Revision of the Genus Nacobbus Thorne and Allen, 1944 (Nematoda: Tylenchoidea)

S. A. SHER¹

Abstract: All four species and one subspecies of the genus Nacobbus Thorne and Allen, 1944 were studied and measured from type specimens. Nacobbus batatiformis Thorne and Schuster, 1956; N. serendipiticus Franklin, 1959; and N. serendipiticus bolivianus Lordello, Zamith and Boock, 1961 are proposed as synonyms of N. aberrans (Thorne, 1935) Thorne and Allen, 1944. Nacobbus aberrans is distinguished from the type species N. dorsalis Thorne and Allen, 1944 by the larger number of body annules between the vulva and anus; the lower position of the vulva in the young female; and the shape and number of eggs retained in the mature female. Key Words: Taxonomy, Nacobbus.

Juveniles, immature females and males of Nacobbus Thorne and Allen 1944, have been found, usually in low numbers (1 to 10 per 477 cc of soil), in soil samples from widely distributed areas (usually uncultivated) in the western United States. Rarely have the mature females been found in the roots, even after repeated sampling of some of these infested areas. Native plants from these places were grown in infested soil in the greenhouse on several occasions without finding mature females in the roots. Because these specimens could not be identified and also because N. batatiformis Thorne and Schuster, 1956 is a class "A" pest subject to strict quarantine regulations in California, this study of the described species and the widely-distributed California specimens was undertaken.

Four species and one subspecies have been described in the genus *Nacobbus*. A key to the four species of *Nacobbus*, adapted from Thorne and Schuster's key of 1956 (14), was presented by Franklin in 1959 (6). These keys, using juvenile, immature female, mature female and male characters were based

on the original descriptions. For this revision preserved type specimens of all the described species were studied and measured. In addition, fresh material of N. *dorsalis* from the type locality was used for comparison.

HISTORY

Thorne and Allen (12) pointed out that Cobb (4) was apparently the first to record specimens of *Nacobbus* from Colorado, U.S.A. Cobb illustrated a male and juvenile which he considered to be *Heterodera schachtii* Schmidt, 1871 but the illustrations clearly indicate they belong to the genus *Nacobbus*.

The first species of *Nacobbus* was described as *Anguillulina aberrans* Thorne, 1935, from a native plant, *Atriplex confertifolia* (Torr. and Frem.), collected in the desert foothills west of Utah Lake, Utah, on May 25, 1927 (11). Additional collections of this nematode were made in 1933 several miles west and about 95 miles south of the original location (11).

In 1944 Thorne and Allen proposed the genus *Nacobbus* (13) based upon pronounced sexual dimorphism, elongated dorsal esophageal glands overlapping the intestine, and the galls or swellings produced on host roots. A new species, *Nacobbus dorsalis* Thorne and Allen, 1944, from southern California was designated as the type species (13). They

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included this genus in the family Tylenchidae and considered it most closely related to *Pratylenchus* Filipjev, 1936 and what is now *Radopholus* Thorne, 1949. *Anguillulina aberrans* was placed in *Nacobbus* by Thorne and Allen, 1944, and it was noted that Cobb's description of 1918 from Colorado could not be identified to species from the information given. *N. dorsalis* was distinguished from *N. aberrans* by the shape of the mature female, male tail and the ratio of tail length to vulva-anus distance in the immature female.

Nacobbus batatiformis Thorne and Schuster, 1956 (14) was described from sugar beets (Beta vulgaris) grown in Mitchell, Nebraska and was reported on the same host from various other areas in Nebraska; Windsor, Colorado; and Torrington, Wyoming. Host range studies by Thorne and Schuster indicated that a number of plants in the Cactaceae, Chenopodiaceae, Cruciferae, and Zygophyllaceae were susceptible, whereas many plants in the Gramineae, Liliaceae, Malvaceae, Iridaceae, Amaranthaceae and Convolvulaceae were not. Some species of the Cucurbitaceae, Umbelliferae, Compositae and Solanaceae were resistant while others were susceptible. In addition, Thorne and Schuster reported on the life cycle of Nacobbus batatiformis. This species was distinguished from the previous two species by the shape of the mature female, strongly developed median bulb and corpus, ratio of tail length to the vulva-anus distance and the position of the phasmids. Later Caveness (2) reported N. batatiformis from 14 counties in six states in the western part of the United States.

The first record of *Nacobbus* outside the western United States was that by Franklin (6) who described a new species from England, *N. serendipiticus* Franklin, 1959. This species, which produced characteristic galls

on the lateral roots, was found on tomato in a glasshouse nursery in only one locality. It was distinguished from the other species by the shape of the mature female, vulva-anus distance in relation to tail length, position of the phasmids, stylet length in the female, shape of first stage juvenile tail and incisures on juvenile tail. In pot tests mangold, lettuce and Solanum nigrum were found to be hosts (6). A later host test, with some of the plants tested by Thorne and Schuster for N. batatiformis, indicated the same reaction to N. serendipiticus in 18 plants and different results with 4 plants (3). Prasad and Webster (10) reported on the effect of temperature on rate of development, and Clark (3) recorded the development and life history of N. serendipiticus. In 1968 de Bruijn and Stemerding (1) reported N. serendipiticus in the Netherlands in a glasshouse, and in an inoculation trial showed the pathogenicity of this nematode to tomatoes.

Nacobbus serendipiticus bolivianus Lordello, Zamith and Boock, 1961 was described from the roots of potato (Solanum andigenum) collected in the Cochabamba Valley in Bolivia at an altitude of 3,200 meters (8). It was distinguished from N. serendipiticus serendipiticus by the inner band of the lateral fields being somewhat narrower than the outer ones, and by the wider males.

Thorne in 1961 (12) considered the H. schachtii reported from Colorado in 1918 by Cobb as a synonym of *Nacobbus batatiformis* on the basis of a survey indicating the widespread distribution of *N*. batatiformis in Colorado (2). He also discussed the history, distribution and control of *N*. batatiformis.

Genus Nacobbus Thorne and Allen, 1944

Nacobbus Thorne and Allen, 1944, pp. 27-28; Thorne, 1961, p. 239; Goodey, 1963, p. 85.

DIAGNOSIS EMENDED: Nacobbinae. Sexual dimorphism present, mature female swollen, monodelphic; sedentary in the galls or swellings of plant roots. Male vermiform, caudal alae not well developed, enveloping tail. Cephalic framework and stylet welldeveloped. Median bulb with strongly developed valve, except in juveniles with normal valve. Esophageal glands elongated, overlapping intestine dorsally.

TYPE SPECIES: Nacobbus dorsalis Thorne and Allen, 1944.

Nacobbus dorsalis Thorne and Allen, 1944 (Fig. 1)

Nacobbus dorsalis Thorne and Allen, 1944, pp. 28-30; Goodey, 1963, pp. 85-86.

Measurements (6 mature \circ topotypes): L = 1.4 mm (1.3-1.6); stylet = 22 μ (20-24).

(10 immature \circ topotypes): L = 0.78 mm (0.59–1.06); a = 30 (26–34); b = 6.1 (5.1–7.3); b' = 2.8 (2.0–3.9); c = 39 (30– 52); c' = 1.1 (0.8–1.4); V = 95 (94–97); VA¹ = 10 (8–14); stylet = 22 μ (19–24).

(10 & topotypes): L = 0.89 mm (0.72– 1.16); a = 30 (25–41); b = 6.6 (5.2–8.7); b'= 3.6 (2.7–4.7); c = 34 (25–38); c' = 1.6 (1.4–1.8); stylet = 23.5 μ (20–27); gubernaculum = 9 μ (8–11); spicules = 30 μ (27– 35).

Mature female (sedentary in roots).—Body enlarged to oval or spherical shape (Fig. 1 G–J), short anterior projection containing lip region to median bulb; elongated posterior portion containing tail, vulva and portion of the uterus, usually with 1 to 4 eggs in tandem.

Swollen spindle-shaped females without eggs but with single, convoluted ovary (Fig. 1 F); as females age body becoming wider and rounder with more eggs (Fig. 1 G-H) to almost spheroidal and completely filled with eggs containing first and second stage juveniles (Fig. 1 I-J).

Immature female (migratory in soil and roots).—Body vermiform. Lip region hemispherical, not set off, with three to four annules. Stylet knobs round. Median bulb well-developed with large conspicuous valve. Esophageal glands elongated, overlapping intestine dorsally more than three times body width. Lateral field with four incisures, incompletely areolated. Tail rounded with 10 to 18 annules, distal annules wider. Phasmids below level of anus, in anterior portion of tail.

Male.—Similar to immature female except for sexual dimorphism; caudal alae inconspicuous, enveloping tail.

Juveniles.—First stage in the egg in female. Labial framework, stylet, esophagus and body annulation not well-developed. Tail rounded (Fig. 1 D). Second stage juvenile in the egg (Fig. 1 E) or free in the soil. Labial framework, stylet, esophagus and body annulation well-developed.

Type material.—Original specimens used in the description of this species are deposited in the USDA Nematode Collection, Nematology Investigations, Beltsville, Maryland, U.S.A. Topotypes collected from the type host, Erodium cicutarium (L.) L'Hér., and at the type locality, Caliente, California, are in the collections of the Departments of Nematology, University of California, Davis and Riverside, California, U.S.A.

Diagnosis.—Nacobbus dorsalis can be identified by the number of annules (8 to 14) between the vulva and the anus (best seen in the immature females), position of the vulva in the immature females (94–97%) and the almost round mature female with elongated posterior region and filled with eggs which usually contain juveniles.

The original slides labeled Nacobbus dorsalis used to describe this species contained, in addition to Nacobbus, specimens of a juvenile Heterodera species and females of a

¹ VA = number of annules between vulva and anus.

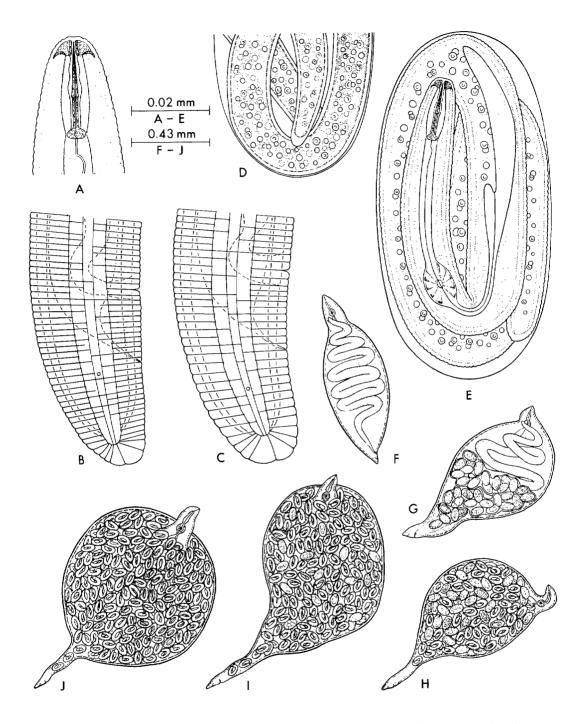


FIG. 1. Nacobbus dorsalis. A. Immature female, anterior region; B-C. Immature female, posterior region; D. Portion of egg with first stage juvenile; E. Egg with second stage juvenile; F-G. Early stages of mature female; H-J. Later stages of mature female.

Pratylenchus species. These are illustrated in Thorne and Allen, 1944 (13) as Fig. 1 F (posterior portion of first stage larva) and Fig. 1 B (posterior portion of young female).

Specimens identified as *N. dorsalis* have been collected from the following habitats and localities in California: *Salvia* sp. roots, 4 miles NW of Desert Springs, Los Angeles County; *Prunus* sp. soil, Mint Canyon, Los Angeles County; barley and melon soil, west side of San Joaquin Valley, Kern County; fallow soil, Bakersfield; soil around unknown plants, Box Springs Mountains, Riverside; and soil around unknown plants, Twin Peaks, San Francisco.

Nacobbus aberrans (Thorne, 1935) Thorne and Allen, 1944

(Fig. 2)

Anguillulina aberrans Thorne, 1935, pp. 510–512. Pratylenchus aberrans: Filipjev, 1936, p. 81.

- Nacobbus aberrans: Thorne and Allen, 1944, p. 30.
- Nacobbus batatiformis Thorne and Schuster, 1956, pp. 131–134, new synonymy.
- Nacobbus serendipiticus Franklin, 1959, pp. 286-292; Clark, 1967, pp. 92-99, new synonymy.
- Nacobbus serendipiticus bolivianus Lordello, Zamith and Boock, 1961, pp. 209-213, new synonymy.

Measurements (6 mature \circ topotypes): L = 1.0 mm (0.8–1.2); stylet = 22 μ (20–24).

(12 immature \circ topotypes): L = 0.84 mm (0.71-0.93); a = 27 (23-40); b = ?; b' = 3.8 (2.8-4.1); c = 37 (24-40); c' = 1.2 (0.9-1.5); V = 93 (92-94); VA = 20 (15-24); stylet = 23 μ (21-25).

(7 & topotypes): L = 0.86 mm (0.71– 0.92); a = 29 (24–31); b = 7.0 (6.4–7.2); b' = 3.6 (3.4–4.0); c = 38 (32–42); c' = 1.3 (1.2–1.4); stylet = 25 μ (23–27); gubernaculum = 7 μ (6–8); spicules = 27 μ (21–30).

(Nebraska 6 mature $9 \ 9$); L = 1.1 mm (1.0-1.4); stylet = 22 μ (20-24).

(6 immature $\varphi \varphi$): L = 0.78 mm (0.74-0.84); a = 30 (27-32); b = 7.6 (7.0-9.3); b' = 4.2 (4.1-4.5); c = 34 (30-38); c' = 1.5 (1.3-2.0); V = 93 (92-94); VA = 22 (18-25); stylet = 21 μ (20-23). (5 $\delta \delta$): L = 0.80 mm (0.68-0.88); a = 33 (28-39); b = 6.7 (6.5-8.3); b' = 4.3 (4.2-4.4); c = 35 (33-36); c' = 1.5 (1.3-1.7); stylet = 24 μ (23-27); gubernaculum = 9 μ (7-11); spicules = 28 μ (24-34).

(England 7 mature $\varphi \varphi$): L = 1.08 mm (0.91-1.45); stylet = 22 μ (20-23).

(10 immature $\circ \circ$): L = 0.71 mm (0.60-0.78); a = 28 (23-31); b = 5.4 (5.1-5.8); b' = 3.3 (2.8-3.9); c = 29 (23-32); c' = 1.5 (1.3-1.6); V = 92 (91-93); VA = 20 (16-24); stylet = 20 μ (19-21). (6 $\delta \delta$): L = 0.78 mm (0.67-0.88); a = 30 (24-32); b = 6.1 (5.6-6.6); b' = 4.5 (3.5-5.4); c = 34 (30-38); c' = 1.2 (1.0-1.5); stylet = 25 μ (23-27); gubernaculum = 8 μ (7-10); spicules = 27 μ (26-32).

Mature Female (sedentary in roots).— Body enlarged, spindle-shaped usually tapering anteriorly and posteriorly. Unsegmented eggs seen in posterior portion of body. Tail terminus often nipple-shaped.

Immature Female (migratory in soil and roots).—Body vermiform. Lip region hemispherical, not set off, with three to four annules. Stylet knobs round. Median bulb well-developed with large conspicuous valve. Esophageal glands elongated, overlapping intestine dorsally more than three times body width. Lateral field with four incisures, incompletely areolated. Tail rounded with 10 to 17 annules; distal annules irregular, wider. Phasmids below level of anus in anterior portion of tail.

Male.—Similar to immature female except for sexual dimorphism.

Juvenile.—Similar to N. dorsalis.

Type Material.—The original specimens used to describe this species were available

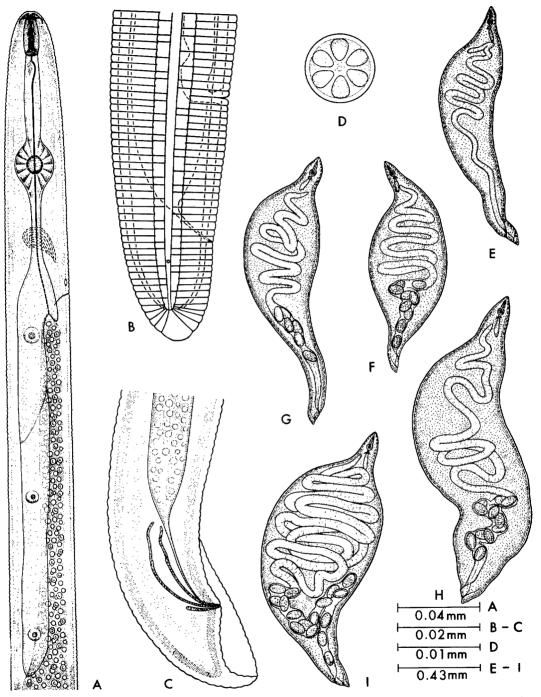


FIG. 2. Nacobbus aberrans. A. Immature female, anterior region; B. Immature female, posterior region; C. Male, posterior region; D. Male, face view; E. Early stage of mature female; F-I. Later stages of mature female.

for study and are deposited in the USDA Nematode Collection, Nematology Investigations, Beltsville, Maryland, U.S.A.

Diagnosis.—N. aberrans can be distinguished from the type species by the number of annules (15 to 24) between the vulva and anus, slightly higher position of the vulva in the immature female, and the spindle-shaped mature females that only have eggs in the posterior portion of the body. The maturing sedentary females of N. dorsalis (Fig. 1 G) are similar to the mature females of N. aberrans (Fig. 2 G–I).

Type material of N. aberrans, N. batatiformis, N. serendipiticus and N. serendipiticus bolivianus was examined and no morphological differences were observed. The posterior position of the phasmids in the immature female and the short caudal alae reported in the original description of N. aberrans were not seen in the type specimens. The spermatheca with sperm reported in N. batatiformis was not seen in the original specimens from Mitchell, Nebraska or other localities in Nebraska, and the stylet in these specimens measures 20–24 μ . In addition, the host range of N. serendipiticus is similar to N. batatiformis (3). Franklin (6) states for the male of N. serendipiticus "the head probably has four annules and a labial disc for the male. Eighteen face views were made of three populations of N. aberrans as follows: England 5 δ , 3 immature 9, 2 juveniles; Wyoming 3 & &, 2 juveniles; and Nebraska 3 & &. Only one of these face views (& England) exhibited what might be considered a labial disc. The other face views are similar to the illustration in Fig. 2D. N. batatiformis, N. serendipiticus, and N. serendipiticus bolivianus are therefore proposed as new synonyms of N. aberrans.

Additional specimens identified as *N*. *aberrans* have been examined from the following hosts and localities: sugar beets, Lin-

coln, Nebraska and Wyoming; and potato, Carhuaz, Peru.

Because of insufficient and poorly preserved material, specific identifications of *Nacobbus* specimens from Imperial County, California; Lake Powell, Utah; and Huamantla, Tlaxcala, Mexico were not made.

DISCUSSION

The genus *Nacobbus* is considered to contain only two closely related species that can be most easily distinguished by the number of annules between the vulva and anus of the immature, vermiform female.

This genus appears to be native to the western part of North and South America where its members parasitize a number of native and agricultural plants causing galls on the roots that are similar to those produced by the genus *Meloidogyne*. This genus apparently has been introduced to England and the Netherlands, where it has been found infecting tomato plants under glasshouse conditions. The report of *Nacobbus* in India (9) could not be confirmed.

The pathogenicity of *Nacobbus* to important agricultural crops, the similarity of its symptoms to those caused by root-knot nematodes, its wide host range and incompletely known geographical distribution, and its classification in the Tylenchoidea make it a most interesting and important genus to observe.

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