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SYNLOPHE OF *NEMATODIRUS NEOTOMA* (TRICHOSTRONGYLOIDEA)

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ABSTRACT: The synlophe of *Nematodirus neotoma* from *Neotoma* spp. is characterized. The cervical synlophe is composed of 30-32 and 36-42 ridges in males and females, respectively. Of these, 14 and 20-22 ridges are continuous in the cervical zone and extend to the base of the cephalic expansion. Six pairs of lateral ridges are discontinuous but extend greater than one-third the length of the cervical region. In both males and females, the number of ridges increases posteriad, terminating near the bursa in the male, and extending the entire length of the body in the female. The synonymy of *N. neotoma* and *N. tortuosus* was confirmed.

Studies have indicated the importance of the synlophe as a character in trichostrongyloid systematics (Durette-Desset, 1971, 1985; Lichtenfels and Pilitt, 1983; Rossi, 1983; and others). Among *Nematodirus* spp. (Trichostrongyloidea: Nematodirinae), detailed studies of the synlophe have largely been limited to those species parasitic in ruminants (Durette-Desset, 1978, 1979; Lichtenfels and Pilitt, 1983; Rossi, 1983; Hoberg et al., 1986; Hoberg and Rickard, 1988).

Nematodirus neotoma Hall, 1916, and *N. tortuosus* Tucker, 1941, were originally described from woodrats in Colorado (*Neotoma desertorum* Cary, *N. mexicana fallax* Merriam, *N. floridana baileyi* Merriam, and *N. cinerea rupicola* Allen) and California (*N. lepida intermedia* Rhoads and *N. fuscipes macrotis* Thomas), respectively (Hall, 1916; Tucker, 1942). Miller and Schmidt (1982) reduced *N. tortuosus* as a synonym of *N. neotoma*.

Although *N. neotoma* can be differentiated from its congeners based on current descriptions, the synlophe and cephalic structures were never defined in previous studies. In the study reported herein, the synlophe and cephalic structures of *N. neotoma* are described, and the synlophe is compared with that of other *Nematodirus* spp. The occurrence of *N. neotoma* in a host-group not typical of its congeners is discussed with references to parasite morphology and parasite-host

biogeography. Additionally, the synonymy of *N. neotoma* and *N. tortuosus* is confirmed based on characteristics of the synlophe in the cervical region.

MATERIALS AND METHODS

The description of the synlophe and cephalic structures is consistent with the methodology and terminology presented by Lichtenfels and Pilitt (1983). In the description, the cervical region is the zone extending anteriad from the cervical papillae and excretory pore to the posterior margin of the cephalic expansion. Specimens of *Nematodirus neotoma* were examined using interference contrast microscopy (Leitz) and scanning electron microscopy. Prior to examination, material for light microscopy was transferred to 70% ethanol/5% glycerine and cleared in glycerine by evaporation. Ten specimens of each sex were prepared as temporary whole mounts, and 5 specimens of each sex were studied in transverse sections cut by hand with a scalpel blade. Eight male and 7 female specimens were examined using SEM (stubs submitted to the USNM Helm. Coll. No. 75507). All measurements are in μm unless stated otherwise.

Specimens examined: *Nematodirus tortuosus*: 2 male specimens (type) from *Neotoma* spp. at West Los Angeles, California, USNM Helm. Coll. No. 36717. *Nematodirus neotoma*: male and female specimens from *Neotoma cinerea rupicola* at northern Weld County, Colorado, and southeastern Laramie County, Wyoming, 15 October 1979 (borrowed from collection of G. D. Schmidt, Nos. GK-7 and GK-8).

RESULTS

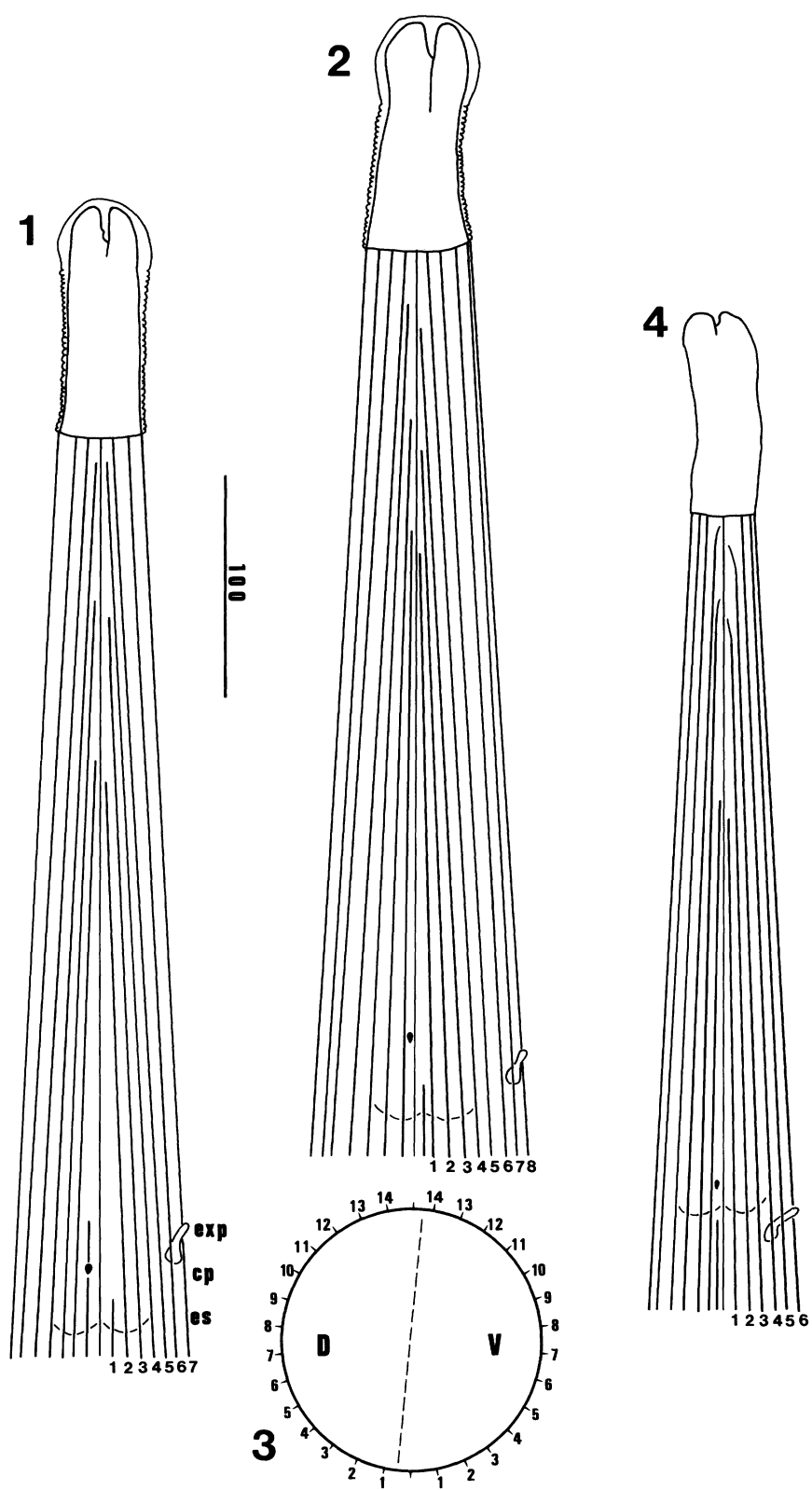
Cuticular morphology of *N. neotoma* (Figs. 1-16)

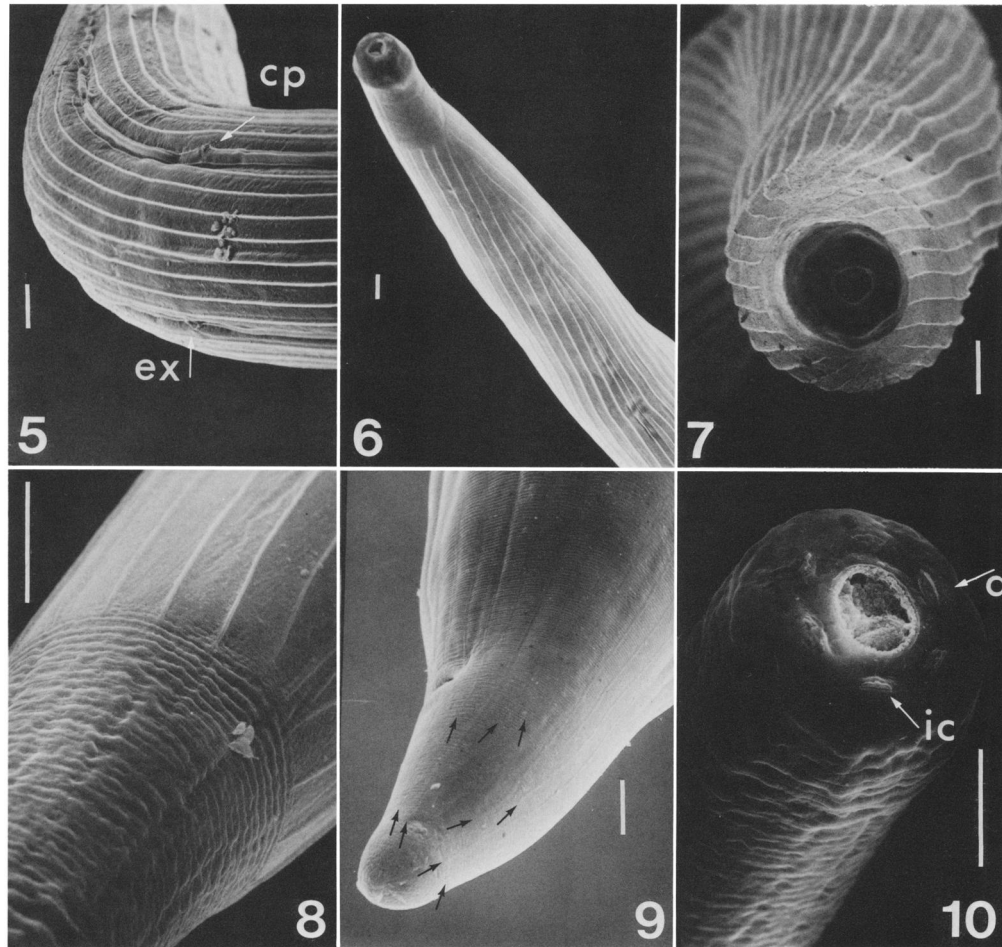
Synlophe: At the level of the esophagus and cervical papillae, the synlophe of *N. neotoma* consists of a bilaterally symmetrical system of 30-32 ridges in males and 36-42 ridges in females. The fine lateralmost cervical ridges originate 1,000-1,500 from the cephalic

Received 20 October 1987; revised 6 January 1988; accepted 15 February 1988.

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FIGURES 1-4. Synlophe of *Nematodirus neotoma*. Scale = 100 μm , same for Figures 1, 2, and 4. 1. Male, cervical synlophe, right lateral view (excretory pore = exp, cervical papilla = cp, and esophagus = es). Origin of fine lateralmost ridge not shown. 2. Female, cervical synlophe, right lateral view. 3. Schematic of transverse section showing synlophe at level of cervical papilla and esophagus in male (not to scale). 4. Synlophe of *N. tortuosus* (= *N. neotoma*), right lateral view in male (type).





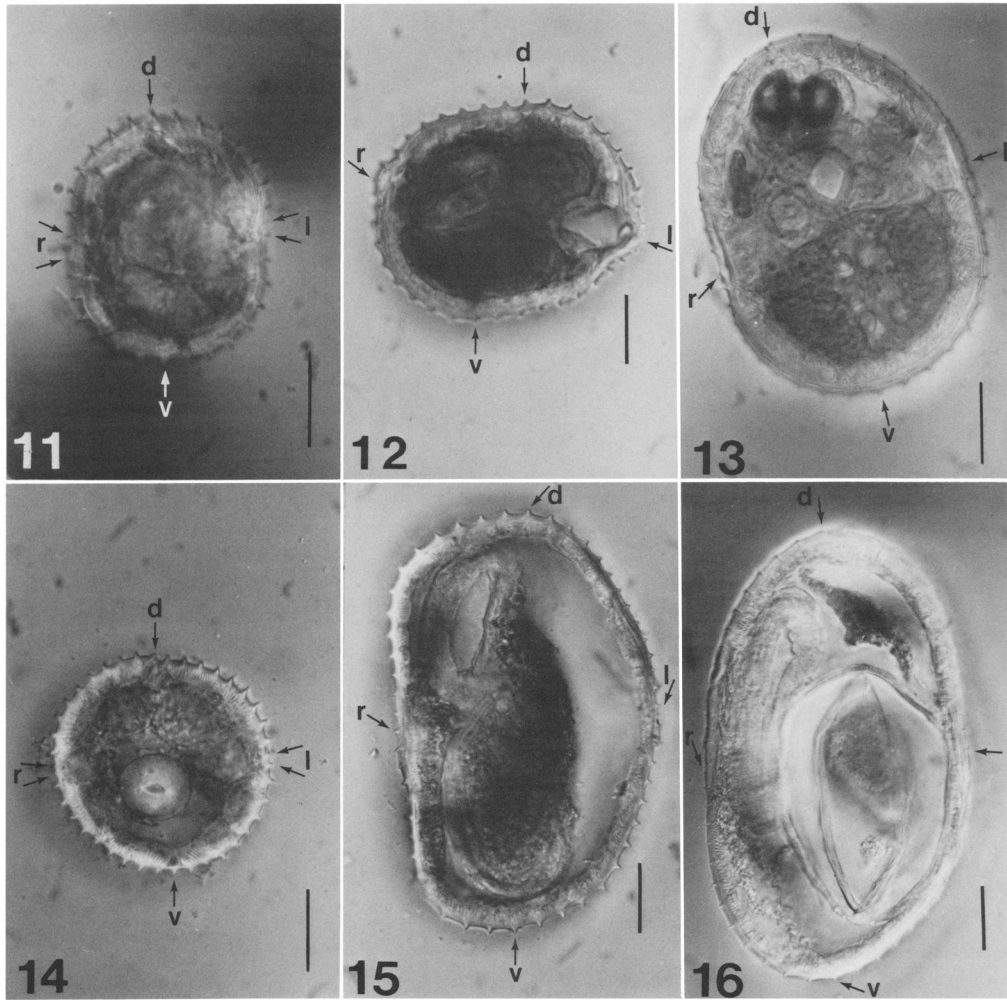
FIGURES 5–10. Scanning electron microscopy of *N. neotoma*. All scales = 10 μ m. 5. Cervical synlophe, left lateral view, showing left cervical papilla (cp) and excretory pore (ex). 6. Cervical synlophe, right lateral view, showing pattern of discontinuous ridges anterior to cervical papilla. 7. En face view of female, showing 20 continuous ridges extending to the base of the cephalic expansion. 8. Detail of synlophe at base of cephalic expansion showing termination of cervical ridges and transverse striations on cephalic expansion. 9. Caudal extremity of female showing minute cuticular ridges adjacent to tail extending posteriad to the vulva. Arrows indicate points of termination for individual ridges. 10. En face view of cephalic extremity of female showing perioral denticles, papillae of inner circle (ic), and amphids (a).

expansion. The right lateral ridge is occasionally interrupted at the level of the cervical papilla. The seventh and eighth ventral ridge is interrupted at the excretory pore in males and females, respectively. Fourteen ridges in males and 20–22 ridges in females are continuous in the cervical zone and terminate at the base of the cephalic expansion. Six pairs of lateral ridges extend greater than one-third the cervical distance but terminate before reaching the cephalic expansion. All ridges are perpendicular and there is no gradient in height.

Posteriad from the cervical zone the numbers of ridges increase in both males and females. Slightly anterior to the midbody in males there are 35–36 ridges; at the midbody, 39–40. At the level of the proximal end of

the spicules, there are 47–49 ridges; dorsally, the ridges become markedly reduced in height. The synlophe terminates 350–400 from the bursa. At the midbody in females, the synlophe is composed of 47–55 ridges; maximum observed posterior to this region is about 60 ridges. Within a distance of 500 anterior to the vulva, the dorsal ridges become reduced in height. Although markedly attenuated posterior to the vulva, and not generally discernible with light microscopy, the synlophe extends to the caudal extremity of females.

Cephalic structures: Cephalic expansion longer than wide, with slight swelling in anterior and distinct transverse striations in posterior. Papillae of internal circle 6 in number, with sclerotized semicircular supports. Papillae of the external circle indistinct. Perioral den-



FIGURES 11–16. Transverse sections of *N. neotoma* showing distribution of cuticular ridges. All figures are oriented with dorsal toward top; arrows indicate dorsal (d), ventral (v), and lateral ridges (l = left; r = right); all scales = 30 μ m. **11.** Cervical region of male with 32 ridges; note small ridges laterally. **12.** Midbody region of male with 39 ridges. **13.** Posterior region of male at level of proximal end of spicules showing 43 ridges. **14.** Cervical region of female with 41 ridges. **15.** Midbody region of female (cut at 11.5 mm from anterior in specimen measuring 23.18 mm) showing 53 ridges. **16.** Posterior to midbody (12.4 mm from anterior) showing 54 ridges; synlophe is no longer easily discernible in interference contrast beyond this point.

ticles 42–52 (46) ($n = 4$) in number for males, 46–59 (52) ($n = 7$) for females.

Comparison with *Nematodirus tortuosus*: The numbers of ridges in the type specimens of *N. tortuosus* could not be accurately determined. However, the pattern of the cervical synlophe, particularly the extent of the lateral ridges and origin and form of the lateralmost ridge appeared identical to that observed in specimens of *N. neotoma*.

DISCUSSION

The number and longitudinal extent of ridges comprising the synlophe of *N. neotoma* in the

present study, as determined by light microscopy, was generally similar to that reported previously. Although the number of perioral denticles was greater (42–52 for males; 46–59 for females) than that reported by Durette-Desset (1979), this and other differences in the numbers of ridges are considered as intraspecific variation. Based on these characters, the synonymy of *N. neotoma* and *N. tortuosus* is confirmed.

Previous descriptions of *Nematodirus* spp. from cricetids did not consider details of the synlophe. Hall (1916), in describing *N. neotoma*, reported

the presence of longitudinal lines in males and females. Tucker (1942) described longitudinal ridges throughout the length of males of *N. tortuosus*, whereas in females, the synlophe was confined to the region anterior to the vulva. Durette-Desset (1979) elucidated some details of the synlophe in *N. tortuosus*. The numbers of ridges increased posteriad attaining a maximum of 40–56 in males and 52–61 in females. The synlophe terminated within 400 μm of the vulva in females and 1,000 μm from the bursa in males. Additionally, about 40 perioral denticles were enumerated. Recently, Miller and Schmidt (1982) reported 22–48 and 26–68 ridges in males and females of *N. neotoma*, respectively (presumably a range from anterior to posterior). The synlophe in female specimens was observed to extend posteriad to the vulva.

Considering the other species of *Nematodirus* previously examined, *N. neotoma* is characterized by a substantially greater number of cervical and midbody ridges. The synlophe in the cervical region (anterior to the cervical papillae) has been characterized for only 8 species of *Nematodirus* that are parasites of the Bovidae (Lichtenfels and Pilit, 1983; Hoberg et al., 1986; Hoberg and Rickard, 1988). A bilateral system of 16 ridges was found in *N. maculosus* Becklund, 1965, an 18-ridge system was typical of *N. filicollis* (Rudolphi, 1802), *N. davtiani* Grigorian, 1949, *N. oratianus* (Raevskaia, 1929), *N. abnormalis* May, 1920, *N. spathiger* (Railliet, 1896), and *N. battus* Crofton and Thomas, 1951, and 26 ridges were reported for *N. helvetianus* May, 1920 (lateral-most extending less than one-third of the cervical distance). The midbody region has been examined in 16 species of *Nematodirus* from the Bovidae, Cervidae, and Camelidae (Becklund, 1963; Durette-Desset, 1978, 1979; Rossi, 1983). Among these only 4 species have 30 or more ridges at the level of the midbody, viz. *N. helvetianus* (30–36) from bovids, *N. europeus* Jansen, 1972 (33–36), *N. roscidus* Railliet, 1911 (34), from palearctic cervids, and *N. lamae* Becklund, 1963, from neotropical camelids (approximately 40). Additionally, *N. odocoilei* Becklund and Walker, 1967, from nearctic cervids has 34–42 ridges at the midbody (Hoberg, unpubl. data).

Species of *Nematodirus* generally are parasites of the Artiodactyla and only 2 species are known from rodents (see Kulmamatov, 1974; Durette-Desset, 1979). In addition to *N. neotoma* from *Neotoma* spp., *N. mugosaricus* Schulz, 1926, was

described from *Citellus* in the Soviet Union (Skrjabin et al., 1954). The distribution of these species appears to represent independent events of colonization of cricetids and sciurids by species of *Nematodirus* typical of ruminants (see Durette-Desset, 1979).

The widespread distribution of *N. neotoma* among *Neotoma* spp. in western North America could indicate that *Nematodirus* became parasites of woodrats prior to geographic isolation resulting in speciation and subspeciation of the host-group in the Pleistocene (see Kurtén and Anderson, 1980). Morphologically, the synlophe of *N. neotoma* appears most similar to some species characterized by a high number of ridges from camelids or cervids (Rossi, 1983; Hoberg, unpubl.). Current evidence thus suggests a possible switch from either of these host-groups to *Neotoma*. Additional study involving phylogenetic analyses will be required to evaluate the degree of relationship among *N. neotoma* and other *Nematodirus* spp.

ACKNOWLEDGMENTS

Partial funding for this study was provided by a grant from the General Research Council, Oregon State University. Dr. J. R. Lichtenfels kindly provided specimens of *N. tortuosus* from the USNM Helminthological Collection, USDA, Beltsville, Maryland. This study would not have been possible without specimens of *N. neotoma* kindly provided by Dr. G. D. Schmidt. Scanning electron microscopy was conducted with Mr. A. H. Soeldner at the Electron Microscopy Facility, Oregon State University. Published as Oregon Agricultural Experiment Station Technical Paper No. 8341, Oregon State University.

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