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Cuticular Ridge Patterns of *Nematodirus* (Nematoda: Trichostrongyloidea) Parasitic in Domestic Ruminants of North America, with a Key to Species

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**ABSTRACT:** The six species of *Nematodirus* parasitic in domestic ruminants of North America have been identified previously on the basis of characteristics of the bursa and tips of the spicules, and females could not be identified. In an effort to find additional diagnostic characteristics of both sexes, cuticular ridges were studied with light and scanning electron microscopy and in whole mounts and cross sections. After the cuticular ridges of males were characterized, females were matched with males by means of cuticular ridges, except for the rare species *N. davtiani*. Five of the six species have variations of an 18-ridge bilaterally symmetrical system in the cervical region. The sixth species has 26 cervical ridges. Two groups of species were recognized on the basis of cuticular characteristics correlated with other morphological characters. The two species in Group I, *Nematodirus filicollis* and *N. dalbani*, lose ridges laterally in the postcervical region and have 14 ridges at midbody. They can be identified by their anteriorly extended pattern of ridges in the cervical region. These two species also share the characteristics of finlike ridges, a small number (30–35) of perioral denticles, a short cephalic expansion, and a large bursa without a separate dorsal lobe. *Nematodirus davtiani* can be distinguished from *N. filicollis* by its prominent dorsalmost and ventralmost ridges and its distinctive dorsal ray. In contrast, the four species of Group II, *N. helvetianus*, *N. oiratianus interruptus* ssp. n., *N. abnormalis*, and *N. spathiger*, share the characteristics of a more posteriorly distributed pattern of ridges in the cervical region, 18 or more ridges near midbody, smaller dorsal and ventral ridges, a larger number (50–65) of perioral denticles, a longer cephalic expansion, and a smaller bursa with separate dorsal lobes. *Nematodirus helvetianus* and *N. oiratianus interruptus* add ridges in the cervical and postcervical regions, and are characterized by having more than 18 ridges for most of their length; they do not add ventral ridges in the last quarter of the males. *Nematodirus helvetianus* has more ridges (30–36 at midbody) than any of the other species. *Nematodirus oiratianus interruptus* can be easily separated from all other species by its discontinuous ridges in the cervical region. *Nematodirus oiratianus oiratianus* from Asia and South America have continuous ridges. *Nematodirus spathiger* and *N. abnormalis* have 18 ridges for most of their length; they lose all dorsal ridges and add a few ventral ridges in the last quarter of the males. *Nematodirus abnormalis* can be distinguished from *N. spathiger* by the cervical discontinuities in ridges numbered 2 and 8, by spicular and bursal characteristics, and a more anterior vulva position. Possible evolutionary relationships among the six species are described in a cladogram and a key to species.
Table 1. Specimens of *Nematodirus* spp. studied and illustrated by host and locality.

<table>
<thead>
<tr>
<th>Species and synonyms</th>
<th>Numbers and lots/specimens (Figs.) by host and locality</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>N. davtiani</em> Grigorian, 1949 syn.: <em>N. rufavastitatis</em> Durbin and Honess, 1951 (Becklund, 1966)</td>
<td>Ovis aries, sheep Wyoming, USA—1/3</td>
</tr>
<tr>
<td><em>N. helvetianus</em> May, 1920</td>
<td>Ovis ammon, Argali sheep British Museum—1/2 Ovis canadensis, bighorn sheep Alberta, Canada—1/1 Montana, USA—1/3 Ovis dalli, Dall sheep Alaska, USA—2/7 (8, 14, 24–28, 34, 35)</td>
</tr>
<tr>
<td><em>N. oiratianus oiratianus</em> (Raevskaia, 1929) syn.: <em>N. oiratianus</em> Raevskaia, 1929 <em>N. lanceolatus</em> Ault, 1944</td>
<td>Gazella subgutterosa, goitered gazelle Iran—1/1 (British Museum) Ovis aries, sheep Argentina—1/1 Cairo, Egypt—1/6 Iran—1/3 Peru—1/3 Saiga tatarica, saiga gazelle Washington, D.C., USA—1/1 (zoo—orig. USSR) USSR—1/5</td>
</tr>
<tr>
<td><em>N. oiratianus interruptus</em> ssp. n. syn.: <em>N. oiratianus</em> Raevskaia, 1929 (only North American records of this species) <em>N. lanceolatus</em> Ault, 1944 (only North American records of this species)</td>
<td>Antilocapra americana, pronghorn antelope New Mexico, USA—1/3 Oreamnos americana, mountain goat Canada—1/1 (37) Ovis aries, sheep Alaska, USA—1/2 Colorado, USA—2/4 Nebraska, USA—1/2 (53–55) New Mexico, USA—2/5 (10, 16) Utah, USA—1/2 Wyoming, USA—1/6</td>
</tr>
</tbody>
</table>
Table 1. Continued.

<table>
<thead>
<tr>
<th>Species and synonyms</th>
<th>Numbers and lots/specimens (Figs.) by host and locality</th>
</tr>
</thead>
</table>
| **N. abnormalis** May, 1920 | **Ovis canadensis**, bighorn sheep  
Montana, USA—7/54 (40, 52)  
Alberta, Canada—1/2 (38, 39, 41)  
**Ovis dalli**, Dall sheep  
Alaska, USA—2/5 |
| **N. spathiger** (Railliet, 1896) Railliet and Henry, 1909  
syn.: **Strongylus spathiger** Railliet, 1896 | **Gazella subgutterosa**, goitered gazelle  
Iran—1/2 (British Museum)  
**Ovis aries**, sheep  
Australia—1/17  
British Columbia, Canada—1/14 (18, 36, 49, 51)  
Colorado, USA—1/1  
Idaho, USA—1/8  
Maryland, USA—1/1  
Peru—2/9  
Utah, USA—2/6  
Vermont, USA—2/2 (47)  
Washington, USA—1/1  
**Ovis canadensis**, bighorn sheep  
Montana, USA—2/9 (12, 48, 50)  
**Saiga tatarica**, saiga gazelle  
Washington, D.C., USA—1/5 (zoo—orig. USSR) |

**Materials and Methods**

The sources and numbers of specimens studied and the figure numbers in which they are illustrated are listed in Table 1. Whole specimens were studied in temporary mounts cleared in phenol–alcohol (80 parts melted phenol crystals and 20 parts absolute alcohol). Regular light microscopy, interference-contrast light microscopy (Leitz), and scanning electron microscopy were used when sufficient specimens were available. Scanning electron micrographs were obtained by the methods of Madden and Tromba (1976). Cross sections were studied in either free-hand cuts made with a cataract knife, or in paraffin-embedded sections. The cuticular ridges were studied first in males identified by other characteristics. Females were then matched with the males on the basis of characteristics of the cuticular ridges. After females were identified by cuticular characteristics, they
Figure 1-6. Nematodirus spp. of North American domesticated ruminants. Diagrammatic drawings of anterior and cervical regions; right lateral views showing cephalic expansions, number and pattern of distribution of cuticular ridges, and positions of cervical papillae (cp), excretory pore (exp), and distal end of esophagus (es). 1. N. filicollis. 2. N. davtiani. 3. N. helvetianus. 4. N. oiratianus interruptus ssp. n. 5. N. abnormalis. 6. N. spathiger.

were studied for additional distinguishing characteristics. Measurements are in micrometers unless indicated otherwise. Drawings were made with the aid of a camera lucida. The cladogram and cladistic analysis followed the methods of Hennig (1966).

Results

Differences in the pattern of distribution and the number of cuticular ridges were found to be sufficient to identify both males and females of the six species of Nematodirus of domestic ruminants of North America. A new subspecies,

*Nematodirus oiratianus interruptus* ssp. n., is proposed, recognizing the distinctive cuticular ridges of the North American populations of this species.

Five of six species of *Nematodirus* of domestic ruminants of North America have variations of an 18-ridge bilaterally symmetrical system in the cervical region (from the posterior edge of the cephalic expansion to the level of the excretory pore and cervical papillae) (Figs. 1, 2, 4–6). The sixth species, *N. helvetianus*, has


Figures 29-33. *Nematodirus helvetianus*. Scale bars 20 μm. 29. Cephalic expansion. 30. Postcervical cross section, showing 26 ridges. 31. Midbody cross section, showing 34 ridges. 32. Spicule tips, dorsoventral view. 33. Spicule tips, lateral view.

Figures 34, 35. *Nematodirus davtiani*. Scale bars 20 μm. 34. Copulatory bursa, lateral view. 35. Dorsal ray, arrow at spurlike ramus.

Figure 36. *Nematodirus spathiger*. Scale bar 20 μm. Copulatory bursa, dorsal view.

Figures 42-46. *Nematodirus abnormalis*. Scale bars 20 μm. 42. Cephalic expansion. 43. Postcervical cross section, showing 18 ridges. 44. Midbody cross section, showing 18 ridges. 45. Spicule tips, dorsoventral view. 46. Spicule tips, lateral view.

Figures 47-51. *Nematodirus spathiger*. Scale bars 20 μm. 47. Cephalic expansion. 48. Postcervical cross section, showing 18 ridges. 49. Midbody cross section, showing 18 ridges. 50. Spicule tips, dorsoventral view. 51. Spicule tips, lateral view.

Figures 52-55. *Nematodirus oiratianus interruptus* ssp. n. Scale bars 20 μm. 52. Female tail, lateral view. 53. Copulatory bursa, ventral view. 54. Copulatory bursa, dorsal view. 55. Spicules, showing junction of proximal and middle thirds where they become joined by a common membrane.
two extra pairs of ridges, for a total of 26 in the cervical region (Fig. 3). The ridges in Figures 1–6 are numbered in two directions (dorsally and ventrally), beginning at the right cervical papilla.

The six species can be divided into two groups by characters A–E (Fig. 56). Group I, with two species (*N. filicollis* and *N. davtiani*), has a cervical ridge pattern in which the lateral ridges are extended more anteriorly than in Group II. The lateralmost pairs of cervical ridges (pairs 1 and 9) extend more than one-third of the cervical distance and ridge pairs 2, 3, 7, and 8 also extend anteriorly, pairs 3 and 8 nearly, or actually, reaching the cephalic expansion (Figs. 1, 2).

The dorsal and ventral ridges of the two species are finlike (Figs. 13, 14), the cephalic expansion is usually less than twice as long as thick (Figs. 19, 24), and the number of ridges is reduced to 10–14 around midbody or slightly posterior to midbody (Figs. 21, 26). In the last quarter of the body all dorsal ridges disappear and the number of ventral ridges increases to 11 in *N. davtiani* and 15 in *N. filicollis*. In addition to the cuticular characteristics that they share, *N. davtiani* and *N. filicollis* share the characteristics of a small number of perioral denticles (Figs. 7, 8) and a large bursa with numerous bosses in which the dorsal ray is not set off in a separate lobe (Becklund and Walker, 1967) (Fig. 34).

The two species of Group I can be separated by cuticular, bursal, and spicular differences. Females of the rare species *N. davtiani* were not available, so a direct comparison of females was not possible. The only known description of female *N. davtiani* is that of *N. davtiani alpinis* Biocca, Balbo, and Costantini, 1974. *Nematodirus davtiani* differs from *N. filicollis* by having exceptionally large dorsalmost and ventrallmost (pair no. 5) ridges (Figs. 25, 26) and by lacking the extra pairs of fine ridges posterior to the cervical papillae of *N. filicollis* (Figs. 1, 2).

Group II includes four of the six species (*N. helvetianus*, *N. oiratianus*, *N. abnormalis*, and *N. spathiger*; Figs. 3–6) that share the cuticular characteristics of the lateralmost cervical ridges extending less than one-third of the cervical distance, the cephalic expansions more than twice as long as thick (Figs. 29, 37, 42, 47), the dorsal and ventral ridges not as finlike as in *N. davtiani* and *N. filicollis*, and the number of ridges near midbody 18 or more (Figs. 31, 39, 44, 49). The four species of Group II also share the characteristics of numerous perioral denticles (Figs. 9–12) and small bursae in which the dorsal rays are set off in separate lobes (Figs. 36, 54).

The four species of Group II can be separated by cuticular differences. In addition, differences in the spicules and copulatory bursae were reported earlier by Becklund and Walker (1967) and Stringfellow (1968). Only cuticular differences will be described below, but other differences are included in the cladogram and in the key to species. The descriptions of the cuticle include both males and females unless noted otherwise.

*Nematodirus helvetianus* can be identified by its large number of ridges. Five dorsal and five ventral ridges reach the cephalic expansion (Fig. 3), four more than in the other three species of Group II, in which only three dorsal and three ventral ridges reach the cephalic expansion. Just posterior to the excretory pore of *N. helvetianus* there are 26 ridges (Figs. 3, 15, 30), and at midbody there are 34 (Fig. 31). In the last quarter of the body of the male all dorsal ridges are lost without an increase in the number of ventral ridges.
Nematodirus oiratianus interruptus ssp. n.  
(Figs. 4, 10, 16, 37–41, 52–55)

When N. oiratianus from other parts of the world (Table 1) were compared with N. oiratianus of North America, the North American specimens were found to differ, but only in the presence of discontinuities in the ridges of the cervical region (Table 3). Because the North American specimens of N. oiratianus were from a wide range of hosts from all over the western half of North America (Table 1), the discontinuous ridges are believed to represent a true genetic difference between the North American populations and other populations of N. oiratianus. In order to provide a handle for the information pertaining to this unique population of N. oiratianus that differs both morphologically and geographically, we propose a subspecies designation for it.

Both males and females of the new subspecies can be identified by the interruptions in the cuticular ridges in the cervical region (Figs. 4, 16). Posterior to the cervical region the ridges gradually become continuous. A strong pair of ridges extends to the level of the cervical papillae and another finer pair of ridges begins a bit more posteriorly (Fig. 4), to bring the total number of ridges just posterior to the cervical region to 22–26 (Fig. 38). Before reaching midbody one or both of the fine lateral ridges are lost on each side so that 22–24 ridges are present at midbody (Fig. 39). Unlike the other species, which lose dorsal ridges a millimeter or more anterior to the bursa, both N. oiratianus interruptus and N. o. oiratianus retain their dorsal ridges to about 0.500 mm anterior to the bursa.

Hosts: Ovis canadensis (type); others (Table 1).
Location: Small intestine.
Locality: Montana, U.S.A. (type); others (Table 1), all North America.
Specimens Deposited: USNM Helm. Coll., USDA, BARC-East, Beltsville, Maryland 20705; holotype, male, No. 77397; allotype, female, No. 77398; paratypes, Nos. 77399–77408, 38054, 39011, 56783, 59498, 59209, 69367, 75420, 75421.

Nematodirus abnormalis can be recognized by the interruptions in the ridges of pairs 2 and 8 (Figs. 5, 17) at the level of the excretory pore and cervical papillae. There are 18 ridges for most of the postcervical body length (Figs. 43, 44), except in the posterior quarter of the male, where the dorsal ridges disappear and the ventral ridges increase in number from nine to a total of 12. An examination of N. abnormalis from South America and Australia found a consistent pattern in this species from different parts of the world. In the specimens from Australia an additional interruption in the ridges of pairs 2 and 8 occurred about 300 μm posterior to the anterior interruption. The posterior interruption was found in only one specimen from North America.

An examination of female N. abnormalis identified by the unique cuticular characters described above revealed that the vulva of this species is located more anteriorly than in any of the other species from North American ruminants (Table 2).

Nematodirus spathiger can be recognized by its lack of most of the specialized cuticular characteristics described for the other species (Fig. 6). It is most similar to N. abnormalis, but it lacks the interruptions in pairs 2 and 8. Nematodirus spathiger is the most variable of the six species. In some specimens the ridges of
Table 2. Morphometrics of female *Nematodirus* spp. from domestic ruminants of North America.

<table>
<thead>
<tr>
<th>Species of <em>Nematodirus</em></th>
<th>N. filicollis</th>
<th>N. daviani</th>
<th>N. helvetianus</th>
<th>N. oiratianus interruptus sp. n.</th>
<th>N. abnormalis</th>
<th>N. spathiger</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of specimens</td>
<td>6</td>
<td>10</td>
<td>2</td>
<td>10</td>
<td>9</td>
<td>9</td>
</tr>
<tr>
<td>Body length (mm)</td>
<td>14.3–17.9</td>
<td>10.1–13.6</td>
<td>29.5</td>
<td>8.6–20.5</td>
<td>11.1–16.0</td>
<td>12.8–19.0</td>
</tr>
<tr>
<td>Excretory pore‡</td>
<td>380–585</td>
<td>672–855</td>
<td>375–600</td>
<td>231–510</td>
<td>375–531</td>
<td></td>
</tr>
<tr>
<td>Anterior ovejector</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphincter</td>
<td>60–69</td>
<td>77–90</td>
<td>48–90</td>
<td>60–75</td>
<td>60–81</td>
<td></td>
</tr>
<tr>
<td>Posterior ovejector</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sphincter</td>
<td>54–75</td>
<td>77–96</td>
<td>54–96</td>
<td>60–75</td>
<td>57–78</td>
<td></td>
</tr>
<tr>
<td>Vulva position as percentage‡ of body length (%)</td>
<td>66–73</td>
<td>74–78</td>
<td>73–76</td>
<td>67–79</td>
<td>55–63</td>
<td>66–72</td>
</tr>
<tr>
<td>Tail length</td>
<td>45–69</td>
<td>50–80</td>
<td>71–94</td>
<td>51–75</td>
<td>51–135</td>
<td>63–84</td>
</tr>
</tbody>
</table>

* Measurements from Biocca et al. (1974).
† Measurements in micrometers unless indicated otherwise.
‡ From anterior end of body.

pairst 1 and 9 extend anterior to the cervical papillae, but in others they do not reach that level (Fig. 18).

**Discussion**

The differences in pattern and number of cuticular ridges among the six species of *Nematodirus* are sufficient to identify males and females to species. This is the

Table 3. Morphometrics of *Nematodirus oiratianus* ssp. males.*

<table>
<thead>
<tr>
<th>Subspecies</th>
<th>N. oiratianus interruptus sp. n.</th>
<th>N. oiratianus oiratianus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Characters†</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of specimens</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Body length (mm)</td>
<td>8.3–12.4</td>
<td>7.2–14.8</td>
</tr>
<tr>
<td>Esophagus length</td>
<td>375–525</td>
<td>396–493</td>
</tr>
<tr>
<td>Excretory pore</td>
<td>417–546</td>
<td>323–608</td>
</tr>
<tr>
<td>Spicule length</td>
<td>729–907</td>
<td>665–900</td>
</tr>
<tr>
<td>Spicule tip length</td>
<td>36–39</td>
<td>28–40</td>
</tr>
<tr>
<td>Length of fusion proximal to spicule tips</td>
<td>6–23</td>
<td>13–29</td>
</tr>
<tr>
<td>Percentage of spicules joined by common membrane (%)</td>
<td>64–66</td>
<td>61–67</td>
</tr>
<tr>
<td>Bursa length</td>
<td>90–141</td>
<td>80–150</td>
</tr>
<tr>
<td>Dorsal ray length</td>
<td>36–54</td>
<td>38–60</td>
</tr>
</tbody>
</table>

* Morphometrics of females of *N. oiratianus interruptus* ssp. n. in Table 2; females of *N. oiratianus oiratianus* unavailable.
† Measurements in micrometers unless indicated otherwise.
Figure 56. Cladogram of possible evolutionary relationships of *Nematodirus* spp. of domestic ruminants of North America. Capital letters in open boxes indicate generalized or ancestral character states; lowercase letters in black boxes indicate specialized character states: (A) lateralmost cervical ridges extend less than \( \frac{1}{3} \) cervical distance, (a) lateralmost cervical ridges extend more than \( \frac{1}{3} \) cervical distance; (B) 30–35 perioral denticies, (b) 50–65 perioral denticies; (C) dorsal rays not in separate lobes from laterals, (c) dorsal rays in separate lobes from laterals; (D) ridges not finlike, (d) ridges finlike; (E) cephalic expansion more than twice as long as broad, (e) cephalic expansion less than twice as long as broad; (F) 18 postcervical ridges, (f) 22–26 postcervical ridges; (G) no added ridges in posterior quarter of male, (g) ridges added ventrally in posterior quarter of male; (H) 18 midbody ridges, (h) 22–24 midbody ridges, (h') 34 midbody ridges, (h") 14 midbody ridges; (I) ridges continuous, (i) ridge pairs 2 and 8 discontinuous at cervical papillae, (i') all cervical ridges discontinuous; (J) two short rami at end of dorsal ray, (j) one spurlike ramus at middle of dorsal ray; (K) dorsalmost and ventralmost ridges not hypertrophied, (k) dorsalmost and ventralmost ridges more than twice height of other ridges; (L) spicule tips short (18–26 \( \mu m \)) and symmetrical, (l) spicule tips elongate (36–38 \( \mu m \)), (l') spicule tips asymmetrical; (M) vulva near junction of middle and posterior fourths of body, (m) vulva in posterior fourth of body, (m') vulva in third fourth of body.

first character found to be useful for identifying female *Nematodirus* to species. Because this character can be observed in living and fresh-frozen specimens, as well as in fixed and cleared specimens, many kinds of studies requiring identified females and males are now possible.
The study of females identified by cuticular characters has so far revealed few additional differences among the species (Table 2). Only differences in vulva position were observed. For the *Nematodirella*, which are believed to have evolved from *Nematodirus* (Durette-Desset, 1979; Lichtenfels and Pilitt, 1983), a more anterior vulva and longer spicules were considered to be evolved characteristics. We interpret the results in Table 2 to indicate that the ancestral (most common) vulva position was near the junction of the middle and posterior thirds. The more anterior vulva of *N. abnormalis* is believed to be a specialized character state. The more posterior vulva reported by Biocca et al. (1974) for *N. davtiani alpinus* may also represent a specialized character state that has evolved in the opposite direction. Of the six species, *N. abnormalis* has the most anterior vulva (Table 2). This character was consistent when samples of nematodes from other widely separated parts of the world were studied (Table 1).

Although the six species that were studied represent less than half of the species of *Nematodirus* parasitic in feral and domestic ruminants of the world, some relationships among the six species are apparent. Thirteen morphological characters and 31 character states were used to reconstruct possible relationships of the six species (Fig. 56), and to construct the following key to species.

**Key to Nematodirus of Domestic Ruminants of North America**

1. Lateralmost pair of cuticular ridges extends anteriorly more than one-third of distance between excretory pore and cephalic expansion (Figs. 1, 2). Cephalic expansion about twice as long as broad, or shorter (Figs. 19, 24). Number of cuticular ridges in region posterior to midbody (the third quarter) 10–14 (Figs. 21, 26). Copulatory bursa large, without separate dorsal lobes (Fig. 34). Spicule tips short (18–30 µm) and symmetrical (Figs. 22, 23, 27, 28) .......................... 2

   Lateralmost pair of cuticular ridges extends less than one-third of distance between excretory pore and cephalic expansion (Figs. 3–6). Cephalic expansion more than twice as long as broad (Figs. 29, 37, 42, 47). Number of cuticular ridges in midbody or in third quarter 18–34 (Figs. 31, 39, 44, 49). Copulatory bursa small, with separate dorsal lobes (Fig. 36). Spicule tips elongate (Figs. 32, 33, 40, 41), asymmetric (Figs. 45, 46), or short and broad (Figs. 50, 51) .......................... 3

2. Extra pairs of ridges present bilaterally in postcervical region for total of 22 ridges (Figs. 1, 13). Dorsalmost and ventralmost ridges not more than twice height of other ridges (Figs. 20, 21). Dorsal rays end with two short rami (similar to Fig. 36). Spicule fused anterior to tips; tips with narrow membrane (Figs. 22, 23) .................................. *N. filicollis*

   Extra pair of ridges absent, total of 18 ridges in postcervical region (Figs. 2, 14, 25). Dorsalmost and ventralmost ridges more than twice height of other ridges (Figs. 25, 26). Dorsal rays with short spurlike ramus at middle of ray and single point at distal end (Fig. 35). Spicule fused only at tips; tips with broad membrane (Figs. 27, 28) .................................. *N. davtiani*

3. Twenty-two to 26 ridges just posterior to excretory pore (Figs. 3, 4, 15, 16, 30, 38). Twenty-two to 34 ridges near midbody (Figs. 31, 39). Number of ventral ridges does not increase in posterior quarter of male .......................... 4
Eighteen ridges just posterior to excretory pore (Figs. 5, 6, 17, 18, 43, 48). Eighteen ridges near midbody (Figs. 44, 49). Number of ventral ridges increases in posterior quarter of male.

4. Ridges continuous in cervical region (Figs. 3, 15). Number of ridges in postcervical region 26 (Figs. 3, 15, 30); in midbody 34–36 (Fig. 31). Only ventral ridges extend within 500 μm of bursa. Spicule tips with ventral membrane proximal to tip (Fig. 33) ___________ N. helvetianus

Ridges discontinuous in cervical region (Figs. 4, 16). Number of ridges in postcervical region 22–26 (Figs. 4, 16, 38); in midbody 22–24 (Fig. 39). Both dorsal and ventral ridges extend to within 500 μm of bursa. Spicule tips with ventral membrane at middle of tip (Fig. 41) ___________ N. oiratianus interruptus ssp. n.

5. Ridges of pairs 2 and 8 discontinuous at level of cervical papillae (Figs. 5, 17). Vulva 55–63% of body length from anterior end (Table 2). Spicule tips asymmetric and twisted (Figs. 45, 46) ___________ N. abnormalis

Ridges in cervical region continuous (Figs. 6, 18). Vulva 66–72% of body length from anterior end (Table 2). Spicule tips symmetrical; short with broad membrane, cup-shaped in lateral view (Figs. 50, 51) ___________ N. spathiger

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