies contained females.

The tail shape (smooth or crenate) of the female used as inoculum did not influence the percent of males or females present. At the time data were taken, no larvae were present in progenies with only one sexual form (Table 1). The females of those progenies possessed very characteristic, thick-walled, empty spermatheca [Fig. 1-(D-F)]. In contrast, the empty spermatheca of newly molted females from progeny with males and females possessed thin walls (Fig. 1-G, H).

Females were more numerous in progenies with both sexual forms than in progenies with one sexual form. All the females

TABLE 1. Number of males, females, and larvae of *Pratylenchus penetrans* from single smooth-tail and crenate-tail females.

Experimental parameters	No. of progeny	Mean no. of nematode/progeny			
		Males	Females	Larvae	Total
Growth chamber [3,870 lux (360 ft-c.)]					
Progeny with females and males:					
From single smooth female	12	12.4	16.1	13.1	41.6
From single crenate female	12	19.1	11.7	11.7	42.5
Progeny without males:					
From single smooth female	9	0	10.1	0	10.1
From single crenate female	9	0	10.2	0.5	10.7
Progeny without females:					
From single smooth female	5	2.8	0	0.4	3.2
From single crenate female	5	5.8	0	0.4	6.2
Greenhouse [21,520 lux (2,000 ft-c.)]					
Progeny with females and males:					
From single smooth female	11	14.4	19.3	11.3	45
From single crenate female	9	9.5	7.1	4.4	21
Progeny without males:					
From single smooth female	3	0	5.7	0	5.7
From single crenate female	5	0	5.0	0	5.0
Progeny without females:					
From single smooth female	0	0	0	0	0
From single crenate female	0	0	0	0	0

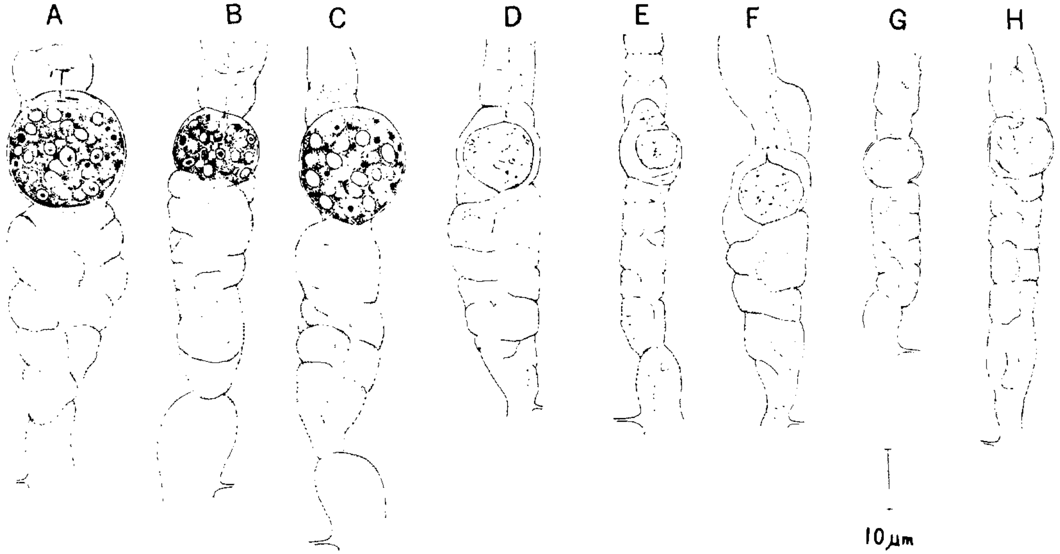

FIG. 1-(A-H). Morphology of spermatheca as observed in *Pratylenchus penetrans* females. *A-C)* Well-developed spermatheca full of sperm— from progenies with females and males. *D-F)* Empty spermatheca— from progenies with females only. *G-H)* Empty spermatheca of newly-molted females from progenies with males and females.

from progenies with both sexual forms possessed well-developed spermatheca full of sperm [Fig. 1-(A-C)].

In progenies where females were present, 64.3 and 67.8% of the progenies from the growth chamber and the greenhouse, respectively, were found to contain females having both types of tails (Table 2). The number of progenies with both types of female tails was higher in progenies with both sexual forms than in progenies with only females, and was also higher in progenies with both sexual forms originating from a smooth-tail female than in similar progenies originating from a crenate-tail female. The remaining progenies possessed females with

TABLE 2. Influence of tail type of a single female of *Pratylenchus penetrans* on the tail type of the female progeny.

Experimental parameters	No. of female progeny with			Mean no. of females/progeny with each tail type	
	Smooth and crenate tails	Smooth tails	Crenate tails	Smooth	Crenate
Growth chamber [3,870 lux (360 ft-c.)]					
Progeny with females and males:					
From smooth-tail female	9	0	3	6.0	12.9
From crenate-tail female	7	0	5	5.7	8.1
Progeny with all females:					
From smooth-tail female	5	1	3	4.4	9.6
From crenate-tail female	6	0	3	1.5	5.7
Total	27	1	14	—	—
Greenhouse [21,520 lux (2,000 ft-c.)]					
Progeny with females and males:					
From smooth-tail female	10	0	1	8.7	10.0
From crenate-tail female	4	0	5	4.7	7.5
Progeny with all females:					
From smooth-tail female	3	0	0	3.0	2.3
From crenate-tail female	2	0	3	1.0	3.5
Total	19	0	9	—	—

only one type of tail, and in 33.2 and 32.1% of the progenies from the growth chamber and the greenhouse, respectively, all of the females had a crenate tail. The majority of these crenate-tail females (69.5%) originated from a crenate-tail female, but 30.5% originated from a smooth-tail female. The number of progenies of this type was also higher in progenies with both sexual forms than in progenies with only females. All the females of only one progeny had smooth tails; this progeny originated from a smooth-tail female in the greenhouse experiment and contained no male.

Generally, in progenies possessing both tail types, crenate-tail females predominated, regardless of the mother's tail type (Table 2). Except for progenies with both sexual forms reared in the growth chamber, however, the percent of females with crenate tails was higher in progenies originating from a crenate-tail female than in progenies originating from a smooth-tail female. Also, the proportion of crenate-tail females was higher in progenies originating from a smooth-tail female in the growth chamber than in similar progenies in the greenhouse.

DISCUSSION

The tail terminus character studied is not evident in males, and therefore, its genetic nature could not be determined precisely. Data on the offspring of single females of *P. penetrans,* however, indicate that tail type may be genetically controlled. This theory is supported by the fact that when crenate-tail females produced progenies containing both crenate- and smooth-tail females, the former always predominated. Furthermore, most of the progenies with 100% crenate tails originated from crenate-tail females, and the only progeny obtained with all smooth tails originated from a smooth-tail female (Table 2).

Some indication that crenate tails are governed by a dominant gene is shown by the fact that progenies with only crenate-tail females were produced by a smooth-tail female, but no crenate-tail female produced offspring with all smooth tails. This hypothesis agrees with the assumption that, if a single gene is involved, then the heterozygotes should not give sizeable progeny that are entirely of the homozygous recessive class. However, no simple genetical analysis can be made because of the selection pressure in favor of crenate-tail females in pea plants (5). Also, the tail type seemed to be affected by environment since the percentage of crenate-tail females originating from a smooth-tail female was higher in the growth chamber than in the greenhouse. The adaptive capability of the crenate genotype on Wando pea plants may be much greater than that of the smooth genotype. Because the genetic constitution of the favored individuals is unknown, very little more can be said in regards to the dominance or recessiveness of either tail type since the proportion of crenate-tail females to smooth-tail females would increase with every generation, and in these tests probably three generations occurred.

While the tail type and sex expression of the progenies involved in this study were being observed, some unusual morphological characteristics were noticed among the females of several single female progenies. For instance, in some progenies, larger nematodes predominated; whereas in others very small nematodes were most numerous. Most or all of the individuals of some progenies possessed rounded stylet knobs; in others, the anteriorly concave shape predominated. Some progenies had great morphological variability, but others were more uniform. Empty spermatheca of females from progenies with no males were similar to those of the monosexual *P. crenatus* (3).

The evidence in favor of the genetic nature of a morphological character suggests the existence of polymorphism in *P. penetrans.* A population described as a different species might have been a polymorphic variant of *P. penetrans* favored by environmental selection pressures.

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