of useful action against the fringed tapeworm: Tetrachlorodifluoroethane [Freon 112], trichlorotrifluoroethane [Freon 113], 2,2′ methylenebis (3,4,6-trichlorophenol) [hexachlorophene], 1,4-bis-trichloromethyl benzene [Hetol], 3,3′-dichloro-5,5′-dinitro-o,o′-biphenol [Bayer 9015], and 1-(3-trifluoromethyl-4-chlorophenyl)-3-(3,4,dichlorophenyl)urea [G 27384].

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Description and Taxonomic Position of the DD-136 Nematode (Steinernematidae, Rhabditoidea) and Its Relationship to *Neoaplectana carpocapsae* Weiser

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INTRODUCTION

In 1954, nematodes isolated from diseased codling moth larvae in Virginia were examined by the late Dr. G. Steiner, who considered them as belonging to the Steinernematidae (anonymous, 1955) and very close to *Neoaplectana chresima* Steiner (Dutky and Hough, 1955). However they were never described and have been known since mainly by the code number, DD-136. Moreover, the original diagnosis given *N. chresima* by Steiner is very scant and, although from the available information similarities with the DD-136 nematode are apparent (Glaser et al. 1942), a description of *N. chresima* Steiner was never published and this species should be designated as a nomen nudum.

The lack of a binomial and accompanying description of the DD-136 nematode has caused no little confusion with nematologists and other scientists working with these forms. The nematodes from the original sample were maintained in the laboratory and, because of their wide host range and potential as a biological control agent of insects, were distributed to a number of insect pathologists throughout the world.

Accounts of the biology of this nematode have already been presented (Anonymous, 1955, 1956; Dutky, 1959; Schmiege, 1962,

1963; Welch and Briand, 1961; Poinar, 1966; Poinar and Thomas, 1966; Poinar and Himsworth, in press).

In 1953, Weiser found and later described *Neoaplectana carpocapsae* Weiser from diseased codling moth larvae in Czechoslovakia (Weiser, 1955).

The relationship between these two nematodes has never been clear and while Schmiege (1964) felt that they were probably the same species (but apparently did not examine living material of *N. carpocapsae* Weiser), Dutky et al. (1964) state that "it appears from the description given by Weiser that the two nematodes are not the same species." Later Weiser (1966) mentioned in regards to the DD-136 nematode (translated from Czech) "a number of differences show that it is a species distinguishable from *N. carpocapsae* which was isolated in Europe from the same host." But he does not mention any specific differences and goes on to say "lack of more detailed data in Dutky's study hinders comparison of both." Moreover, Jackson (1965) found several types of differences between them and treated the two as separate species, regarding the DD-136 nematode as *N. dutkii.* However, this name is invalid and remains a nomen nudum since there was no formal publication of the specific epithet nor an accompanying description.

The present study was undertaken to characterize the DD-136 nematode and reexamine the relationship between this form and *N. carpocapsae*. This study also focuses attention on the problems of variation associated with such groups as the neoaplectanid nematodes.

MATERIALS AND METHODS

Axenic populations of *Neoaplectana carpocapsae* Weiser were received from Dr. J. Weiser of Prague. Infective juveniles were removed from the culture tubes, and then injected with a suspension of *Achromobacter nematophilus* Poinar and Thomas into larvae of *Galleria mellonella*. The resulting infective juvenile progeny later emerged from these insects and contained cells of the above bacterium in their intestine, as is characteristic for the DD-136 nematode (Poinar, 1966). Cultures of the DD-136 nematode were sent to this laboratory in 1963 from the USDA Insect Pathology Laboratory, at Beltsville, Md. Thus both *N. carpocapsae* and DD-136 were maintained in the laboratory on *Galleria mellonella* larvae in the presence of *A. nematophilus*, and any other naturally occurring microorganisms from the insect. This was done to insure that environmental conditions were similar during the development of both nematodes.

For comparative measurements, care was taken to introduce approximately equal numbers of infective juveniles into the oral cavity of last instar insect larvae. After holding the diseased insects for 4 days at 70 F, first generation adult nematodes were removed, suspended in saline, killed with gentle heat and placed in 3% formalin for measurements. Some were later placed in lactophenol for detailed studies of the mouth and caudal region. Measurements were made on heat-killed infective juveniles that emerged naturally from *Galleria* larvae about 15 days after infection.

Detailed examinations of the lateral line of the third-stage infective nematodes were made with the electron microscope. Juveniles were fixed with 1% osmium in veronal acetate buffer (pH 7.2), embedded in maraglas and ultra-thin sections examined with an RCA-F-3 electron microscope.

Squash mounts were made for chromosome counts. The gonads were removed and stained with aceto-orcein.

For controlling matings, infective-stage juveniles of both nematodes were placed individually in hanging drops of insect blood with *Achromobacter nematophilus*. After reaching the adult stage, males and females of one nematode were transferred to drops containing females and males of the other nematode, respectively. As a control, nematodes were transferred to the opposite sex of the same nematode and females of both nematodes were held isolated in separate drops.

RESULTS

All of a total of 18 paired matings attempted were successful, showing that the DD-136 nematode and *N. carpocapsae* could interbreed, producing viable, normal progeny, which in turn produced repeated generations when introduced into *Galleria* larvae. Similar results were obtained whether males or females

TABLE 1. Comparative measurements of females of the Czechoslovakian and DD-136 strains of *N. carpocapsae* Weiser.[1]

Character	DD-136 (N = 25)			Czechoslovakian (N = 21)		
	X	Range		X	Range	
Total length (mm)	3.68	2.80	5.16	3.31	1.97	5.81
Greatest width	148.0	123.2	184.8	156.3	123.2	192.5
Stoma length	6.5	4.7	9.3	5.9	3.1	7.8
Stoma width	8.3	6.2	9.3	9.3	6.2	12.4
Length head to excretory pore	61.1	46.5	74.4	56.7	34.1	86.8
Width at excretory pore	76.9	65.1	87.0	82.2	65.1	108.5
Length head to nerve ring	137.3	117.8	161.2	140.1	108.5	170.5
Width at nerve ring	103.2	86.8	124.0	116.9	91.0	133.3
Length head to base of esophagus	191.0	161.2	217.0	201.5	155.0	241.8
Width at base of esophagus	112.0	99.2	133.3	131.4	111.6	145.7
Length tail	36.3	27.9	46.5	34.7	18.6	55.8
Width tail	69.1	49.6	86.8	62.9	46.5	77.5
Per cent vulva	54.1	51.5	56.0	52.0	50.0	58.0

[1] All measurements in microns unless otherwise specified.

of the DD-136 nematode were mated with *N. carpocapsae*. These experiments establish that the nematodes are conspecific. Isolated females produced ova, but did not deposit viable eggs, indicating that these nematodes are dioecious and zygogenetic.

No consistent qualitative morphological characters were found which could be used to separate the two nematodes. Structurally, both nematodes are very similar and the variation that occurred in the shape of the tail, stoma, spicules, gubernaculum, and position of the male anal papillae restricted the use of these structures as diagnostic characters. Jackson (1965) used some of the above structures for differentiating DD-136 from *N. carpocapsae*, however, after having examined several hundred adults of both nematodes, the present author feels that the variability is too great for definite conclusions to be drawn. However, it should be pointed out that Jackson examined axenic nematodes maintained on artificial media and thus possibly with less overall variation.

Quantitative data obtained for comparison of the sexual stages and infective juveniles of both nematodes are presented in Tables 1, 2, and 3. These data are comparative and, since they include only measurements of the first generation adults, do not represent the complete variability which would also cover the smaller succeeding generations in the insect. Differences between the measurements of *N. carpocapsae* presented here and those presented by Weiser (1955, 1956) reflect the variation within this species. While first generation adults were measured in this study, Weiser probably measured adults of the succeeding generations, thus obtaining significantly smaller values. Further variation would probably arise from the host parasitized, associated microorganisms and physical factors of the environment.

Tests of significance (*t*-test) were made on the quantitative data presented in Tables 1, 2, and 3. Even under these relatively stable conditions, values obtained for the females were too variable to be significant at the 5% level. A similar condition existed in the male populations, although a significant difference in length and reflection of testis was recorded. This may be due to the quicker maturation of DD-136, since populations measured 5 or 6 days after infection showed no significant difference in length or reflection of testis. Variation was less in the infective juveniles as shown in Table 3, and several values were found to be significantly different, especially the distance from the head to the excretory pore. This value remained significantly different over several samples taken, even though further sampling showed that variation in length and distance from head to nerve ring was too great for these characters to be used for diagnostic purposes.

Measurements of the distance from the head to excretory pore made on the infective juveniles resulting from the crossing experiments usually fell between those obtained for the parental populations (Table 4).

TABLE 2. Comparative measurements of males of the Czechoslovakian and DD-136 strain of *N. carpocapsae* Weiser.[1]

Character	DD-136 (N = 25)			Czechoslovakian (N = 12)		
	$\bar{X}$	Range		$\bar{X}$	Range	
Total length (mm)	1.45	1.09	1.71	1.32	1.25	1.40
Greatest width	101.6	77.0	130.9	117.0	107.8	130.9
Stoma length	5.6	2.6	7.8	5.6	5.2	7.8
Stoma width	4.9	3.9	6.5	4.6	2.6	6.5
Length head to excretory pore	61.4	46.5	74.4	71.3	55.8	74.4
Width at excretory pore	47.7	37.2	58.9	52.1	46.5	58.9
Length head to nerve ring	110.1	93.0	124.0	127.7	108.5	155.0
Width at nerve ring	58.9	46.5	71.3	68.5	62.0	86.8
Length head to base of esophagus	154.7	136.4	167.4	151.9	145.7	155.0
Width at base of esophagus	64.5	49.6	77.5	70.7	65.1	77.5
Length bent portion of testis to base of esophagus	128.6	53.9	284.9	136.3	84.7	192.5
Length tip of testis to tail	1,150.0	780.0	1,560.0	1,000.0	780.0	1,090.0
Reflection testis	563.6	400.4	808.5	385.0	284.9	477.4
Length tail	30.4	23.4	39.0	31.2	22.1	35.1
Width anus	42.6	32.5	54.6	44.5	39.0	52.0
Length spicula	64.6	58.5	71.5	66.3	62.4	70.2
Width spicula	11.1	9.1	13.0	12.5	10.4	13.0
Length gubernaculum	47.1	39.0	55.9	47.1	42.9	52.0
Width gubernaculum	5.2	3.9	6.5	6.4	5.2	7.8

[1] All measurements in microns unless otherwise specified.

The infective third-stage juveniles of both nematodes possess conspicuous lateral fields. The number and shape of the folds and striae constituting these fields are sometimes characteristic and used in the differentiation of nematode species. Electron micrographs show that these fields are similar in both nematodes and at midbody consist of six longitudinal ribs, comprising two pairs of pronounced outer ribs on either side of a pair of finer inner ribs (Fig. 1, A, B).

Smears of testicular tissue from both nematodes showed a chromosomal condition of four bivalents and a single univalent. This indicates a 2N condition of nine chromosomes for the males and ten for the females (Fig. 1, C, D).

A qualitative description of the DD-136 nematode follows.

Steinernematidae Chitwood and Chitwood 1937, 1950; *Neoaplectana* Steiner 1929.

Adult forms (Figs. 2 and 3). Cuticle smooth, head truncate to slightly rounded, lips united, setae obscure; two circles of anterior papillae, six inner labial papillae and six outer cephalic papillae. Amphids small, porelike, near level of cephalic papillae. Stoma partially collapsed with only an anterior vesibule remaining. Collar lacking, esophageal tissue close to mouth opening, reaching to the base of the vestibule. Cheilorhabdions represented as lightly sclerotized areas lining the inside of the lip region anterior to the esophagus. A small sclerotized area just beneath the cheliorhabdions probably represents the modified prorhabdions. Meso-, meta-, and telorhabdions vestigial, although sometimes rarely represented as refractive edges lining the collapsed walls of the stoma.

Esophagus muscular, the anterior portion of the procorpus slightly expanded just behind the vesetibule, then extending into a slightly enlarged nonvalvulated metacorpus, followed by an isthmus and terminating in a basal bulb containing a small haustrum with three bulb flaps lined with refractive ridges. Base of esophagus often inserted into the anterior portion of the intestine. Nerve ring surrounding isthmus just anterior to the basal bulb. Excretory pore usually anterior to nerve ring. Lateral field and phasmids inconspicuous.

Female amphidelphic with opposed reflexed ovaries. Variable in size, some giant forms reaching 10 mm. Vulva a transverse slit, bearing two prominant ventral protuberances. Vagina short with muscular walls leading into a prouterus which serves as an egg chamber—a small constriction separates this from the remainder of the uterus, where fertilization occurs. Well developed glandular oviduct leads into the growth zone of the ovary and finally into the elongate germinal zone. Fe-

TABLE 3. Comparative measurements of the 3rd stage infective juveniles of the Czechoslovakian and DD-136 strain of *N. carpocapsae* Weiser.[1]

Character	DD-136 (N = 25)			Czechoslovakian (N = 25)		
	$\bar{X}$	Range		$\bar{X}$	Range	
Total length	547.0	438.0	625.0	572.0	488.0	613.0[2]
Greatest width	24.0	22.0	28.0	26.0	25.0	28.0
Head to excretory pore	35.7	34.0	40.0	42.1	39.0	56.0[3]
Head to excretory pore (sample 2)	38.6	36.4	40.3	43.2	39.0	58.5[3]
Head to nerve ring	85.0	81.0	90.0	88.0	84.0	93.0[2]
Length tail	53.0	50.0	59.0	53.0	47.0	59.0

[1] All measurements in microns.
[2] Means significantly different at 5% level.
[3] Means significantly different at 1% level.

male tail bluntly conical to dome shaped—with or without a short spine on the tip. Second and succeeding generation females in the host are correspondingly smaller in size. Pigmy forms or swollen miniature females were never found.

Male with single reflexed testis consisting of a germinal and growth zone leading into a seminal vesicle containing spermatophores. Vas deferens conspicuous, with glandular walls. Spicules paired, symmetrical, curved and bearing a more or less pronounced arch on their ventral surface (Fig. 3 C). Shape of capitulum variable—from slightly pointed to round or flat. Surface and edge of calamus and lamina bearing ridges. A thin velum present. The gubernaculum is also variable, ranging from completely flattened to bow shaped in lateral view, with the proximal portion bent at various angles and sometimes even bluntly bifurcate (Fig. 3, D, E). In dorsal view, the distal portion consists of two lateral projections with a thin sclerotized spine between them. The area between the lateral projections is connected by a thin membrane. Male tail with a complement of 23 anal papillae (11 pairs and a single median adanal) comprising two rows of six ventrolateral papillae and five paired post anal papillae. Of the latter group, two pair are situated laterally on the tail, one near the terminus and the other in the vicinity of the gubernaculum. This latter pair is variable in position and often difficult to observe. Tip of tail conical with a small appendage. Bursa absent.

Infective-stage juveniles (3rd stage) (for illustration, see Poinar, 1966) much narrower than corresponding parasitic juvenile. Mouth and anal opening closed, esophagus and intestine collapsed; tail pointed; lateral fields distinct.

The development and bionomics of both nematodes were studied and compared under laboratory conditions. The observations made here on *N. carpocapsae* were similar to those Weiser (1966) reported earlier and the infection pattern of this nematode is similar to that previously reported for the DD-136 nematode (Poinar and Himsworth, in press). Aside from a quicker development of the DD-136 nematode to the adult stage in the insect, no major differences were discerned between the two nematodes during the course of this investigation and it is concluded that both belong to a single species.

DISCUSSION AND CONCLUSIONS

Although breeding studies establish that the nematodes are conspecific, there is evidence indicating that they are not identical. Morphological variability prevents the use of structural characters for differentiating between the two nematodes. However, Jackson (1965, 1966) detected differences in response to axenic growth media and in serological reactions. Although both nematodes behaved similarly on solid media, in fluid environments DD-136 normally developed to the adult stage, while *N. carpocapsae* usually did not develop at all. In further investigations along this line, Hansen and Yarwood (1967) found that in axenic liquid media distributed as a film over glass wool (for method, see Hansen and Cryan, 1966), very few of the infective juveniles of *N. carpocapsae* exsheathed and reached

TABLE 4. Distance from head to excretory pore in infective juveniles of the Czechoslovakian and DD-136 strain of *N. carpocapsae* Weiser and their cross F_1 progeny.[1]

Date	DD-136	F_1	Czechoslovakian
1 March 1966	37.7	38.4[2]	40.8
12 March 1966	37.0	39.0	42.0
20 March 1966	37.7	38.4	40.8

[1] Each figure represents the average of 50 individuals.
[2] Means not flanked by lines are significantly different at the 5% level.

the adult stage where reproduction would occur, while most of the DD-136 nematodes reached the adult stage and reproduced. However, when developing stages of *N. carpocapsae* were placed in the same environment, reproductive cultures were readily established, suggesting that a major difference between the two nematodes is the ability of the infective juveniles to exsheath and initiate development when placed in liquid media.

Do these differences warrant subspecific status for these organisms? Subspecies are populatations capable of interbreeding, yet which differ from each other taxonomically and are isolated ecologically or geographically. These nematodes interbreed, but the great degree of variability rules out morphological separation on any practical basis. The distance from the head to the excretory pore in the infective juveniles was the only consistent difference found in this study. Yet it should be pointed out that a relatively small population of both nematodes was examined and this difference may represent only a relative one between isolated populations. Both nematodes were discovered in geographically isolated areas, DD-136 from Virginia and *N. carpocapsae* from Czechoslovakia. However, there is no way of knowing the precise range of either nematode, especially since DD-136 has now been introduced into Europe for field tests.

Host specificity here probably is not as important as in other groups, since both nematodes do not develop on host tissue alone, but on a mixture of host tissue and bacteria. This association with certain bacteria permits them to parasitize a wide range of insects. The DD-136 nematode was found to be associated with a characteristic bacterium, *Achromobacter nematophilus* Poinar and Thomas. A closer association between these nematodes would have been established if the bacterial flora of *N. carpocapsae* could have been examined for the presence of *A. nematophilus*, or a closely related form. Unfortunately, natural xenic colonies of this nematode were recently lost (Weiser, personal communication).

It is possible that adaptation to hosts in a particular physical environment occurs, however since both nematodes were originally found in codling moth larvae, differentiation along these lines may not yet have developed.

It is the author's impression that this and related species are composed of a complex of separate populations throughout a major part of the world, all modified to a greater or lesser extent and perhaps adapted to a particular environmental or host "niche."

The author feels that taxonomic (morphological and physiological) differentiation between these two nematodes has not yet reached the point where they can be called distinct subspecies. On this basis, these nematodes should be assigned to an infrasubspecific rank. Although they may be considered populations from the zoological standpoint, a more appropriate term might be strain. This is an infrasubspecific category which is used in microbiology and is defined in the International code of nomenclature of bacteria and viruses (1958) as being "made up of the descendants of a single isolation in pure culture." This may be especially appropriate here since both nematodes can be maintained in the laboratory continuously on living insects or artificial media, similar to bacterial cultures. It is realized that this term has no official standing in the zoological code of nomenclature.

It is proposed that the DD-136 nematode now be considered as the DD-136 strain of *N. carpocapsae* Weiser and what was originally *N. carpocapsae* Weiser be known as the Czechoslovakian strain of *N. carpocapsae* Weiser.

In studying the DD-136 nematode, Schmiege (1962, 1963) obtained a wide range of deMan values when he compared adults of the first and second generation, finding that during growth of the female, the size of the body organs did not vary proportionally to the total body size, and he concluded that the deMan

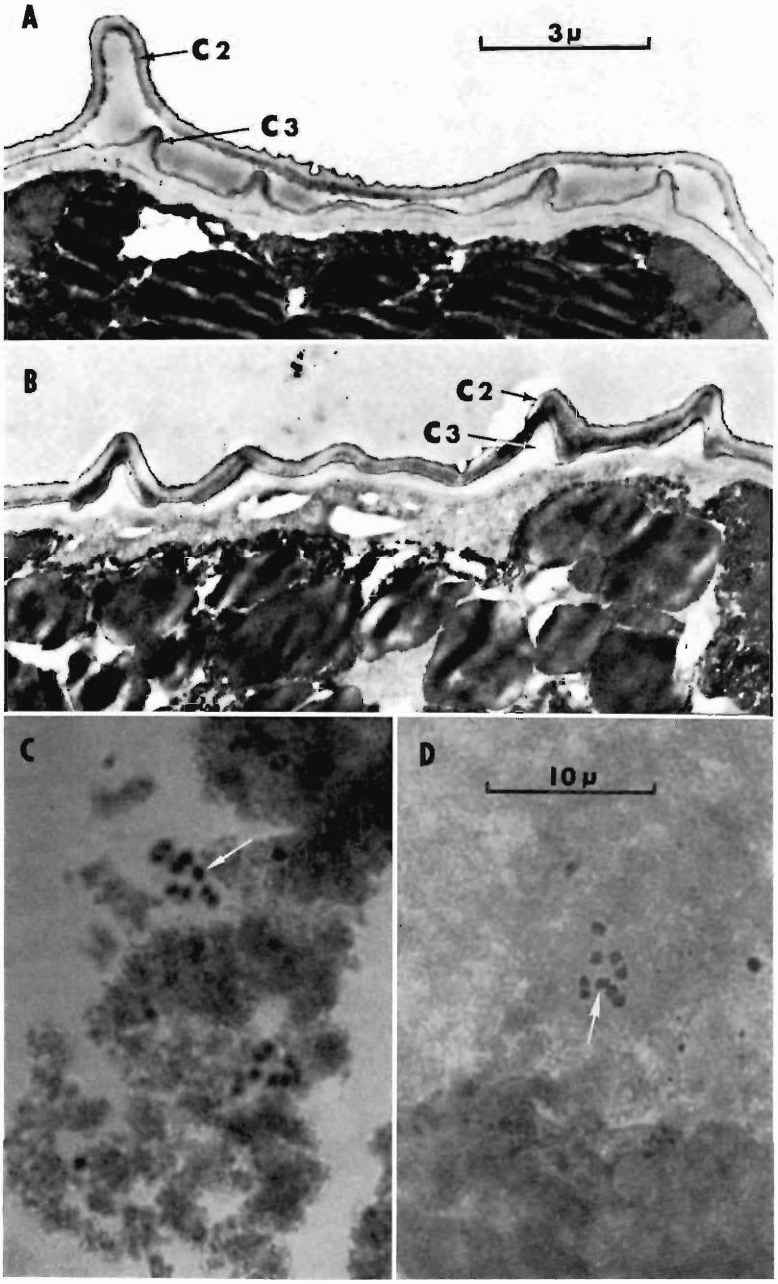

Figure 1. *Neoaplectana carpocapsae* Weiser. A. Electron micrograph of the lateral field of the infective juvenile of the Czechoslovakian strain. B. Same of the DD-136 strain (magnification same as A). C. Male chromosomes of the DD-136 strain (magnification same as D). D. Same for the Czechoslovakian strain. (Arrow points to the univalent sex chromosome.) C2—second stage cuticle, C3—third stage cuticle.

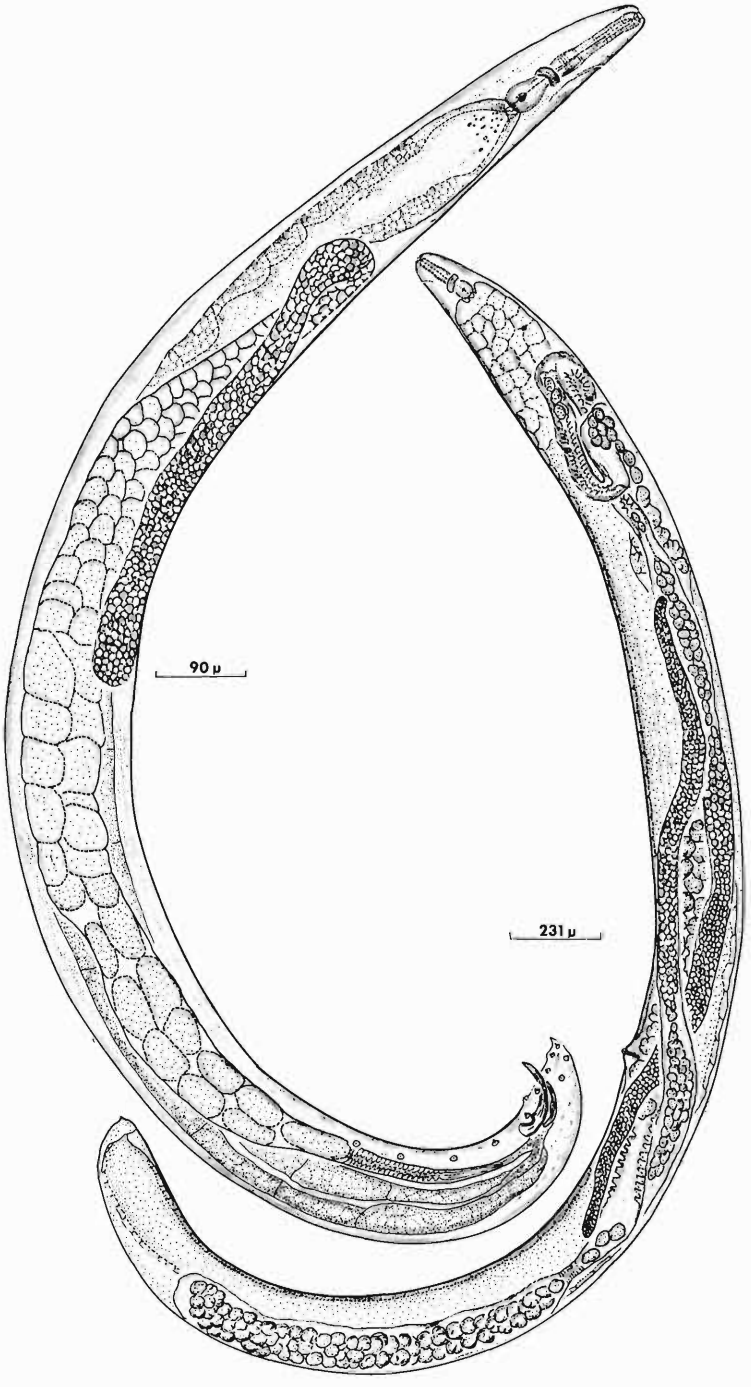

Figure 2. Adult forms of the DD-136 strain of *Neoaplectana carpocapsae* Weiser.

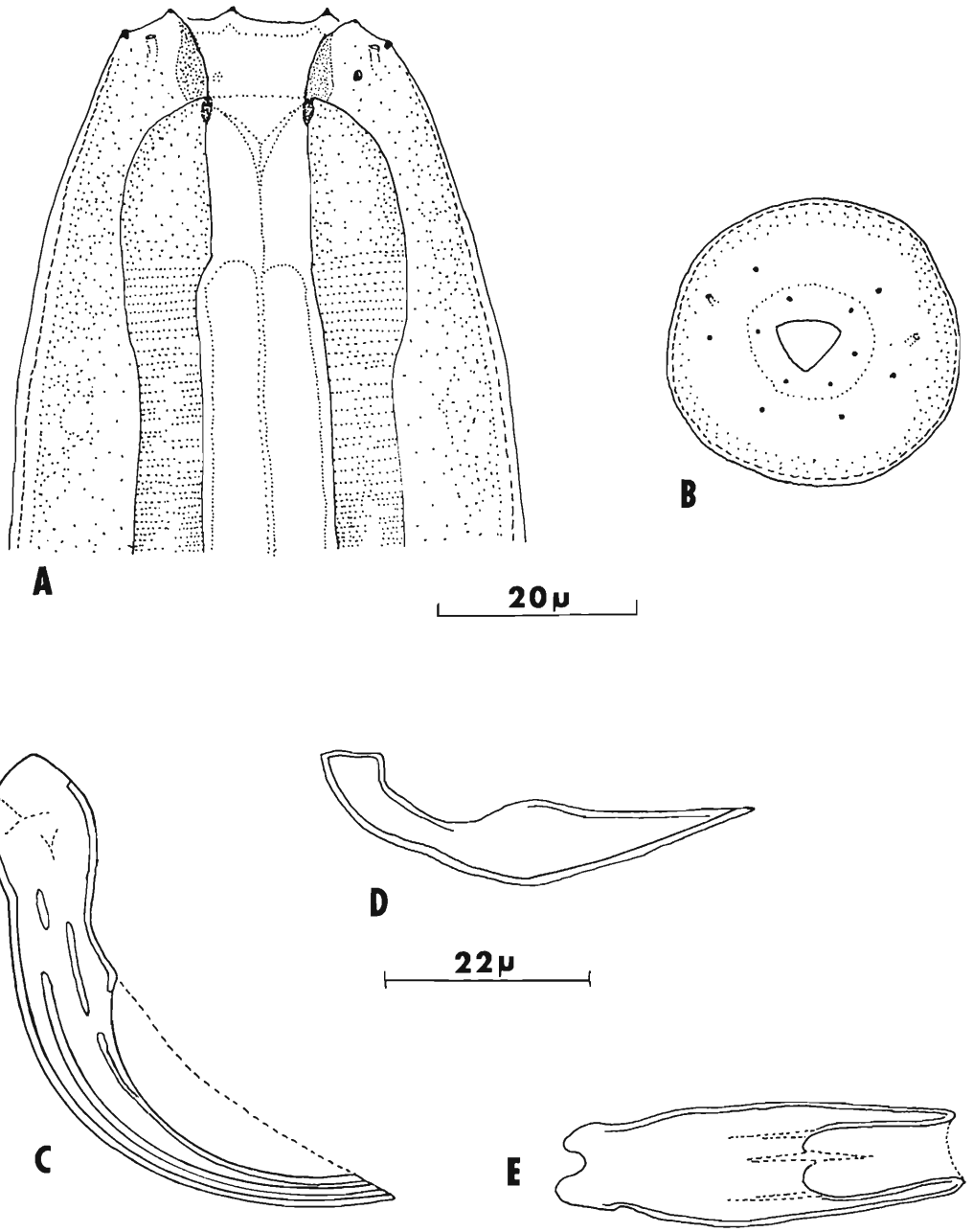

Figure 3. DD-136 strain of *Neoaplectana carpocapsae* Weiser. A. Dorsal view of head region of the female. B. "En face" view of female. C. Lateral view of spicule. D. Lateral view of gubernaculum. E. Dorsal view of gubernaculum.

index was not a good character to distinguish species of this group. Weiser (1966) also mentioned the extreme size variation in the Czechoslovakian strain, and results in the present study support these observations. The variable index values occur because of differential growth rates of various body areas. When there is ample nourishment, usually the condition for the first generation adults, the nematodes, especially the females, enlarge after reaching the adult stage. The amount of growth that occurs in the body between the base of the esophagus and anus is proportionally greater than that which occurs in the esophageal and caudal region, resulting in variable indices. Added variability arises from the diminishing adult size with each new generation in the host.

With the limited value of measurements for diagnosis we see that distinguishing *N. carpocapsae* Weiser from previously described members of the genus is difficult. Weiser (1955) listed no diagnostic characters with the original description of *N. carpocapsae* and in a later publication (Weiser and Kohler, 1955) used various morphological characters, both quantitative and qualitative, for the separation of species. However, many of these characters have never been evaluated, and since many of the earlier descriptions gave no reference to variation, the validity of these characters for diagnosis is questionable. The manner of treating the nematode prior to measurement is also of considerable importance. The structure of the stoma for instance varied considerably depending on how the nematodes were killed and fixed. Thus before *N. carpocapsae* Weiser can be clearly separated from previously described species, some knowledge of the variability and breeding potential of the latter should be acquired. When living material is available, further hybridizing studies will be conducted to determine the biological relationship between *N. carpocapsae* and other neoaplectanid nematodes.

The diagnostic value of biological characters such as the presence of pigmy females in the 2nd and 3rd generation, and the retention of eggs in the uterus resulting in viviparity should be evaluated.

In general, nematode species have been defined mainly on a morphological and host preference basis, thus establishing morphological rather than biological species. Although many morphological species are probably also true biological species, when clear-cut differences are not apparent, reproductive isolation can serve as the final decision for specific identity. Neoaplectanid and free living nematodes lend themselves well for this type of study, while other forms can be examined when adequate methods of handling and rearing are developed.

Studies involving hybridization have already been done with some of the biological races of *Ditylenchus dipsaci* (Kühn). Races occur which are morphologically indistinguishable and restricted to certain host plants. This host specificity breaks down on callus tissue and interbreeding occurs, indicating that the races are conspecific (Eriksson, 1965). Roberts et al. (1954) used this criterion in determining if the ovine and bovine strains of *Haemonchus contortus* were distinct species and Augustine (1939) held the same view when comparing *Strongyloides* from different animal hosts. Duke (1964) recently established conspecificity between the simian and human strains of *Loa loa* and found that the characters of size and periodicity of microfilariae, which varied in both strains, segregated out according to a simple Mendelian pattern in the F_1 and F_2 generations.

Further study on the strains of *N. carpocapsae* Weiser may reveal other differences between them, however it appears that both nematodes diverged relatively recently from a common stock and the differences found so far (mainly physiological) reflect the state of continued isolation under different environmental conditions.

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SUMMARY

A description of the DD-136 nematode is given. Detailed qualitative and quantitative comparative studies were made on *Neoaplectana carpocapsae* Weiser and the DD-136 nematode. These nematodes are able to inter-

breed and on this basis are considered conspecific. After a discussion of the similarities and differences between these nematodes and the variation associated with them, it was concluded to assign them to the infrasubspecific rank of strain. It is proposed that the DD-136 nematode be considered as the DD-136 strain of *N. carpocapsae* Weiser and what was originally *N. carpocapsae* be known as the Czechoslovakian strain of *N. carpocapsae* Weiser.

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