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A Redescription of *Ostertagia bison* is (Nematoda: Trichostrongyloidea) and a Key to Species of Ostertagiinae with a Tapering Lateral Synlophe from Domestic Ruminants in North America

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A Redescription of *Ostertagia bisonis* (Nematoda: Trichostrongyloidea) and a Key to Species of Ostertagiinae with a Tapering Lateral Synlophe from Domestic Ruminants in North America

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ABSTRACT: *Ostertagia bisonis* Chapin, 1925, is an abomasal worm of the American buffalo, *Bison bison,* and other ruminants including cattle in which it can cause clinical nematodiasis. This report describes characteristics of *O. bisonis,* especially details of the synlophe and esophagus, that are necessary for constructing a key to the species of medium stomach worms (Ostertagiinae) parasitic in domestic ruminants in North America. The synlophe of *O. bisonis* is most similar to the single ridge tapering lateral synlophe of *Ostertagia ostertagi.* Ducts of the subventral glands of the esophagus empty anterior to the cervical papillae and the esophageal–intestinal valve is more than twice as long as wide. We follow earlier workers in considering *Ostertagia orloffi* Sankin, 1930, a synonym of *O. bisonis. Ostertagia bisonis* may have more generalized characters than any other species with a tapering lateral synlophe that are parasites of domestic ruminants in North America, but polarization of some characters cannot be considered reliable until additional outgroups are studied.

KEY WORDS: *Ostertagia bisonis* (=*O. orloffi*), synlophe, redescription, nematode morphology, Nematoda, *Bison bison,* Trichostrongyloidea, Ostertagiinae, *Ostertagia ostertagi, Ostertagia lyrata, Teladorsagia circumcincta* (=*Teladorsagia davtiani*), *Teladorsagia trifurcata,* cuticle, ruminants, SEM.

Ostertagia bisonis Chapin, 1925, is one of a group of medium stomach worms that is among the most serious nematode pathogens of ruminants (Anonymous, 1983). It was described from the American buffalo, *Bison bison,* and has been reported from a wide range of ruminants including Bovidae, Cervidae, and Antilocapridae. It is of interest to veterinary parasitologists because of the clinical nematodiasis it can cause in cattle (Worley and Sharman, 1966).

The present study is part of an effort to prepare an identification key to the species of medium stomach worms of domestic ruminants of North America. Several characters of primary importance in the identification keys, including the synlophe (longitudinal surface cuticular ridges) and structure of the esophagus, have not been described for *O. bisonis,* and are described herein. An earlier redescription of *O. bisonis* by Becklund and Walker (1967) included excellent drawings of spicules and the copulatory bursa. The structure of the genital cone was described in detail by Stringfellow (1971). In order to separate female *O. bisonis* from other species with a similar synlophe, a detailed study of females of 3 species was necessary including *O. bisonis, O. ostertagi,* and *Teladorsagia circumcincta.* A key to males of 5 species and females of 3 species is presented at the end of the Discussion section. This group includes all species with a tapering lateral synlophe.

Materials and Methods

Nematodes

Specimens were obtained from the National Parasite Collection maintained in this laboratory and others were provided by Drs. David E. Worley and Newton Kingston (Table 1). Among specimens studied were paratypes of *Ostertagia bisonis* (USNM Helm. Coll. Nos. 25960 and 26103).

Microscopy

Specimens were studied as: (1) temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with regular light microscopy or interference-contrast microscopy at a magnification of 400 to 1,000; (2) cross sections in free-hand cuts made with a cataract knife and mounted in glycerine jelly; (3) critical point dried, coated with gold palladium, and viewed at 5–20 kV with scanning electron microscopy (SEM) (Madden and Tromba, 1976).

Characters studied

Male specimens were identified to species on the basis of the morphology of the spicules and genital cones (Andreeva, 1958; Dróżdż, 1965; Becklund and Walker, 1967, 1971; Stringfellow, 1971) prior to study of the synlophe and esophagus. Bursal ray patterns were determined and described using the system of Durette-Desset and Chabaud (1981). Papillae of the genital cone and rays of the copulatory bursa followed the numbering system of Chabaud et al. (1970). The lengths of the esophageal–intestinal (E-I) valves, determined to extend from the posterior end of the cuticular lining of the triradiate lumen of the esophagus to the posterior end of the esophagus (Figs. 14–16), were measured (Table 2). For measurements of the

Table 1. Specimens of *Ostertagia bisonis* and related species* studied by host, locality, and sex.

Species and synomyms	Number of lots/number of specimens by host, locality and sex	
Ostertagia bisonis Chapin, 1925	*Ammotragus lervia,* Barbary sheep	
=*O. orloffi* Sankin, 1930	New Mexico	1/2 males
=*O. bellae,* nomum nudum	*Antilocapra americana,* pronghorn	
	South Dakota	4/15 males, 1 female
	Wyoming	1/5 males
	Bison bison, buffalo	
	Alberta, Canada	2/6 males, 6 females
	South Dakota	1/6 males, 7 females
	Bos taurus, cattle	
	Colorado	1/1 male
	Montana	5/25 males, 16 females
	Wyoming	6/20 males, 1 female
	Odocoileus hemionus, mule deer	
	Montana	2/7 males, 6 females
	South Dakota	2/4 males
	Ovis aries, sheep	
	USSR, Leningrad	1/1 male, 1 female
*Ostertagia ostertagi**	*Antilocapra americana,* pronghorn	
	South Dakota	1/1 female
	Bos taurus, cattle	
	England, Weybridge	1/2 males, 1 female
	Georgia	2/3 females
	Louisiana	1/7 males
	Maryland	5/11 males,† 14 females
	Montana	3/13 males, 15 females
	New York	1/2 males
	Wyoming	1/7 males, 1 female
	Odocoileus hemionus, mule deer	
	Montana	1/3 females
*Teladorsagia circumcincta**	*Capra hircus,* goat	
	England, Weybridge	3/4 males, 8 females
	Oreamnos americanus, mountain goat	
	South Dakota	1/1 female
	Ovis aries, sheep	
	England, Weybridge	1/1 male‡
	Georgia	1/2 males, 5 females
	Indiana	1/1 male
	Maryland	1/5 females
	Virginia	1/1 female

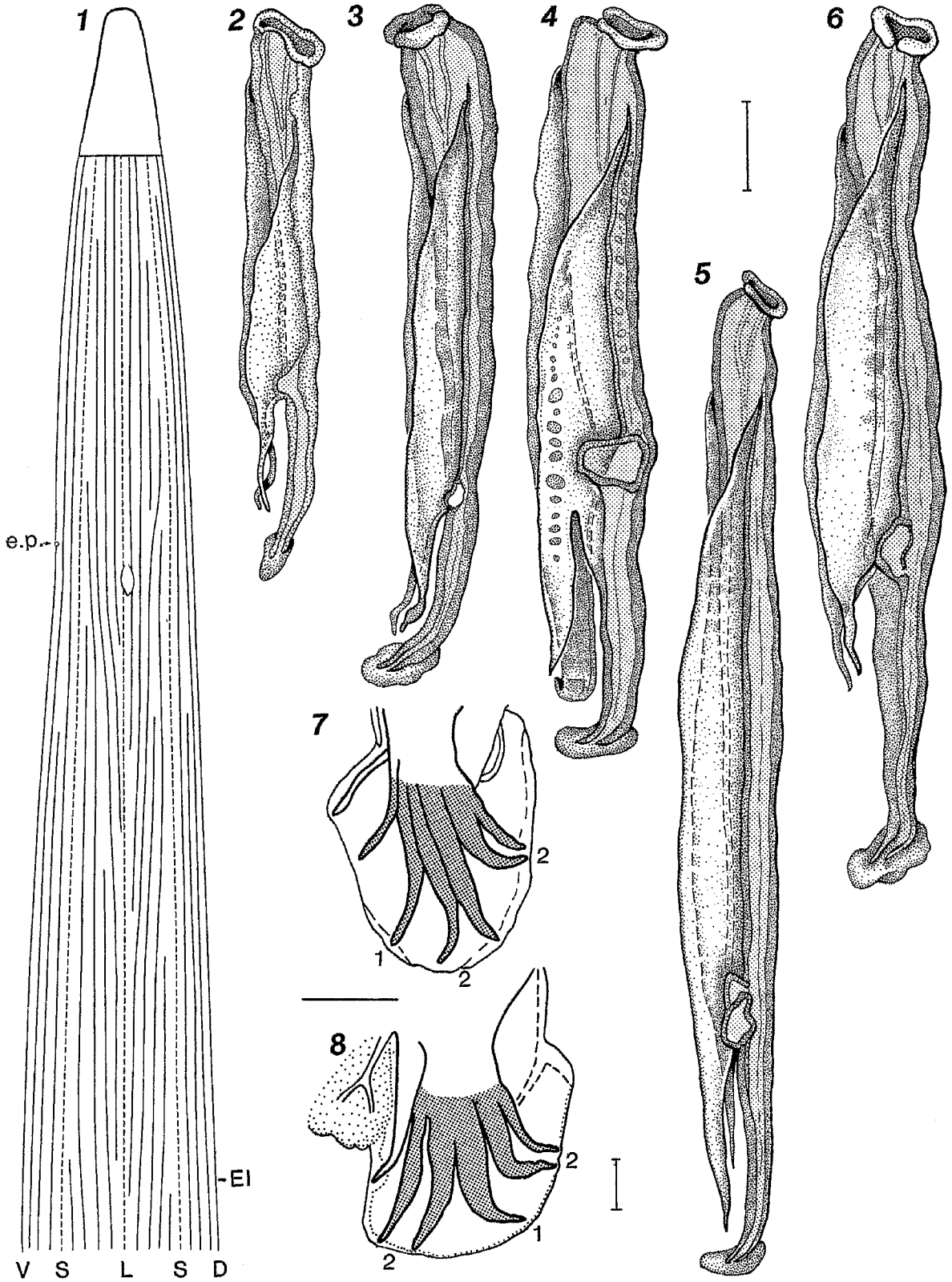
* For additional specimens studied and synonymies see Lichtenfels et al. (1988a).
† Includes 1 male *Ostertagia lyrata.*
‡ *Teladorsagia trifurcata.*

infundibula and sphincters of the ovejectors (Table 3), the edge of the muscular portion of the sphincter was used as a dividing line between them, and the fluffy coat around the sphincter and the portion of the infundibulum overlapped by the muscles of the sphincters were ignored (Figs. 36–38). Because the separation of the vestibule from the sphincter was difficult or impossible to determine, the vestibule was counted as part of the sphincter. The measurement for length of the sphincter includes the distance from the distal end of the sphincter to the vulva. Measurements are in micrometers unless indicated otherwise. Synonymies in Table 1 follow Dróżdż (1965) and Skrjabin et al. (1954).

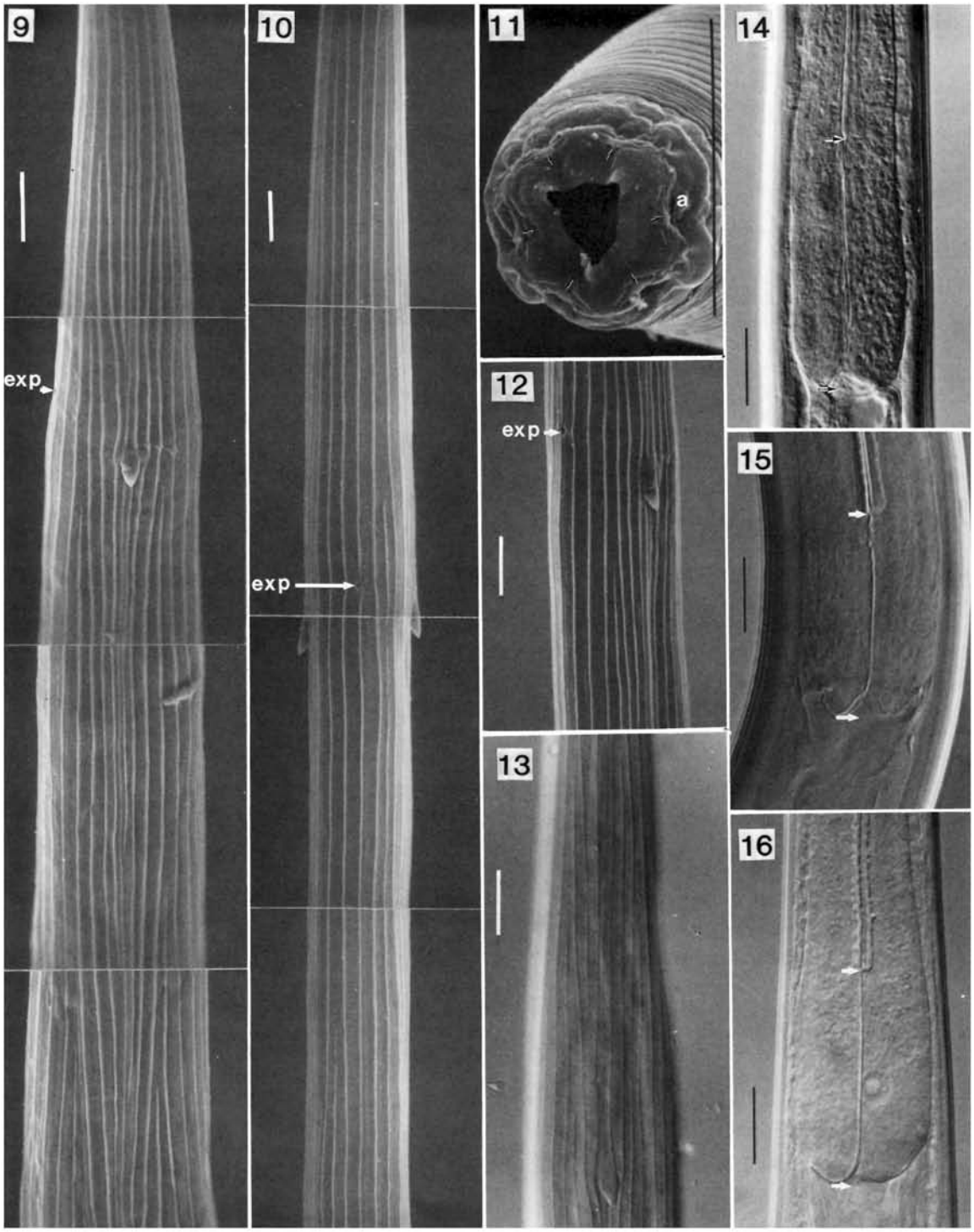
Results

Synlophe of *Ostertagia bisonis*

There were about 20–38 ridges in the region of the esophagus (Fig. 1) with the smaller number anteriorly. The pattern observed was the Type I lateral synlophe (Lichtenfels et al., 1988a) in which there is 1 continuous lateral ridge (L in Fig. 1) running just ventral to the cervical papilla and other adjacent ridges in the lateral field angle posteriorly toward the lateral ridge and end adjacent to it (Figs. 1, 9, 12, 13). This pattern was



Figures 1–8. Drawings of 5 species of Ostertagiinae. 1. Synlophe of *Ostertagia bisonis,* diagram of left lateral view. Note: Dashed lines for emphasis only; ridges are not interrupted (see Figs. 9, 10, 12, 13). 2. Spicule of *Ostertagia bisonis.* 3. Spicule of *Ostertagia ostertagi.* 4. Spicule of *Ostertagia lyrata.* 5. Spicule of *Teladorsagia circumcincta.* 6. Spicule of *Teladorsagia trifurcata.* 7. Bursal ray pattern of the *Teladorsagia* species. 8. Bursal ray pattern of *Ostertagia bisonis* (from Becklund and Walker, 1967). e.p., excretory pore; EI, esophageal–intestinal junction; L, lateral ridge; S, sublateral ridges; V, ventral ridge; D, dorsal ridge. All scale bars = 25 μm.



Figures 9–16. Lateral tapering synlophe of *Ostertagia bisonis* and esophageal–intestinal (E-I) valves of 3 species of Ostertagiinae. 9. Synlophe, left lateral view, SEM. 10. Synlophe, ventral view, SEM. 11. En face view, SEM, showing 6 labial papillae (arrows), 1 of the 2 lateral amphids (a). Outer circle of 8 cephalic papillae not discernable. 12. Synlophe showing number of ridges between excretory pore and cervical papilla, SEM. 13. Synlophe, left lateral view, light microscopy. 14. E-I valve of *Ostertagia bisonis* showing anterior and posterior ends of valve between arrows. 15. E-I valve of *Ostertagia ostertagi* showing anterior and posterior ends of valve between arrows. 16. E-I valve of *Teladorsagia circumcincta* showing anterior and posterior ends of valve between arrows. exp, excretory pore. All scale bars = 25 μm.

Table 2. Morphometrics (in micrometers; range with mean in parentheses) of male *Ostertagia bisonis, Ostertagia ostertagi, Ostertagia lyrata, Teladorsagia circumcincta,* and *Teladorsagia trifurcata.*

Character	*Ostertagia bisonis* (*N* = 40)	*Ostertagia ostertagi** (*N* = 18)	*Ostertagia lyrata** (*N* = 16)	*Teladorsagia circumcincta** (*N* = 35)	*Teladorsagia trifurcata** (*N* = 24)
Body length (mm)	5.64–8.64 (7.23)	5.40–7.44 (6.12)	5.04–7.32 (6.23)	5.40–11.4 (8.13)	6.24–10.7 (8.44)
Subventral esophageal gland orifices†	225–350 (285)	204–280 (248)‡	224–293 (260)	188–256 (219)	188–280 (236)
Cervical papillae†	225–388 (312)	296–372 (339)	278–392 (344)	264–408 (332)	296–396 (352)§
Esophagus length†	604–869 (741)	556–764 (672)	525–740 (665)	502–892 (620)	528–684 (618)
Esophageal–intestinal valve length	82–141 (108)	51–89 (76)	50–77 (64)	53–97 (79)	51–99 (79)
Esophagus as percent of body length	8.4–12.3 (10.3)	7.6–13.1 (11.1)	7.9–13.9 (10.8)	5.6–10.3 (7.7)	6.3–8.8 (7.4)
Spicule length	129–188 (162)	212–264 (238)	229–268 (238)	242–408 (317)	188–319 (252)
Genital cone shape	Normal	Proconus	Sjöberg's organ	Normal	Sjöberg's organ
Bursal ray formula‖	2-1-2	2-1-2	2-1-2	2-2-1	2-2-1

* Emended measurements published by Lichtenfels et al. (1988a).
† From anterior end.
‡ *N* = 16.
§ *N* = 23.
‖ Pattern of rays in lateral lobes of bursa following system of Durette-Desset and Chabaud (1981).

repeated through the anterior half of the specimen. In the posterior half of the nematode the lateral ridges became more parallel to each other. In the region of the esophagus posterior to the cervical papillae, 1–4 pairs of lateral ridges ended adjacent to the lateral ridge. Most specimens had 3 parallel ventral ridges with the ventralmost ridge being interrupted by the excretory pore (Fig. 10). However, 3 or 4 of the 130 specimens studied had only 1 ventral ridge and 1 or more ridges beginning near the excretory pore next to the ventral ridge rather than running parallel to the ventral ridge anteriorly to the cephalic region. At the level of the excretory pore *O. bisonis* had 28 ridges (Fig. 12). More posteriorly in the body the number of ridges increased to 38–40 at the E-I junction (Figs. 1, 9). The number of ridges remained relatively constant through the middle three-fourths of the nematode (Fig. 39). In the prebursal or postvulvar region only the lateral ridges remained (Table 4).

Esophagus

The most useful characteristic of the esophagus, as in other related species, was the length of the E-I valve (Tables 2, 3). The valve was found to be longer than that of other species (Figs. 14–16) with a similar tapering lateral synlophe, but shorter than related Ostertagiinae with a parallel lateral synlophe. In addition other characteristics of the esophagus were studied (Tables 2, 3). The length of the esophagus as a percentage of the total body length was found to differ among similar species and was useful in identifying females (Table 3). The subventral esophageal gland orifices (SVGO) were anterior to the excretory pore (Table 3).

Male characters

We confirmed the presence of a gubernaculum (Figs. 18, 32) and found it to have an expanded proximal portion. The paired spicules are mirror images of each other, of medium to slender thickness, split into 3 branches in the distal third, with a central shaft that ends distally in a medially curved point covered with a fleshy pad, and a pair of thin branches supported by membranous alae that extend from the proximal shaft and end in slightly sinuous tips of nearly equal length (Figs. 2, 18, 19). The ventral surface of the genital cone does not have a proconus (Fig. 18). In lateral view the genital cone is bilobed with ventral and dorsal lobes, and with the saclike dorsal ray of the bursa the appearance is trilobed (Fig. 18). In ventral view the ventral lobe (Fig. 17) of the genital cone appears to be a bipartite velum that encloses the paired number 0 papillae. The dorsal part of the genital cone bears an oval accessory bursal membrane (Figs. 17, 18) that encloses the paired papillae number 7. The dorsal lobe is

Table 3. Morphometrics (in micrometers; range with mean in parentheses) of female *Ostertagia bisonis*, *Ostertagia ostertagi*, and *Teladorsagia circumcincta*.

Character	*Ostertagia bisonis** (*N* = 18)	*Ostertagia ostertagi* (*N* = 16)	*Teladorsagia circumcincta* (*N* = 15)
Body length (mm)	6.38–8.90 (7.95)	8.90–10.5 (9.07)	9.10–12.4 (10.7)
Nerve ring†	199–280 (249)	229–293 (267)	235–304 (266)
Subventral esophageal gland orifices†	252–328 (290)	194–296 (262)§	209–310 (246)
Excretory pore†	269–328 (300)	259–343 (309)	308–386 (349)
Cervical papillae†	280–353 (322)	289–369 (341)	323–418 (372)
Esophagus length†	643–849 (743)	651–825 (724)	548–688 (615)
Esophageal–intestinal valve length	89–124 (107)	56–86 (76)	63–82 (74)
Esophagus as percent of body length	8.6–10.3 (9.4)	7.1–8.9 (8.0)	5.1–6.8 (5.8)
Vulva percent†	79–83 (81)	84–87 (85)	80–85 (83)
Anterior infundibulum	124–199 (163)	131–189 (162)	136–196 (168)
Anterior sphincter to vulva length‡	168–332 (257)	114–196 (140)	159–253 (203)
Posterior infundibulum	112–178 (143)	128–180 (151)‖	129–175 (150)
Posterior sphincter to vulva length‡	145–295 (224)	103–159 (123)	147–211 (171)
Eggs (l × w)	70–84 (78) × 30–43 (39)	70–86 (77) × 39–49 (41)¶	84–101 (91) × 40–56 (49)
Tail length	126–164 (148)	105–168 (136)‖	133–164 (154)¶

* Includes 5 paratypes.
† From anterior end.
‡ Sphincter to vulva includes vestibule and sphincter length.
§ *N* = 14.
‖ *N* = 15.
¶ *N* = 13.

about half to two-thirds as long as the lateral lobes of the bursa, saclike in lateral view, and usually has a granular appearance (Fig. 18). The fleshy rays of the lateral lobes of the copulatory bursa are oriented in a 2-1-2 pattern with the ventroventral (No. 2) and the lateroventral (No. 3) rays close together, the anterolateral (No. 4) ray by itself and the mediolateral (No. 5) and posterolateral (No. 6) rays close together (Fig. 8).

Female characters

The vulva is located about one-fifth of the body length from the posterior end. The vulva is a ventral transverse slit, usually without a vulval flap and with a thickened cuticle around the opening (Fig. 36). In 2 of 20 specimens studied, a small cuticular lobe was present on 1 side, slightly anterior to the vulva. The ovejectors fill most of the diameter of the body cavity (Fig. 36). The infundibula are slightly shorter than the distance from the vulva to the junction of the sphincter and infundibulum. The anterior ovejector is longer than the posterior ovejector in all specimens. The tip of the tail is completely covered by annulated cuticle and is usually slightly swollen or digitiform (Fig. 33). Eggs are cylindrical with rounded ends 70–84 (78) long by 30–43 (39) wide.

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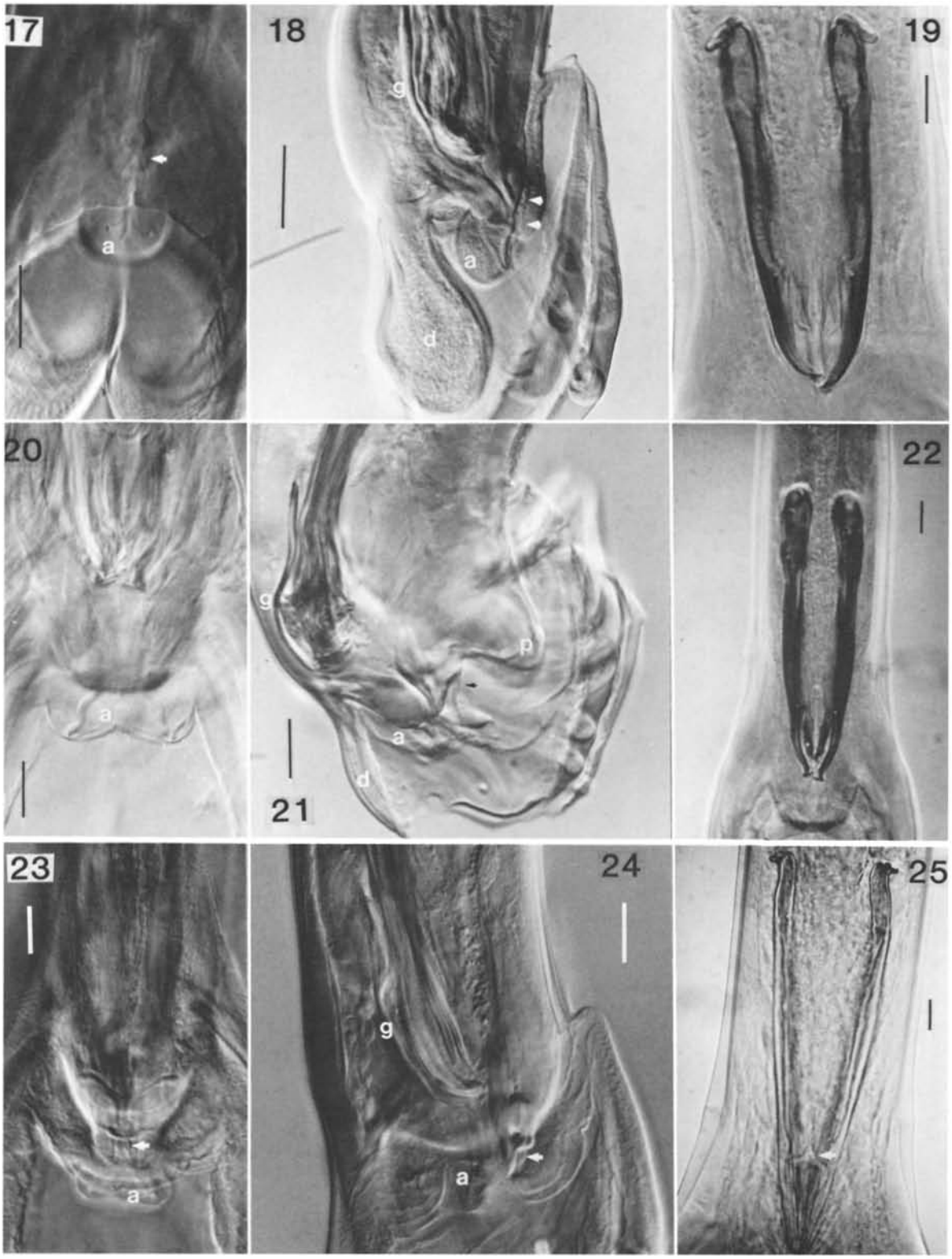
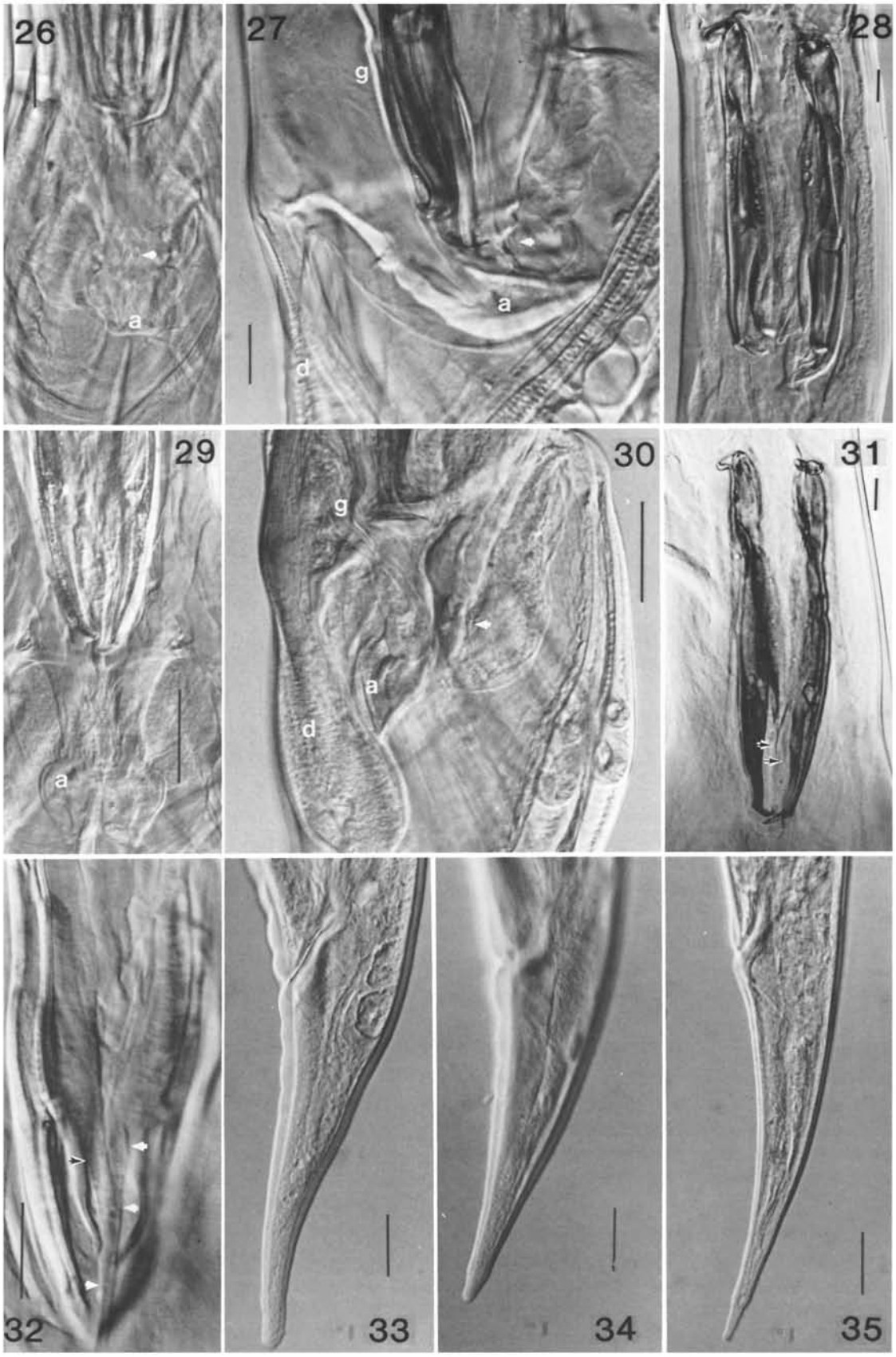
Figures 17–25. Genital cones, spicules and gubernacula of some male Ostertagiinae. 17–19. *Ostertagia bisonis*. 17. Genital cone, ventral view, showing paired papillae number 0 (arrow) within the ventral velumlike expansion, and paired papillae number 7 within accessory bursal membrane (a). 18. Genital cone and dorsal bursal lobe (d), lateral view, showing ventral lobe of genital cone enclosing 1 of paired papillae number 0 (arrows), and dorsal lobe of genital cone bearing accessory bursal membrane (a) enclosing 1 of paired papillae number 7. 19. Spicules, ventral view, showing 3 distal branches on each spicule. 20–22. *Ostertagia ostertagi*. 20. Genital cone, ventral view, showing accessory bursal membrane (a) enclosing paired papillae number 7 and distal ends of central branches of spicules. 21. Posterior extremity of male, lateral view, showing dorsal bursal lobe (d), gubernaculum (g), distal end of spicules and genital cone with accessory bursal membrane (a), and 1 of paired papillae number



0 (arrow), and proconus (p). 22. Spicules and gubernaculum, ventral view. 23–25. *Teladorsagia circumcincta*. 23. Genital cone, ventral view, showing ventral velumlike expansion of genital cone enclosing papillae number 0 (arrow), and accessory bursal membrane (a) enclosing papillae number 7. 24. Genital cone, lateral view, showing distal end of spicules, gubernaculum (g), ventral expansion of cone enclosing 1 of paired papillae number 0 (arrow) and accessory bursal membrane (a) enclosing 1 of paired papillae number 7. 25. Spicules, ventral view and gubernaculum (arrow). All scale bars = 25 μm.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Discussion

New information on *Ostertagia bisonis* presented herein includes the description of the synlophe and the esophagus. This new information was required in order to develop an identification key to both males and females of *O. bisonis* and related species. The tapering lateral synlophe described herein for *O. bisonis* is very similar to that described earlier (Lichtenfels et al., 1988a) for *O. ostertagi* and *Teladorsagia circumcincta.* Lichtenfels et al. (1988a) reported that the tapering pattern was more marked in *T. circumcincta* than in *O. ostertagi* with 2 or 3 pairs of ridges tapering toward and ending near the lateral ridge in the region of the esophagus in *T. circumcincta,* but only 1 pair ending in that region in *O. ostertagi.* However, in *O. bisonis* there was a greater range of variation in this character with 1–4 pairs of ridges ending near the lateral ridge in the region of the esophagus (Figs. 1, 9). The variability of the ventral synlophe pattern in *O. bisonis* was similar to that reported earlier (Lichtenfels et al., 1988a) for *O. ostertagi.* Most specimens had 3 parallel ventral ridges (Fig. 10), but fewer than 5% of *O. bisonis* specimens were similar to the single ventral ridge pattern described by Lichtenfels et al. (1988a) for *T. circumcincta.* In number of ridges in 1 circumference at various points along the body, *O. bisonis* is very similar to *O. ostertagi* except for its smaller number of postvulvar and prebursal ridges (Table 4). The cross sections also show, in addition to the number and distribution of ridges, that *O. bisonis* is only about half as thick as the 2 related species (Figs. 39–41).

Two characteristics of the esophagus were found to be consistent within species, variable among species, and easily observable making them useful key characters for identifying females of *O. bisonis, O. ostertagi,* and *T. circumcincta.* The length of the E-I valve of *O. bisonis* (Fig. 14) is longer than that of *O. ostertagi* (Fig. 15) or *T. circumcincta* (Fig. 16) (Tables 2, 3). The length of the esophagus as a percentage of total body length is smaller in *T. circumcincta* than in the other 2 species, and is especially useful in separating females of *O. bisonis* and *T. circumcincta* (Tables 2, 3) as a supplementary character to the length of the E-I valve.

The ducts of the subventral glands of the esophagus empty anterior to the cervical papillae (Tables 2, 3). As reported earlier (Lichtenfels et al., 1988a), the position of these ducts relative to the nerve ring, cervical papillae, and excretory pore has a wide variability because of the degree of shrinkage or stretching of the esophagus. In addition, the position of the ducts is difficult to determine compared to the length of the E-I valve which we recommend, along with the length of the esophagus as a percentage of total body length, as key characters for this group of species.

The most useful characteristics for identifying males to species, in addition to the length of the E-I valve, are the morphology of the spicules and genital cone, lateral bursal ray pattern, and presence or absence of a proconus. The spicules, gubernaculum, genital cone, and copulatory bursa of *O. bisonis* were illustrated in detailed drawings by Becklund and Walker (1967). Herein we provide, for comparison with related species, drawings of the left spicule (Figs. 2–6) and photomicrographs of the genital cone, gubernaculum, and spicules (Figs. 17–32) of 5 species with a tapering lateral synlophe. The spicules of *O. bisonis* (Figs. 2, 18, 19) appear to be typical for the Ostertagiinae with a central main stem and 2 medial branches (Figs. 3–6). In characteristics of the genital cone, especially in lacking a proconus, *O. bisonis* (Fig. 18) is more similar to *T. circumcincta* (Fig. 24) than to *O. ostertagi* (Fig. 21). The

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Figures 26–35. Genital cones, spicules and gubernacula (26–32), and female tails (33–35) of some Ostertagiinae. 26–28. *Ostertagia lyrata.* 26. Genital cone and spicule tips, ventral view, showing paired papillae number 0 (arrow) and accessory bursal membrane (a). 27. Genital cone and spicule tips, lateral view, showing 1 of paired papillae number 0 (arrow), sclerotized accessory bursal membrane (a), gubernaculum (g), and proximal portion of dorsal bursal lobe (d). 28. Spicules, ventral view, showing 3 distal branches on each spicule. 29–31. *Teladorsagia trifurcata.* 29. Genital cone and spicule tips, ventral view, showing accessory bursal membrane (a) enclosing paired papillae number 7. 30. Genital cone and spicule tips, lateral view, showing ventral lobe of cone enclosing 1 of paired papillae number 0 (arrow), accessory bursal membrane (a), dorsal bursal lobe (d), and gubernaculum (g). 31. Spicules, ventral view, showing 3 distal branches with arrows indicating 2 medial branches of left spicule. 32. *Ostertagia bisonis* gubernaculum (between arrows), dorsal view. 33–35. Female tails, left lateral views. 33. *Ostertagia bisonis.* 34. *Ostertagia ostertagi.* 35. *Teladorsagia circumcincta.* All scale bars = 25 μm.

Figures 36–38. Ovejectors of some female Ostertagiinae. 36. *Ostertagia bisonis*. 37. *Ostertagia ostertagi*. 38. *Teladorsagia circumcincta*. V, vulva; sp, sphincter; in, infundibula (lateral view). All scale bars = 25 μm.

2-1-2 pattern of rays in the copulatory bursa of *O. bisonis* is like that of *O. ostertagi*.

Additional characters for separating females of *O. ostertagi* and *T. circumcincta* include the synlophe, vulval morphology, and egg size. Differences in the synlophes of *O. ostertagi* and *T. circumcincta* were described by Lichtenfels et al. (1988a). The lateral synlophe between the cervical papillae and the posterior end of the esophagus of *O. ostertagi* has a single pair of ridges ending adjacent to the lateral ridge, but *T. circumcincta* has 2 or 3 pairs of ridges ending next

Table 4. Number of longitudinal cuticular ridges in cross sections at various body regions of 3 species of Ostertagiinae.

Body region	*Ostertagia bisonis*		*Ostertagia ostertagi**		*Teladorsagia circumcincta*†	
	Male ($N = 2$)	Female ($N = 5$)	Male ($N = 4$)	Female ($N = 4$)	Male ($N = 4$)	Female ($N = 5$)
Junction of E-I	29–38	36–40	39–40	33–39	31–36	30–43
End of first quarter	36–38	38–40	38–41	33–40	29–36	33–43
Midbody	38–41	36–38	39–41	32–36	25–39	29–42
End of third quarter	29–37	38–40	37–41	36–44	25–34	28–36
Prebursal or postvulvar‡	18–30§	16–32§	30–36§	39–49	14–28§	36–54§

* Includes 1 male *Ostertagia lyrata.*

† Includes 1 male *Teladorsagia trifurcata.*

‡ Sectioned 200–300 μm anterior to prebursal papillae or midway between vulva and tail tip.

§ Total number distributed in 2 equal lateral fields, no ridges dorsally or ventrally.

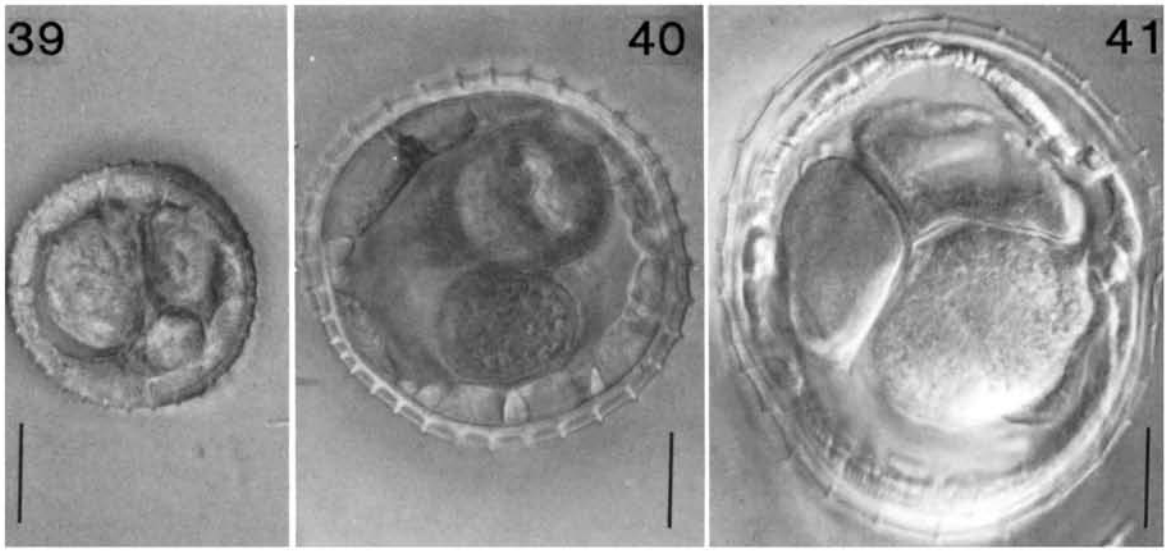
to the lateral ridge in this region. Ventrally ridges beginning between the area of the excretory pore and the posterior end of the esophagus are lateral to a single ventral ridge in *T. circumcincta,* but usually lateral to 3 parallel ventral ridges in *O. ostertagi.* The vulval flap of *O. ostertagi* is usually present and it usually wraps around the body almost 360° (Fig. 37). However, Michel et al. (1972a, b) described considerable variation in the degree of development of the vulval flap in *O. ostertagi.* Specimens may be found that vary from smooth to a fully developed flap that wraps around the body almost 360°. In *T. circumcincta* if a vulval flap is present it wraps 180° or less of the body circumference (Fig. 38). This character has limited use in a key, however, since flapless or specimens with incompletely developed flaps would not be identified. The egg size of *O. bisonis* is almost identical to that of *O. ostertagi,* but differs from the larger eggs of *T. circumcincta* (Table 3).

Two additional characteristics of females, morphometrics of the ovejectors and shape of the tail, were useful for identifying some specimens but were variable enough to disqualify them as key characters. The anterior ovejectors were longer than the posterior ovejectors in all 3 species, *O. bisonis, O. ostertagi,* and *T. circumcincta* (Figs. 36–38). It will be interesting to determine how widespread this asymmetry in ovejectors is within the Ostertagiinae. Morphometrics of the ovejectors were found to be useful in separating most specimens of *O. ostertagi* from *O. bisonis* and *T. circumcincta* (Table 3). In most specimens of *O. ostertagi* the infundibula were longer than the combined length of the sphincter and vestibule but the reverse was true in the other 2 species (Figs. 36–38). This was true for both anterior and posterior ovejectors. In characteristics of the ovejectors and vulvar morphology, *O. bisonis* is more similar to *T. circumcincta* than to *O. ostertagi.* The shape of the tip of the female tail of most specimens of *O. bisonis* is slightly swollen or digitiform (Fig. 33) while the tail tips of *O. ostertagi* and *T. circumcincta* females usually are sharply tapered (Figs. 34, 35, respectively).

Recently, characteristics useful for identifying 4 species of female Ostertagiinae were described by Lancaster and Hong (1990). They did include *O. ostertagi* and *T. circumcincta,* but not *O. bisonis,* and they used different characters than used here.

The possible synonymy of *O. orloffi* with *O. bisonis* was discussed by Becklund and Walker (1967) and they preferred to recognize both species because of possible minor differences in shape of the gubernaculum and medial branches of the spicules. The original description of *O. bisonis* indicated a gubernaculum was not present. The presence of a gubernaculum in *Ostertagia orloffi* Sankin, 1930, was the primary difference between the 2 species until a gubernaculum was described in *O. bisonis* by Olsen (1949). After studying the synlophe, spicules, gubernaculum, genital cone, esophagus, ovejectors, and other characteristics of 1 male and 1 female *O. orloffi* collected from *Ovis aries* in Leningrad in 1936, we regard *O. orloffi* Sankin, 1930, to be a junior synonym of *O. bisonis* following Karamendin (1967). However, Dróżdż (1979) and Petrov (1983) continued to use the name *O. orloffi* for the Palaearctic populations.

Since the review of *O. bisonis* literature in North America by Becklund and Walker (1967), this species has been reported in *Antilocapra americana, Bison bison,* and *Odocoileus hemionus* in



Figures 39–41. Mid-body cross sections of some female Ostertagiinae. 39. *Ostertagia bisonis* showing 39 ridges. 40. *Ostertagia ostertagi* showing 36 ridges. 41. *Teladorsagia circumcincta* showing 30 ridges. All scale bars = 25 μm.

South Dakota (Boddicker and Hugghins, 1969), in *O. hemionus* in Montana (Worley and Eustace, 1972), and in cattle in Wyoming (Honess and Bergstrom, 1971). A review of the literature on *O. orloffi* in Asia and North America supports the conclusions of Worley and Sharman (1966) that *O. bisonis* (=*O. orloffi*) normally occurs in wild ruminants and appears in cattle and sheep in specialized conditions when grazing land is shared. It is clear, however, that *O. bisonis* can be an important pathogen of cattle under those conditions (Worley and Sharman, 1966).

The Ostertagiinae of domestic ruminants of North America is a group of 10 species with unsettled generic level taxonomy (Lichtenfels et al., 1988b). Recently, Durette-Desset (1989) placed *O. bisonis* in the genus *Camelostrongylus* Orloff, 1933, based on characteristics of the copulatory bursa and synlophe. The species she transferred to *Camelostrongylus* included *O. lyrata,* but not *O. ostertagi.* We prefer to retain *O. bisonis* and *O. lyrata* in the genus *Ostertagia* with *O. ostertagi.* Realignment of species at the generic level will be required in the Ostertagiinae, but must await clarification of relationships in future studies.

Several synlophe patterns have been identified in the Ostertagiinae from domestic ruminants (Lichtenfels et al., 1988a, b). The following key includes only species with a tapering lateral synlophe. Data on all key characters for 5 species of males are included in Table 2. Comparative data on the main characters of females include only 3 species in both Table 3 and the key, because females of *O. lyrata* and *T. trifurcata* have never been identified. Dróżdż (1974) reported that species pairs were common within the Ostertagiinae. Lancaster and Hong (1981) and Lancaster et al. (1983) have proposed that *O. lyrata* (Figs. 26–28) and *T. trifurcata* (Figs. 29–31) (=*T. davtiani* Andreeva and Satubaldin, 1954) are morphotypes of *O. ostertagi* and *T. circumcincta,* respectively. Included among 14 species pairs proposed by Dróżdż (1974) were *O. orloffi* (which we consider to be a synonym of *O. bisonis*) and *Teladorsagia kazakhstanica* Dikov and Nekipelova, 1963. In North America no associated minor species has been identified for *O. bisonis.* The associated minor species in Asia (*T. kazakhstanica*) was described (Dikov and Nekipelova, 1963) as similar to *T. trifurcata* (=*T. davtiani*) but with longer branches on the spicules, longer ventral papillae on the genital cone (pair number 0), a dorsal ray that bifurcates in its proximal third, and lateral rays in a 2-1-2 pattern rather than 2-2-1 as in *T. trifurcata.* In addition, we can predict that *T. kazakhstanica* will share characteristics of the synlophe and esophagus as described herein with *O. bisonis* (=*O. orloffi*).

The comparisons with other species have been limited to those species with a tapering lateral

synlophe that are parasitic in domestic ruminants in North America. Two species, *Ostertagia leptospicularis* Assadov, 1953, and *O. mossi* Dikmans, 1931, without a tapering lateral synlophe are sufficiently similar in other characteristics, especially in size and spicule morphology, that distinguishing characteristics for separating them from *O. bisonis* are given here. Both *O. leptospicularis* and *O. mossi* have 3 parallel lateral ridges, and both sexes of both species can be distinguished from *O. bisonis* on that character alone. In addition, males of *O. leptospicularis* and *O. mossi* have a proconus, but *O. bisonis* males do not.

Ostertagia bisonis includes some characteristics of both genera *Ostertagia* and *Teladorsagia*. Like *Ostertagia* it has a 2-1-2 arrangement of lateral bursal rays. Like *Teladorsagia* it lacks a proconus. In characteristics of the ovejectors and vulval morphology, *O. bisonis* is more similar to *T. circumcincta* than to *O. ostertagi*. In egg size *O. bisonis* is almost identical to *O. ostertagi*, and both differ from *T. circumcincta*. The synlophe pattern and other characteristics shared by this group of species may indicate that they are each other's closest relatives, but this cannot be determined until sufficient information is available for these key characters to be polarized. Additional characters, including DNA comparisons, should be completed prior to making generic level changes.

Key to Male Ostertagiinae with a Tapering Lateral Synlophe from Domestic Ruminants in North America

1a. Esophageal–intestinal valve length more than twice its width (Fig. 14); spicules 129–188 μm long, dorsal and ventral medial branches longer than half of distance from branching point to distal end of central branch (Figs. 2, 19); proconus absent (Fig. 18) ..... *O. bisonis*

1b. Esophageal–intestinal valve length less than twice its width (Figs. 15, 16); spicules usually longer than 200 μm 2

2a. Lateral rays of copulatory bursa with fleshy rays in 2-1-2 pattern (Fig. 8); proconus present (Fig. 21) or absent (Fig. 27) 3

2b. Lateral rays of copulatory bursa with fleshy rays in 2-2-1 pattern (Fig. 7); proconus absent (Figs. 24, 30) 4

3a. Proconus present, remainder of genital cone not prominent (Figs. 20, 21); spicules as in Figures 3, 21, 22 ..... *O. ostertagi*

3b. Proconus absent, dorsal part of genital cone enlarged and sclerotized (Figs. 26, 27); spicules as in Figures 4, 27, 28 ..... *O. lyrata*

4a. Spicules divided in distal fourth, dorsal and ventral branches more than half as long as main branch (Figs. 5, 25); dorsal genital cone unsclerotized (Figs. 23, 24) ..... *T. circumcincta*

4b. Spicules divided at beginning of distal third, dorsal and ventral medial branches about half as long as main branch (Figs. 6, 31); dorsal genital cone enlarged and sclerotized (Figs. 29, 30) ..... *T. trifurcata*

Key to Female Ostertagiinae with a Tapering Lateral Synlophe from Domestic Ruminants of North America

1a. Esophageal–intestinal valve length more than twice its width (Fig. 14); esophageal length 643–849 (743) μm long and is 8.6–10.3 (9.4) percent of body length (Table 3) ..... *O. bisonis*

1b. Esophageal–intestinal valve length less than twice its width (Figs. 15, 16) 2

2a. Lateral synlophe with 1 pair of ridges ending next to lateral ridge between cervical papilla and posterior end of esophagus; in region of esophagus shorter ventral ridges usually begin lateral to 3 parallel ventral ridges; esophagus length 651–825 (724) μm long and is 7.1–8.9 (8.0) percent of body length (Table 3); egg length 70–86 (77) μm; egg width 39–49 (41) μm ..... *O. ostertagi*

2b. Lateral synlophe with 2 or 3 pairs of ridges ending next to lateral ridge between cervical papilla and posterior end of esophagus; in region of esophagus shorter ventral ridges begin next to single ventral ridge; esophagus length 548–688 (615) μm long and is 5.1–6.8 (5.8) percent of body length; egg length 84–101 (91) μm; egg width 40–56 (49) μm ..... *T. circumcincta*

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