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Cuticular Ridge Pattern in *Ostertagia gruehneri* and *Ostertagia arctica* (Nematoda: Trichostrongyloidea) from Caribou, *Rangifer tarandus*

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ABSTRACT: Two species of medium stomach worms are common parasites of the caribou, *Rangifer tarandus*. The 2 species, *Ostertagia gruehneri* Skrjabin, 1929, and *O. arctica* Mitzkewitzsch, 1929, differ so markedly in morphology of the spicules and genital cone that many nematode systematists place them in different genera. Recent studies of similar pairs of species parasitic in other ruminants have provided evidence that such pairs of species may be morphotypes of 1 species. The 2 species from caribou are redescribed with emphasis on the pattern of surface cuticular ridges and the structure of the esophagus, characters considered useful for distinguishing species of trichostrongyloid nematodes. *Ostertagia gruehneri* and *O. arctica* were found to have identical ridge patterns and esophageal characteristics. Both species had 5 lateral ridges, a long eosphageal valve, and ducts for the subventral esophageal glands that opened internally posterior to the level of the cervical papillae.

KEY WORDS: *Ostertagia gruehneri, Ostertagia arctica,* Nematoda, Trichostrongyloidea, Ostertagiinae, synlophe, nematode morphology, cuticle, ruminants.

Two species of "medium stomach worms" (Ostertagiinae: Trichostrongylidae) are commonly found as coparasites of the caribou, *Rangifer tarandus*. *Ostertagia gruehneri* Skrjabin, 1929 was found in virtually 100% of abomasa of Norwegian *Rangifer tarandus* by Bye (1987) and it comprised 85–99% of the nematode population. Another species frequently found with *O. gruehneri* is *O. arctica* Mitzkewitsch, 1929. Recently, Lancaster et al. (1983) proposed that polymorphism is common in the Ostertagiinae and that species with morphological characteristics of the genus *Skrjabinagia* may be morphotypes of associate dominant species such as *O. gruehneri*. We have studied several suspected pairs of species or associates from other ruminants using newly employed characters to supplement characters commonly used to identify trichostrongyloid species such as the shape of the spicules, genital cone, and copulatory bursa (Lichtenfels et al., 1988a, b; Lichtenfels and Pilitt, 1989). These newly employed characters include the pattern of surface cuticular ridges (synlophe) and the structure of the esophagus.

The objective of the present study was to describe the synlophe and esophageal characteristics of *O. gruehneri* and *O. arctica*. Previous studies have shown the synlophe to be one of the most useful morphological characters for separating species of the Trichostrongyloidea (Lichtenfels, 1977; Lichtenfels and Pilitt, 1983a, b; Measures and Anderson, 1983; Fukumoto, 1986; Lichtenfels et al., 1986; Hoberg and Rickard, 1988). Our hypothesis was that if *O. gruehneri* and *O. arctica* are different species, they would have different synlophes.

Materials and Methods

Nematodes

All specimens were obtained from the USDA Parasite Collection maintained in the Beltsville laboratory. Host and locality data (Table 1) were obtained from the records of the collection. Common and scientific names of hosts and synonymies of nematodes are provided (Table 1). The species identities of male nematodes were confirmed on the basis of spicule and genital cone morphology (Drozdz, 1965). Females were identified by matching synlophes to that of the males.

Hosts

Both woodland caribou, *Rangifer tarandus caribou,* and barren-ground caribou, *R. tarandus groenlandicus,* were included in the collections from Canada (Fruetel and Lankester, 1989). The subspecies in Norway was the Svalbard reindeer, *Rangifer tarandus platyrhynchus,* and the host subspecies for the collection from Russia was *Rangifer tarandus sibiricus*. Common names frequently used for these ruminants are caribou in North America and reindeer in Europe and Asia. For simplicity herein we will refer to all as *Rangifer tarandus* or caribou.

Microscopy

Specimens were studied either as (1) temporary whole mounts cleared in phenol–alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with ordinary light microscopy or interference-contrast light microscopy; or, (2) critical point-dried, coated with gold palladium, and viewed at 5–20 kV with scanning electron microscopy (SEM) (Madden and

Table 1. Specimens of *Ostertagia gruehneri* and *Ostertagia arctica* studied by host and locality.

Species and synonyms	Host, locality (number of lots/number of specimens by host, locality, and sex)
Ostertagia gruehneri Skrjabin, 1929 Syn. *Grühneria grühneri* Sarwar, 1956	*Rangifer tarandus,* Canada 2/9 ♂, 4 ♀ Norway 1/10 ♂, 4 ♀ USSR 1/1 ♂ Alaska 2/4 ♂
Ostertagia arctica Mitzkewitsch, 1929 Syn. *Sjobergia arctica* (Mitzkewitsch, 1929) Sarwar, 1956; *Ostertagiella arctica* (Mitzkewitsch, 1929) Andreeva, 1957; *Skrjabinagia arctica* (Mitzkewitsch, 1929) Drozdz, 1965	*Rangifer tarandus,* Canada 2/7 ♂ Norway 1/15 ♂ USSR 1/2 ♂ Alaska 1/1 ♂

Tromba, 1976). Measurements are in millimeters unless indicated otherwise.

Characters studied

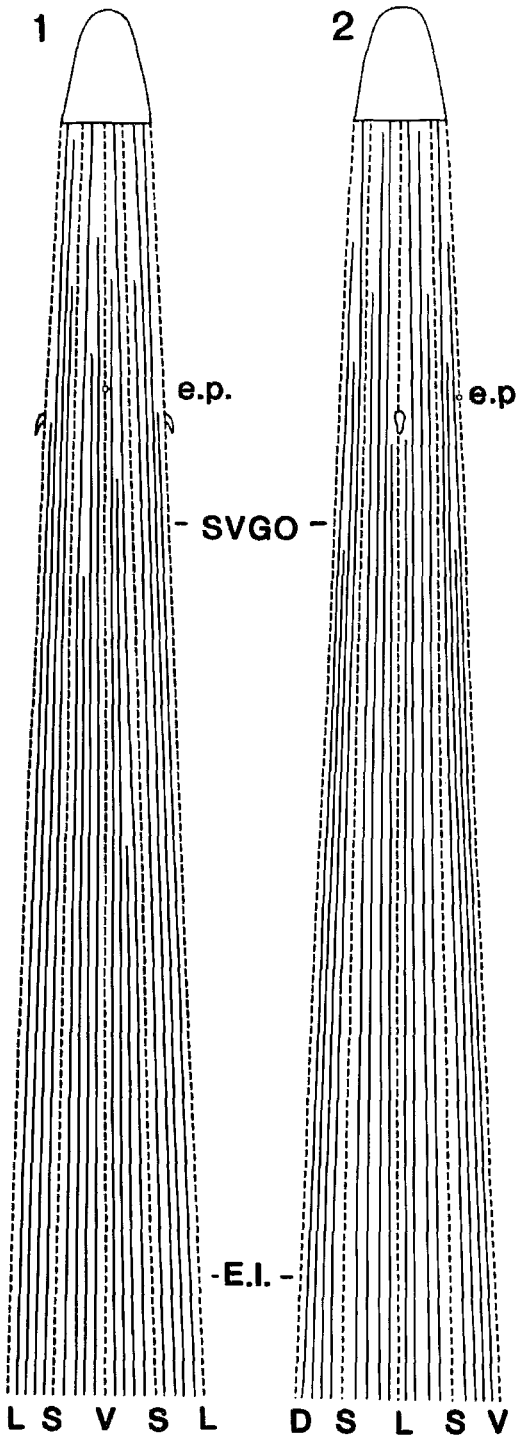
In addition to the synlophes of the nematodes, several morphometric characteristics were studied (Table 2). Student's *t*-test was employed to test apparent difference among mean measurements.

Results

Synlophe

The synlophes of *O. gruehneri* and *O. arctica* were found to be identical. Because no differences between the 2 species were found they are described together below and in the drawings (Figs. 1, 2). The most distinctive and easily recognizable feature of the synlophe of these 2 species is the group of 5 closely spaced ridges in each lateral field (Figs. 1–5). The 5 lateral ridges can be recognized because they are closer together than other ridges. There is a gradient toward less space between ridges in lateral areas than in dorsal and ventral areas (Figs. 3–5). The pattern of ridges in the region of the esophagus is illustrated in lateral and ventral views (Figs. 1, 2). Like other members of the Ostertagiinae the synlophe of these 2 species consisted, in the region of the esophagus, of 40 ridges. For convenience in understanding the pattern the ridges can be grouped into 4 symmetrical and relatively equal fields. The ventral and dorsal fields include 9 ridges each and the lateral fields include 11 ridges each.

The lateral ridge (dashed line L in Fig. 1) is ventral to the cervical papilla. The 5 closely spaced lateral ridges include the lateral, a pair of



Figures 1, 2. Diagrammatic drawings of synlophe present in both *Ostertagia gruehneri* and *Ostertagia arctica,* with lateral (L), ventral (V), and subventral and subdorsal (S) ridges indicated by dashed lines. Other abbreviations: ep = excretory pore; E-I = esophageal-intestinal junction; SVGO = subventral esophageal gland duct opening. 1. Ventral view. 2. Lateral view. Note: dashed lines are for emphasis only; the ridges are not interrupted.

Table 2. Morphometrics (in micrometers; range with mean in parentheses) of males* of *Ostertagia gruehneri* and *Ostertagia arctica* in *Rangifer tarandus*.

Character	Species	
	Ostertagia gruehneri ($N = 23$)	*Ostertagia arctica* ($N = 20$)
Body length	6,600–9,600 (7,950)	5,280–10,500 (7,250)
Cephalic inflation length†	85–120 (100)	82–130 (097)
Nerve ring†	221–288 (259)	223–296 (256)
Execretory pore†	269–332 (305)	257–344 (300)
Cephalic papillae†	284–446 (322)	280–371 (315)
Subventral gland orifices†	296–395 (348)	296–387 (353)
Esophagus length†	806–999 (905)	802–1,149 (948)
Esophageal–intestinal valve length	96–143 (120)‡	110–171 (131)
Spicule length	182–226 (204)	181–263 (206)
Soberg's organ	Absent	Present
Bursal ray pattern§	2-1-2	2-1-2
Length of dorsal ray of bursa	68–96 (81)‖	75–143 (111)‖
Length of bursa#	211–304 (251)	190–365 (272)

* Females not measured.
† Distance measured from anterior end.
‡ $N = 22$.
§ Pattern following system of Durette-Desset (1983).
‖ Significant differences between means with Student's t-test; probability of greater t value less than 0.001.
Measured from prebursal papillae; $N = 20$.

adjacent ridges (1 ventral and 1 dorsal) anterior to the cervical papilla that like the lateral ridge extend from the cephalic expansion to the posterior end of the nematode, and a second pair of ridges that flank the lateral ridge between it and the first pair. The second pair usually begin just posterior to the cervical papilla but may begin slightly anterior to the cervical papilla (Fig. 3) or as much as 200–300 μm posterior to the papilla. Each lateral field also includes 2 additional pairs of ridges for a total of 9 ridges each.

The ventral ridge (dashed line "V" in Figs. 1, 2) intersects with the excretory pore and extends anteriorly to the cephalic inflation. The pair of ridges that flank the ventral ridge extend anteriorly about half of the distance from the excretory pore to the cephalic expansion. The next 2 pairs of ridges flank the 3 ventralmost ridges and are variable in length, extending anteriorly to the middle of the esophagus or in some specimens to a point slightly anterior to the excretory pore. The lateralmost 2 pairs of ridges in the ventral field both extend anteriorly to the cephalic expansion.

The ridges in the dorsal field are a mirror image of those in the ventral field. Each dorsal and ventral field includes 11 ridges. The lateralmost ridge of the ventral field is drawn with a dashed line and labeled "S" in Figures 1 and 2.

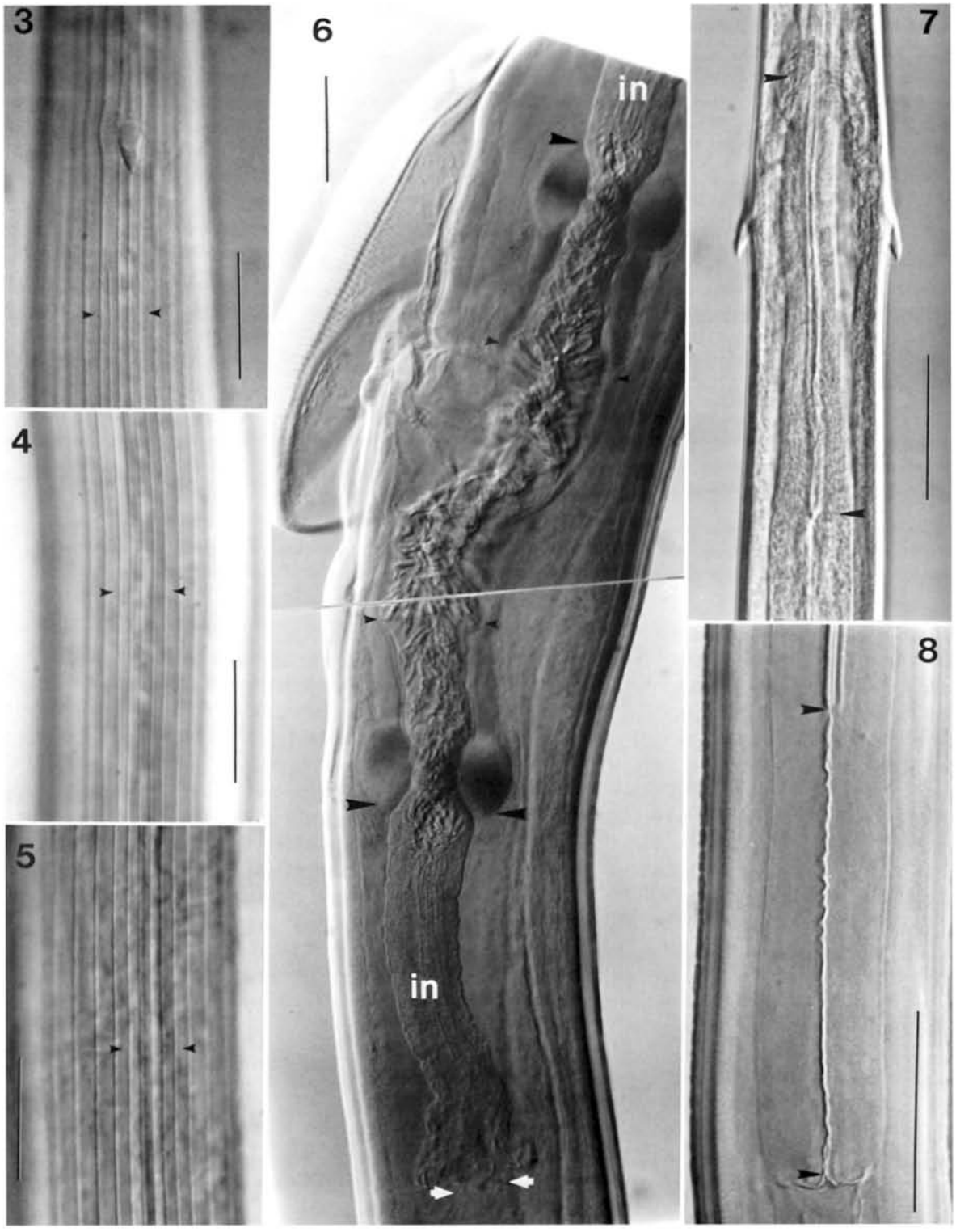
The total number of ridges at the level of the esophageal valve and for most of the rest of the nematode is 40. The ridges are exceptionally straight and continuous with few crossovers, interruptions, or additions. In the posterior half of the lateral fields, 1 or 2 of a group of 5 closely spaced ridges may branch to form a group of 6 or 7 closely spaced ridges (Fig. 5). Near the copulatory bursa in the males the lateral ridges extend almost to the level of the prebursal papillae, but ventral and dorsal ridges end 400–500 μm anterior to the bursa. In the female the ridges are interrupted at the vulva and the vulval flap (if the flap is present), but most of the ridges extend almost to the tip of the tail.

Esophagus

The esophageal valves of *O. gruehneri* and *O. arctica* were found to be similar in length (Table 2). The valves were more than 3 times as long as thick (Fig. 8). The position of the openings of the subventral esophageal gland ducts (SVGO) in relation to the position of the cervical papillae was variable, but was usually posterior to the papillae (Table 2; Fig. 7) in both species.

Bursal rays

The bursal ray formula (2-1-2) described by Durette-Desset (1983) for the genus *Ostertagia* was present in both species studied herein. The only difference noted in the copulatory bursae



Figures 3–8. Synlophe and other morphological features of *Ostertagia gruehneri* and *Ostertagia arctica*. Light micrographs with the aid of interference microscopy. All scale bars, 50 μm. 3. Lateral synlophe of male *O. gruehneri* in region of left cervical papilla showing 5 closely spaced lateral ridges (between arrows). 4. Lateral synlophe of male *O. arctica* in region of esophageal-intestinal junction showing 5 closely spaced lateral ridges (between arrows). 5. Lateral synlophe of male *O. gruehneri* near midbody showing 5 closely spaced lateral ridges (between arrows). 6. Female reproductive system of *O. gruehneri* showing vulva with vulval flap, vestibule (between upper and lower small arrows), sphincters (between small and large arrows), and infundibula (in). The white arrows indicate the end of the posterior infundibulum where it joins the uterus. The anterior infundibulum (only

between the 2 species was in the lengths of the dorsal ray. In *O. gruehneri* the dorsal ray was significantly ($P < 0.001$) shorter than that of *O. arctica* (Table 2).

Genital cones

The genital cones of the 2 species were quite different. Ventrally, *O. gruehneri* had a prominent proconus (Fig. 10), but this structure was completely lacking in *O. arctica* (Fig. 12). Dorsally, in *O. arctica* the accessory bursal membrane was enlarged and sclerotized (Figs. 11, 12), but this structure was small and unsclerotized in *O. gruehneri* (Figs. 9, 10).

The spicules of the 2 species were similar in length (Table 2) but differed markedly in shape. The spicules of *O. gruehneri* were slender and divided into 3 dissimilar branches in their distal third (Figs. 13, 14). The spicules of *O. arctica* are relatively thicker and divided into 3 dissimilar branches in their distal half (Figs. 15, 16). A gubernaculum is present in both species (Figs. 10, 14, 15).

Females

We found no differences among the females so they were all regarded to be *O. gruehneri.*

Discussion

The original spelling, *Ostertagia grühneri,* is not acceptable because of the umlaut sign. The International Code of Zoological Nomenclature (Third Edition, 1985), Article 32(d)(i), clearly requires the deletion of the umlaut from a vowel and the insertion of the letter "e" after the vowel. Accordingly, we have spelled the species name as *O. gruehneri* herein, although most earlier workers either followed the original spelling with the umlaut or dropped the umlaut but did not add the required "e" after the "u."

Females of the 2 species have never been clearly distinguished; being separated by some workers (see Skrjabin et al., 1954) as without a vulval flap (*O. gruehneri*) or with a vulval flap (*O. arctica*). We do not regard presence or absence of a vulval flap to be a useful character for identifying species (Hong and Timms, 1989), and, as no differences were found among the females, they were all regarded to be 1 species.

In recent studies of other species of the Ostertagiinae, Lichtenfels et al. (1988a, b) and Lichtenfels and Pilitt (1989) found that characteristics of the synlophe and the esophagus were useful for identifying species. In the present study however, no differences in these characters were found between *O. gruehneri* and *O. arctica.* Thus, the results are consistent with the hypothesis proposed by Lancaster and Hong (1981) that species such as *O. arctica,* with the characteristics of the genus *Skrjabinagia* as described by Drozdz (1965), may be morphotypes of associate dominant species such as *O. gruehneri.*

The unique synlophe described herein for *O. gruehneri* and *O. arctica* provides a new useful character for identifying both males and females of this species. The distinctive 5 lateral ridges in the region of the esophagus can be observed with light microscopy (at 400× or greater magnification) in whole mounts of living, frozen, or cleared and fixed specimens. Cross sections were not made because an insufficient number of specimens of *O. arctica* were available. Therefore, in order to have comparative data for both species, studies were made on whole specimens.

The newly described characters of the cuticle and esophagus provide new insight into the evolutionary relationships of the Ostertagiinae. The 5 lateral ridge synlophe appears to be very similar to the 3 lateral ridge synlophe present in *O. leptospicularis* (=*O. kolchida*) and *Marshallagia marshalli* (=*O. occidentalis*). Those species also share with *O. gruehneri* (=*O. arctica*) a long esophageal valve and a bursal ray pattern of 2-1-2 (Lichtenfels et al., 1988b). In addition, *O. gruehneri* shared with *O. leptospicularis* the characteristics of 3 ventral ridges, a relatively posterior SVGO, and cervid hosts. It appears that the species from cervids may be more closely related to each other than they are to the Ostertagiinae parasitic in bovids. Lichtenfels and Pilitt (1983a, b) and Hoberg et al. (1989) came to similar conclusions for *Nematodirella* and *Nematodirus,* respectively. However, *O. odocoilei* and *O. mossi* have yet to be redescribed, and an hypothesis on the evolution of the Ostertagiinae is beyond the scope of this work.

The percentage of the population consisting of the minor species, *O. arctica,* in the present study

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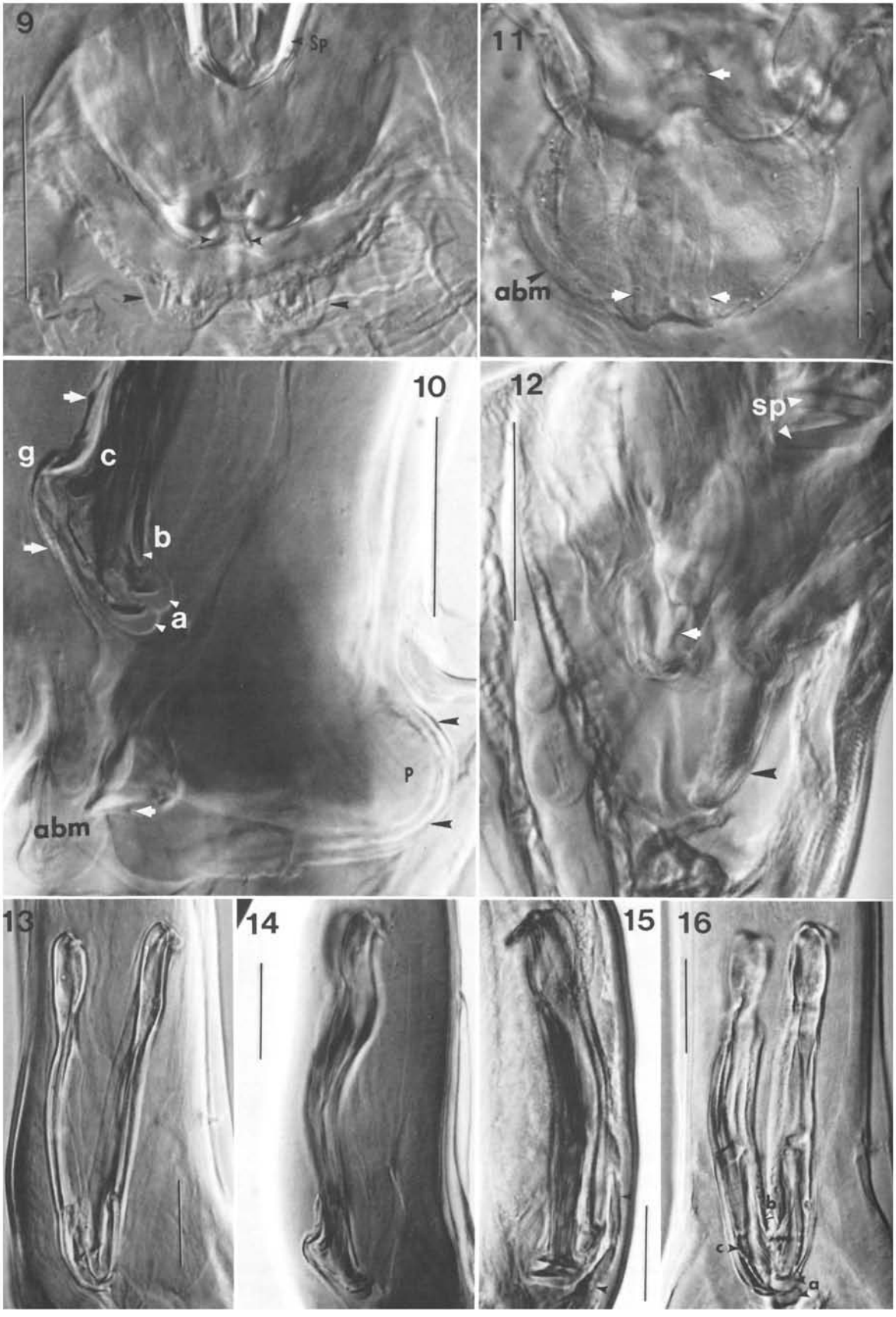
partially shown) is the same size as the posterior one. 7. Male *O. gruehneri,* dorsoventral view, showing the position of the nerve ring (upper arrow) and the anterior margin of the subventral esophageal gland (lower arrow) in relation to the prominent cervical papillae. 8. Esophageal valve of male *O. gruehneri* showing thick cuticular lining of esophagus anterior to the valve (above upper arrow) and the posterior end of the valve (lower arrow).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(0–11%, mean 2%) was similar to that reported for other minor species. In all pairs of species examined previously (Lichtenfels et al., 1988a, b; Lichtenfels and Pilitt, 1989) and suspected to be examples of polymorphism (Lancaster and Hong, 1981), the member of the pair with the relatively slender spicules and unsclerotized accessory bursal membrane has comprised the major proportion of the nematode population (85–99%); and the species with relatively stout spicules and an enlarged and sclerotized dorsal part of the genital cone has comprised a minor proportion of the population (1–15%). This consistent pattern of differences has been described previously by Lancaster and Hong (1981). Others (Fruetel and Lankester, 1989) have published excellent drawings of the spicules and genital cones of the males of these 2 species. However, photomicrographs of these structures as presented herein have not been published previously. The photomicrographs of the spicules and genital cones do not provide new information on their structure, but do provide an example of these structures as seen with interference light microscopy.

The distribution of *O. gruehneri* and *O. arctica* extends throughout the range of *Rangifer tarandus*. We were able to study specimens from that host from North America, Europe, and Asia. Both nematode species have been reported also from many other cervids and bovids. We have determined however, that errors in identifying these species are common because of the difficulty earlier workers had in distinguishing *O. gruehneri* and *O. arctica* from *O. ostertagi* and *O. lyrata*. Therefore, caution is urged in accepting reports in the literature. The new characters described herein and by Lichtenfels et al. (1988a, b) make the identification of these 2 pairs of species exceptionally simple. Although the spicules and genital cones of the 2 pairs of species are quite similar, characteristics of the synlophe and esophagus indicate that *O. gruehneri* and *O. arctica* probably are not closely related to *O. ostertagi* and *O. lyrata*. With the aid of the newly described characteristics, an accurate host range for the species of *Ostertagia* in caribou can be developed.

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Figures 9–16. Genital cones and spicules of *Ostertagia gruehneri* and *O. arctica*. All scale bars, 50 μm. 9. Genital cone, ventral view, of *O. gruehneri* showing dorsal bilobed accessory bursal membrane (large arrows), ventral paired papillae (small arrows), and distal end of spicules (sp). 10. Genital cone, lateral view, of *O. gruehneri* showing accessory bursal membrane (abm), 1 of paired ventral papillae (lowest white arrow), proconus (p, between black arrows), and distal ends of spicules (a—main branch of each spicule with cuticular pad; b—bladelike ventral branch of 1 spicule; c—dorsal curved branch of 1 spicule; g—gubernaculum, upper white arrows). 11. Genital cone, ventral view, of *O. arctica* showing enlarged, oval, sclerotized accessory bursal membrane (abm) with elongate papillae (lower arrows) and paired ventral papillae out of focus (upper arrow). 12. Genital cone, lateral view, of *O. arctica* showing enlarged, sclerotized accessory bursal membrane (large arrow), 1 of the ventral paired papillae (small arrow), and the broad, flat, distal ends of the spicules (sp). 13, 14. Spicules of *O. gruehneri* showing shape and 3 distal branches separated in distal quarter. 13. Subventral view. 14. Lateral view showing gubernaculum. 15, 16. Spicules of *O. arctica* showing shape and 3 distal branches (a, b, c) separated in distal half. 15. Lateral view showing gubernaculum (arrows). 16. Ventral view.

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