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SYNLOPHE STRUCTURE FOR SPECIES OF *LONGISTRONGYLUS* (NEMATODA: TRICHOSTRONGYLOIDEA), ABOMASAL PARASITES AMONG UNGULATES FROM SUB-SAHARAN AFRICA, WITH COMPARISONS TO THE GLOBAL OSTERTAGIINE FAUNA

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ABSTRACT: The synlophe, or system of longitudinal cuticular ridges characteristic of some trichostrongyloid nematodes, is examined in detail for 6 of 8 species in *Longistrongylus* (Ostertagiinae) that occur in ungulates across sub-Saharan Africa. Among the species of *Longistrongylus* examined, 5 are characterized by a tapering pattern laterally in the cervical zone (anterior to the esophageal-intestinal junction), which is largely consistent among multiple male and female specimens; in contrast, for *Longistrongylus meyeri* the lateral pattern is parallel. The synlophe is bilaterally symmetrical, with ridges extending from the base of the cephalic expansion to near the caudal extremity in males and females. Ridges are acutely pointed, with perpendicular orientation and absence of gradient as viewed in transverse section. Species-specific patterns in conjunction with the numbers of ridges may serve to augment an array of diagnostic characters for species of *Longistrongylus* and contribute to increasingly accurate identification of female specimens. Among 5 of 6 species examined in the current study, the numbers of ridges in males was equal to or exceeded that observed in females, a pattern seen only in *Africanastrongylus* among the 15 genera of the Ostertagiinae. The differential numbers of ridges in males and females may represent another character among the suite of attributes that in part diagnose the genus *Longistrongylus*.

Species of *Longistrongylus* Le Roux, 1931, are characteristic medium stomach worms (Ostertagiinae), which reside in the abomasum and infect ungulate hosts endemic to sub-Saharan Africa (Gibbons, 1977; Hoberg et al., 2008). Currently 8 species are recognized in the genus, including *Longistrongylus meyeri* Le Roux, 1931 (type), *Longistrongylus albifrontis* (Mönnig, 1931), *Longistrongylus sabie* (Mönnig, 1932), *Longistrongylus schrenki* (Ortlepp, 1939), *Longistrongylus namaquensis* Ortlepp, 1963, *Longistrongylus banagiense* (Gibbons, 1972), *Longistrongylus curvispiculum* (Gibbons, 1973), and *Longistrongylus thalae* (Troncy and Graber, 1973), based on decisions outlined in redescrptions and revisions of this group (Gibbons 1977, 1981; Boomker and Durette-Desset, 1997). Additional nominal taxa, *Longistrongylus muraschkinzevi* (Shul'ts and Kadenatsii, 1950) and *Longistrongylus neveulemairei* (Gutteres, 1947), are considered as species inquirendae (Gibbons, 1977). Collectively, species of *Longistrongylus* are characterized by narrow filamentous spicules, a reduced dorsal lobe and ray, filamentous, arcuate “0” papillae that terminate in bulbous expansions, a reduced and highly modified accessory bursal membrane in males, and by irregular cuticular inflations at the level of the vulva in females of some species (Gibbons, 1977; Gibbons and Khalil, 1982; Hoberg et al., 1993a, 2008).

Although congeners are reasonably well characterized, there remains limited information about the structure of the synlophe among species of *Longistrongylus* (Gibbons, 1977). The synlophe, or system of longitudinal cuticular ridges, typical of many taxa among the Trichostrongylina, has been shown to be a useful and important character for differentiation of higher taxa, genera, and species (Durette-Desset, 1983, 1985). In the Ostertagiinae the synlophe has been used extensively to distinguish among genera and species, and to provide the basis for unequivocal identification of female nematodes, which often have few definitive diagnostic attributes (Lichtenfels et al., 1988, 1993; Lichtenfels and Hoberg, 1993). Essential data for the structure, pattern, distribution, and extent of ridges have been developed for representatives of most of the 15 genera among the Ostertagiinae

(Hoberg, Abrams, and Pilitt, 2009) and has been critical for understanding the taxonomic context for polymorphism among male conspecifics, particularly among species of *Marshallagia* (Orloff, 1933), *Orloffia* Drózdź, 1965, *Ostertagia* Ransom, 1907, and *Teladorsagia* Andreeva and Satubaldin, 1954 (e.g., Lichtenfels and Pilitt, 1989; Lichtenfels et al., 1990, Lichtenfels and Hoberg, 1993; Drózdź, 1995; Hoberg et al., 1999; Hoberg and Abrams, 2001).

In the present study, we provide new data for the structure of the synlophe among 6 of 8 species in *Longistrongylus*. These observations complement those presented in original descriptions and in revisions of this genus (Gibbons, 1977). Further, characteristics of the synlophe are compared among genera of other Ostertagiinae and *Longistrongylus* as a basis for understanding general patterns for ridge systems within the subfamily.

MATERIALS AND METHODS

Specimens examined

Specimens representing 6 of 8 species of *Longistrongylus* were examined (Table I). Specimens of *L. namaquensis* and *L. albifrontis* suitable for evaluation of the synlophe could not be located for the present study. Specimens of *L. meyeri* were not available for sectioning; transverse sections suitable for illustration were not available from all species. Nematodes were identified based on morphological criteria previously defined for the genus and respective species (Le Roux, 1931; Gibbons, 1977, 1981; Boomker and Durette-Desset, 1997; Hoberg et al., 2008, Hoberg, Abrams, and Pilitt, 2009). Nomenclature for ungulate hosts is consistent with Wilson and Reeder (1993).

Microscopy

Nematodes were prepared as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with interference contrast microscopy. The synlophe was examined in whole mounts with particular attention given to the pattern of ridge systems in the cervical zone and their extent posteriad in males and females consistent with prior studies among the ostertagiines (Lichtenfels et al., 1988; Hoberg et al., 1999). Patterns in the cervical region are defined according to Lichtenfels et al. (1988) as follows: (1) Laterally, Type 1a weakly tapering (usually 1 or 2 pairs convergent on the lateral-most system), Type 1b strongly tapering (usually 3 or more pairs converging), and Type 2 parallel; and (2) ventrally, Type A with 3 continuous and parallel ventral ridges, and Type B with a single continuous ventral ridge. Transverse sections were hand cut with a

TABLE I. Species and entire specimens of *Longistrongylus* examined from Africa ungulates.

Accession*	Species	Host	Locality	♂†	♀†
OHC T2032	<i>Longistrongylus albifrontis</i>	<i>Damaliscus albifrons</i>	South Africa	Not available‡	
RVC (IIP) 1586	<i>L. banagiense</i>	<i>Damaliscus korrigum</i>	Tanzania	3	-
RVC (IIP) 1753	<i>L. banagiense</i>	<i>Ourebia ourebi</i>	Kenya	-	2
USNPC 81213	<i>L. curvispiculum</i> §	<i>Ovis aries</i>	Texas, USA	3	1
USNPC 81214	<i>L. curvispiculum</i> §	<i>Capra hircus</i>	Texas, USA	1	1
USNPC 83054	<i>L. curvispiculum</i>	<i>Oryx biesa</i>	Texas, USA	2	-
USNPC 83055	<i>L. curvispiculum</i>	<i>Addax nasomaculatus</i>	Texas, USA	1	-
RVC (IIP) 1755	<i>L. curvispiculum</i>	<i>Connochaetes taurinus</i>	Kenya	5	5
BMNH 1998.11.20. 312–317 (coatypes)	<i>L. meyeri</i>	<i>Alcelaphus caama</i>	Southwest Africa	1	3
RVC (IIP) 1673	<i>L. meyeri</i>	<i>Gazella thomsoni</i>	Kenya	5	4
OHC (type series)	<i>L. namaquensis</i>	<i>Ovis aries</i>	South Africa	Not available‡	
USNPC 77484	<i>L. sabie</i>	<i>Aepyceros melampus</i>	South Africa	4	3
RVC (IIP) 2006	<i>L. sabie</i>	<i>Aepyceros melampus</i>	Kenya	4	4
USNPC 66325	<i>L. schrenki</i>	<i>Ourebia ourebi</i>	Uganda	5	4
USNPC 66323	<i>L. schrenki</i>	<i>Kobus kob</i>	Uganda	3	5
USNPC 86098	<i>L. schrenki</i>	<i>Ourebia ourebi</i>	Uganda	1	—
RVC (IIP) 1695	<i>L. schrenki</i>	<i>Kobus</i> sp.	Kenya	3	3
USNPC 66324	<i>L. thalae</i>	<i>Alcelaphus buselaphus jacksoni</i>	Uganda	5	5
USNPC 66327	<i>L. thalae</i>	<i>Redunca redunca</i>	Uganda	2	4

* Collection and specimen numbers from the U.S. National Parasite Collection (USNPC), the Onderstepoort Helminthological Collection (OHC), the Natural History Museum, London (BMNH), and the Royal Veterinary College (RVC). Collections of the RVC contain materials from the International Institute of Parasitology and Commonwealth Institute of Helminthology (IIP).

† Number of male and female specimens examined.

‡ Suitable specimens were not available for study.

§ *Longistrongylus curvispiculum* represent vouchers from an introduced population in western Texas (Craig, 1993) and are from experimental infections in domestic sheep and goats based on larvae recovered from *Oryx biesa*.

cataract knife and mounted in glycerin jelly for specimens of all species when available. Sections were used to count the number of ridges in a minimum of single male and female nematodes (when available) at the esophageal-intestinal junction (EIJ), first quarter, midbody, third quarter, and fourth quarter of total body length as determined from the anterior. Additionally, the spacing between lateral ridges, which can vary because of tapering patterns, is best assessed in transverse sections.

RESULTS

General description of synlophe

In all species of *Longistrongylus*, the synlophe is well developed and bilaterally symmetrical, with ridges extending from the base of the cephalic expansion to near the caudal extremity in males and females (Figs. 1–12; Table II). Ridges are acutely pointed, with perpendicular orientation and absence of gradient as viewed in transverse section. Each species has a characteristic pattern laterally and ventrally in the cervical zone, and along with numbers of ridges at varying levels of the body can complement other diagnostic characters (Table II).

Synlophe of *Longistrongylus banagiense* (Figs. 2, 7)

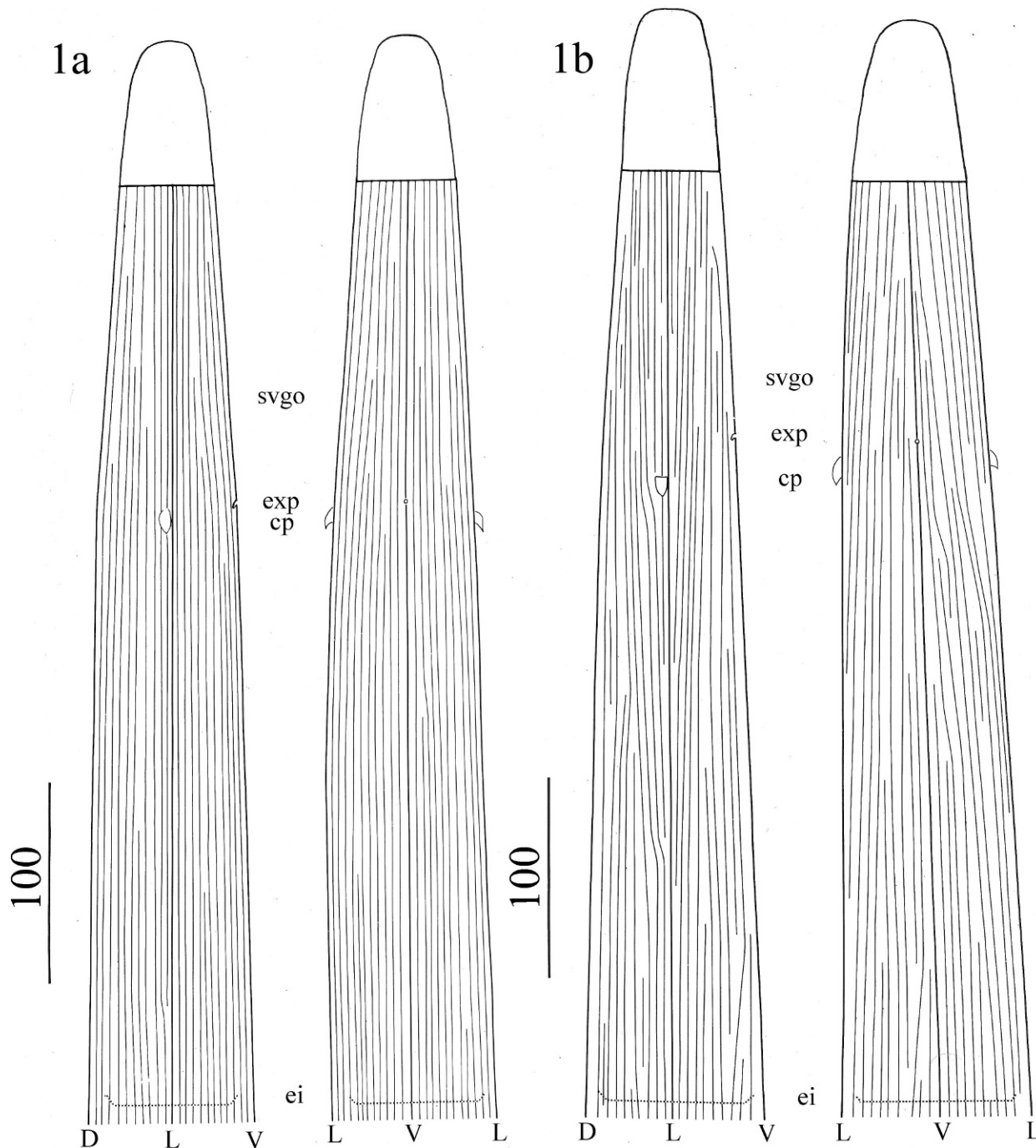
Anterior to the EIJ, the cervical pattern is of Type 1a laterally and Type A ventrally and is similar in males and females irrespective of host species. Continuous subventral and sublateral ridges in the cervical region are present. In each lateral field there are up to 4 narrowly spaced ridges. The numbers of ridges increase posteriorly from the cervical zone attaining a maximum near the midbody. At the EIJ in males, there are 36–37 ridges, and at the midbody 40; data for numbers of ridges among females are not available, and structure of the synlophe at the level of the

vulva was not evaluated. In males, the synlophe terminates ventrally at near 200 µm and dorsally near 100 µm anterior to the prebursal papillae (PBP); ridges are retained in left and right lateral fields to the level of the PBP.

Gibbons (1972) reported 33–43 ridges among males and 33–38 in females at the midbody based on transverse sections in the original description of *L. banagiense*. In contrast, data in a redescription of this species revealed 24–25 ridges at the midbody based on a whole mounted female specimen (Gibbons, 1973).

Synlophe of *Longistrongylus curvispiculum* (Figs. 1, 12)

Anterior to the EIJ, the cervical pattern was variable among the specimens examined. The predominant pattern was Type 1a laterally and Type A ventrally and was similar in males and females irrespective of host species, excluding specimens in *Connochaetes taurinus*. A second pattern was defined as Type 1b laterally and Type B ventrally as seen only among specimens in *C. taurinus*. Thus, ridge systems comprising the lateral field demonstrated variation ranging from nearly parallel to strongly tapering. Continuous subventral and sublateral ridges in the cervical region are present. In specimens with a tapering pattern, 1 to 3 pairs of ridges terminated along the lateral-most ridge in the cervical zone. In 5 of 6 specimens, the ventral field was parallel; in a specimen with the most strongly tapering lateral pattern, the addition of ridges occurred along the single ventral ridge. In each lateral field, there are up to 4–5 narrowly spaced ridges. The synlophe begins with 24–30 ridges at the base of the cephalic expansion, and numbers of ridges increase posteriorly from the cervical zone, attaining a maximum from the EIJ to the end of the first quarter. At the EIJ in males, there are 38–44 ridges, in females 35; in the first quarter 41–42 and 37; at the midbody 35–

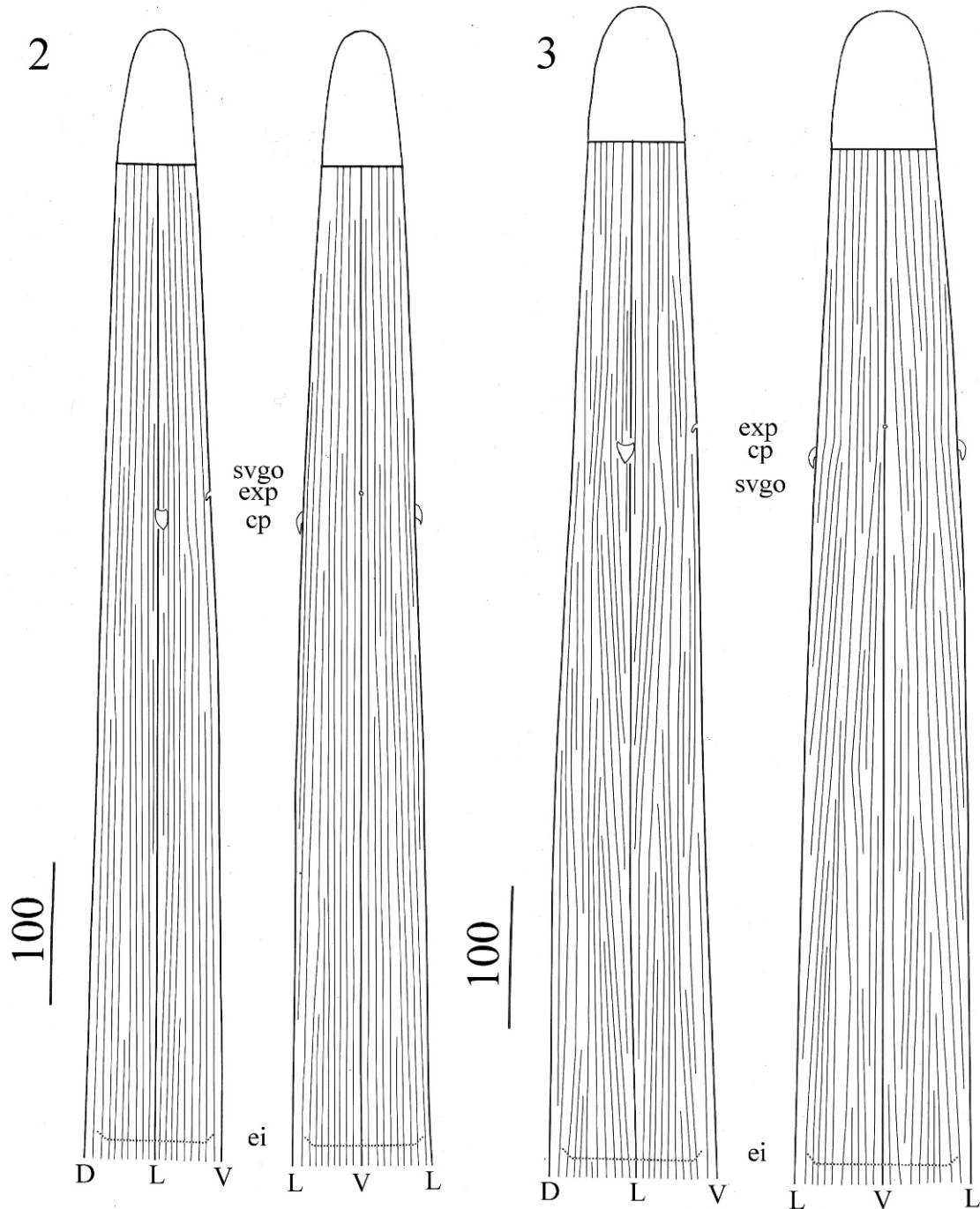


FIGURES 1a–1b. *Longistrongylus curvispiculum* showing pattern for the synlophe in lateral (right) and ventral fields in the cervical zone anterior to the base of the esophagus in representative female specimens. (a) USNPC 81214 in *Capra hircus*, with Type 1a weakly tapering lateral system and parallel Type A ventral system. Note cervical papillae (CP) adjacent to lateral-most ridge and excretory pore (EXP) on ventral-most ridge; orifices of the subventral esophageal glands (SVG0) are situated anterior to the EXP and CP; orientation is indicated by L = lateral, D = dorsal, and V = ventral. Labeling is consistent for Figures 1–7. (b) RVC 1755 in *Connochaetes taurinus*, with a Type 1b strongly tapering lateral system and Type B ventral system with single ventral-most ridge.

37 and 35; and in the third quarter 36 and 35. In males, the synlophe terminates ventrally at near 260–342 μ m and dorsally near 270 μ m anterior to the PBP; about 8 ridges in total are retained in the left and right lateral fields to the level of the PBP.

In females, the synlophe becomes discontinuous and irregular, and cuticular inflations are present at the level of the vulva.

Gibbons (1973), in the original description of *L. curvispiculum*, reported 31–39 ridges at the level of the midbody in males; data



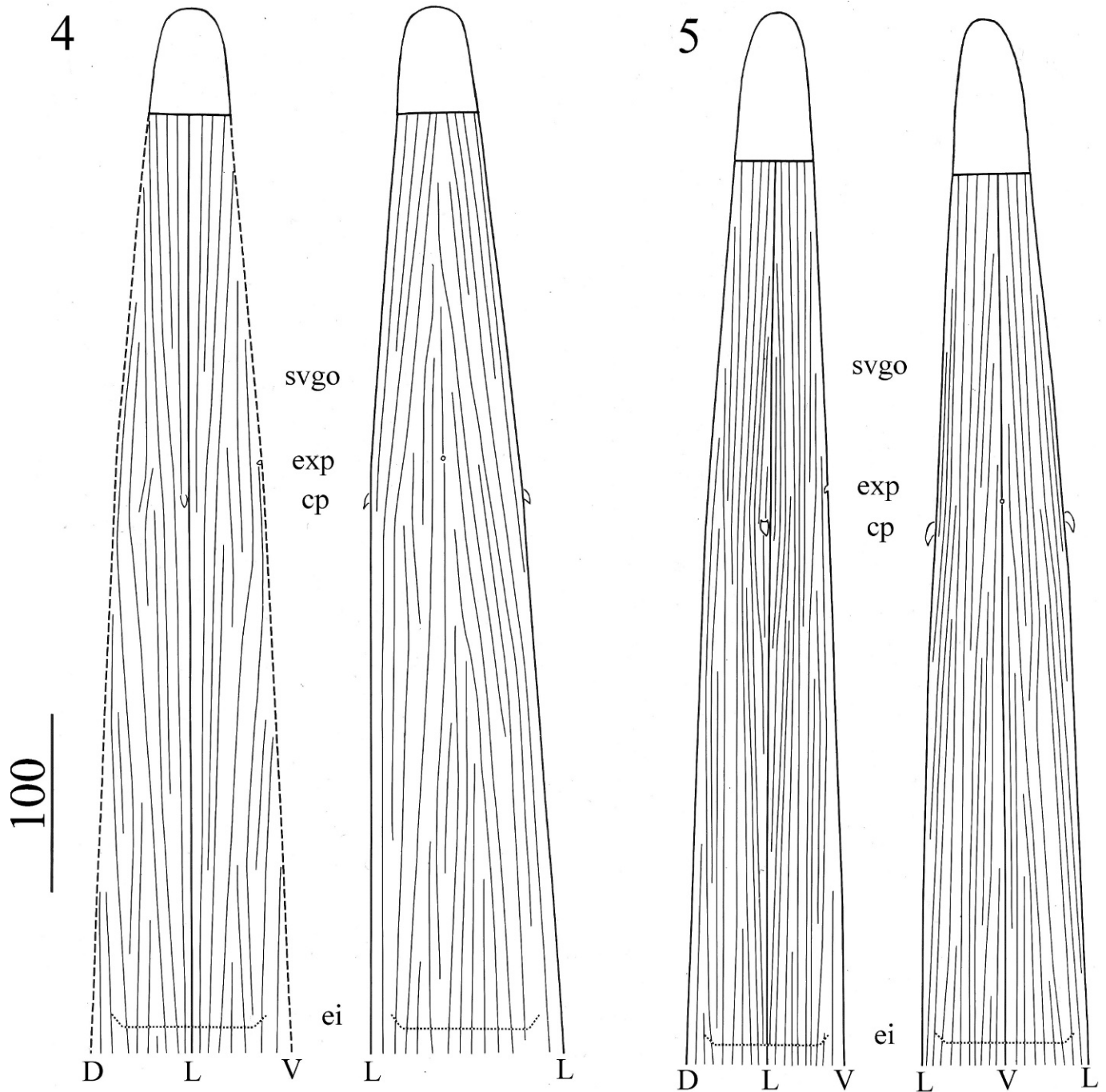
FIGURES 2-3. *Longistrongylus banagiense* and *L. thalae* showing pattern for the synlophe in lateral (right) and ventral fields in the cervical zone anterior to the base of the esophagus in representative male specimens. (2) *L. banagiense* (RVC 1586 in *Damaliscus korrigum*) with a weakly tapering Type 1a lateral and parallel Type A ventral system; (3) *L. thalae* (USNPC 66324 in *Alcelaphus buselaphus jacksoni*) with a strongly tapering Type 1b lateral system and ventral Type B system with single ventral-most ridge interrupted by EXP.

for females were not reported. In a redescription of this species, Gibbons (1977) reported 22-39 ridges at the midbody in males.

Synlophe of *Longistrongylus meyeri* (Fig. 6)

Anterior to the EIJ, the cervical pattern is of Type 2 laterally and Type A ventrally and is similar in males and females. Continuous subventral and sublateral ridges in the cervical region

are present. The synlophe begins with about 30 ridges at the base of the cephalic expansion, and numbers of ridges increase posteriorly from the cervical zone, attaining a maximum near the midbody; posteriorly from the midbody, numbers of ridges diminish rapidly. At the EIJ in males, there are 40-52 ridges, and in females there are 48-56; at the midbody 44-58 and 50-58; and in the third quarter 33-36 and 34-48. In females the synlophe is continuous at the vulva, and irregular cuticular inflations are



FIGURES 4-5. *Longistrongylus sabie* and *L. schrenki* showing pattern for the synlophe in lateral (right) and ventral fields in the cervical zone anterior to the base of the esophagus in representative male specimens. (4) *L. sabie* (USNPC 77484 in *Aepyceros melampus*) with strongly tapering Type 1b lateral and ventral Type B (atypical) system, note absence of single, continuous, ventral-most ridge in this specimen; dotted lines in lateral view show the margins of the body wall, and the absence of continuous ventral or dorsal ridges; (5) *L. schrenki* (USNPC 66325 in *Ourebia ourebi*) with strongly tapering Type 1b lateral and ventral Type B system.

absent. Ridges terminate adjacent to the PBP in males and near the anus in females.

In both male and female specimens of *L. meyeri*, the number of ridges at any level of body length is independent of diameter of the individual worm. For example, the cotype specimens of this species are very large, attaining about 22 mm in length and up to 400 µm in maximum diameter. In contrast, voucher specimens have consider-

ably smaller dimensions near 12 mm in length and less than 200 µm in width. The number of ridges at the midbody across this range of variation in body size does not vary substantially (Table II).

In the original description for *L. meyeri*, Le Roux (1931) found "40 to about 50 well developed longitudinal lines towards the posterior part of the body" in males and females. These ridges extended from near the level of the nerve ring to the anus in

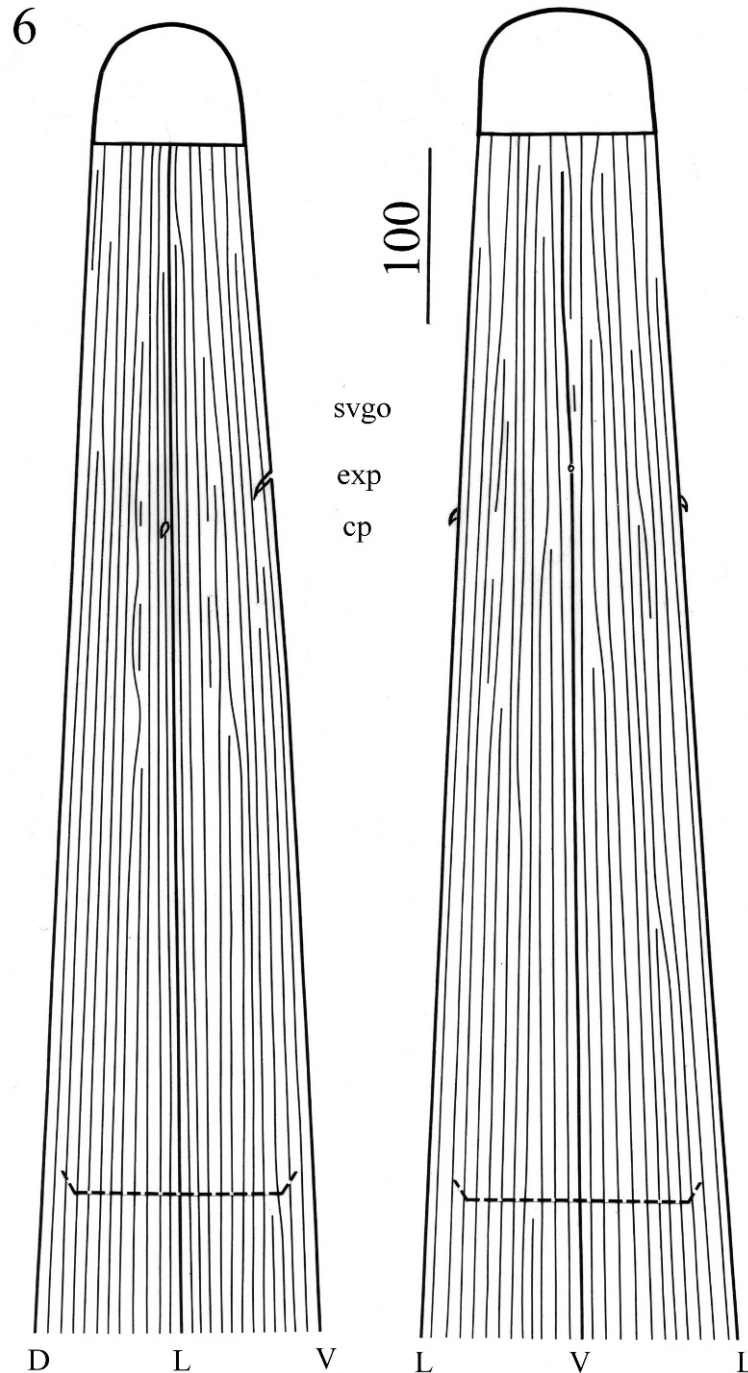


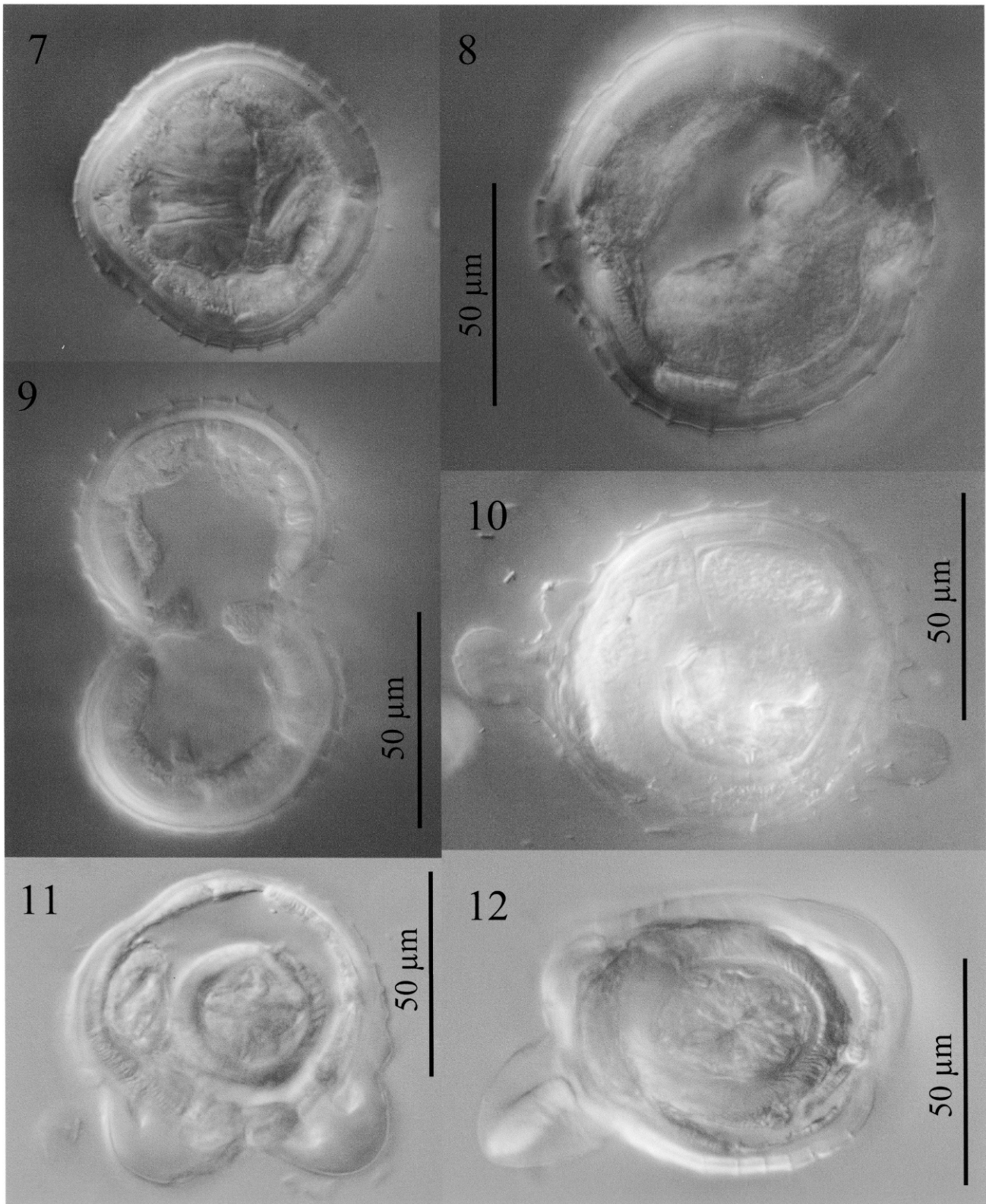
FIGURE 6. *Longistrongylus meyeri* showing pattern for the synlophe in lateral and ventral fields in the cervical zone anterior to the base of the esophagus in representative female specimen. Specimen depicted is from RVC 1673 in *Gazella thomsoni* showing parallel Type 2 lateral system and Type A ventral system.

females and to the PBP in males, and increased in number from the anterior to posterior. Gibbons (1977), in a redescription of this species, reported 40–52 ridges in males based on transverse sections; 5 ridges in each lateral field are narrowly spaced.

Synlophe of *Longistrongylus sabie* (Figs. 4, 8, 10)

Anterior to the EIJ, the cervical pattern is of Type 1b laterally and Type B (atypical) ventrally and is similar in males and

females. Laterally, 1–3 pairs of ridges terminate along the lateral-most ridge in the cervical region. In the ventral field, a short or isolated ventral ridge begins 30 to 108 μm anterior to the excretory pore and trends toward either the right or left lateral field ending from 38 μm anterior to 125 μm posterior to the EIJ. Additional ridges making up the ventral field trend toward the lateral fields. In ventral and dorsal systems, a single continuous ridge is not evident; a single ridge is interrupted at the excretory pore ventrally, but is not continuous through the cervical



FIGURES 7–12. Synlophe in some species of *Longistrongylus* as seen in transverse section at the midbody (7–9) or at the level of the vulva (10–12). Sections are oriented with dorsal to top and ventral to bottom as viewed from the posterior; scale bars are the same for Figures 7 and 8. Refer to Gibbons (1977) and Boomker and Durette-Desset (1997) for additional images of the synlophe in transverse sections at the midbody. (7) *Longistrongylus banagiense* male, RVC 1586, showing 40 ridges; (8) *Longistrongylus sabie*, male USNPC 77484 showing 31 ridges; (9) *Longistrongylus thalae*, male USNPC 66324 showing 42 ridges; (10–12) synlophe and cuticular inflations at level of ovejector, anterior to vulva in female specimens: inflations of cuticle may be irregular to bilateral depending on species; synlophe becomes discontinuous at level of vulva when inflations are present; (10) *Longistrongylus sabie* USNPC 77484, showing bilateral inflations at level adjacent to vulva; (11) *Longistrongylus schrenki* USNPC 66325, showing ventrally directed bilateral inflations adjacent to vulva; (12) *Longistrongylus curvispiculum* USNPC 81213, showing single hypertrophied region of cuticle at level of vulva.

TABLE II. Attributes of the synlophe among species of *Longistrongylus* in African ungulates.

Species*	Cervical pattern† Lateral/ventral	EIJ‡ ♂/♀	1st quarter‡ ♂/♀	Midbody‡ ♂/♀	3rd quarter‡ ♂/♀	4th quarter‡§ ♂/♀
<i>L. banagiense</i>	Type 1a/Type A	36–37/—	—/—	40/— (33–43/33–38) (—/24–25)	—/—	—/—
<i>L. curvispiculum</i>	Type 1a/Type A Type 1b/Type B#	38–44/35	41–42/37	35–37/35 (31–39/—) (22–39/—)	36/35	8/—
<i>L. meyeri</i> ¶	Type 2/Type A	40–52/48–56	—/—	44–58/50–58 (40–52/—)	33–36/34–48	32–36/—
<i>L. sabie</i>	Type 1b/Type B	26–28/30–33	34/26–28	30–31/24–31 (23–31/23–29)	27/25–30	18/—
<i>L. schrenki</i>	Type 1b/Type B	39/38–43	40/42	42–43/39–40 (40–47/37–49)	32–34/—	8–10/—
<i>L. thalae</i>	Type 1b/Type B	42–46/—	45/—	42–45/— (44–51/42–45)**	45–48/—	6–10/—

* Suitable specimens of *L. albifrontis* and *L. namaquensis* were not available.

† Pattern of the cervical synlophe in males and females (anterior to esophageal-intestinal junction) as determined from whole-mounted specimens and based on definitions outlined by Lichtenfels et al. (1988).

‡ Counts of ridges as determined from transverse sections and from intact specimens in specific regions of the body; esophageal-intestinal junction = EIJ.

§ In the fourth quarter and anterior to prebursal papillae and spicules in males the synlophe is reduced to 2 lateral fields. Loss of ridges occurs first ventrally and later dorsally.

|| Data for numbers of midbody ridges as determined by Gibbons (1972, 1973, 1977) in parentheses.

Distinct patterns for the ventral cervical synlophe were observed in *L. curvispiculum* as exemplified by Type 1b/B for IIP1755-1 in *Connochaetes taurinus* from Kenya; Type 1a/A, USNPC 81214 in *Capra hircus* based on larvae derived from *Oryx biesia*.

¶ Specimens including cotypes in *Alcelaphus caama* and vouchers identified as *L. meyeri* in *Gazella thomsoni*.

** Data for numbers of midbody ridges in *L. thalae* as determined by Boomker and Durette-Desset (1997) in parentheses.

zone, and the pattern is considered a modification of Type B. Continuous subventral or sublateral ridges in the cervical region are absent. In each lateral field the interval between ridges is not narrow, and lateral ridges are not grouped. The synlophe begins with 12–18 ridges at the base of the cephalic expansion, and numbers of ridges increase posteriad from the cervical zone, attaining a maximum near the midbody. At the EIJ in males, there are 26–28 ridges and in females 30–33; in the first quarter 34 and 26–28; at the midbody 30–31 and 24–31; and in the third quarter 27 and 25–30. In males, the synlophe terminates ventrally near 200–400 µm anterior to the PBP and dorsally near the PBP; about 18 ridges total are retained in left and right lateral fields and dorsally to the level of the PBP. In females, the synlophe becomes discontinuous, and a bilateral cuticular inflation is present at the level of the vulva; about 22 ridges extend to the level of the anus.

In the original description of *L. sabie*, Mönnig (1933) reported 32 longitudinal striations beginning 800 to 900 µm from the cephalic extremity. In a later redescription, Gibbons (1977) reported 23–31 ridges in males and 23–29 in females at the midbody. Additionally, the transverse section from the midbody of a male showed lateral ridges that are evenly spaced, which contrasts with most species in the genus.

Synlophe of *Longistrongylus schrenki* (Figs. 5, 11)

Anterior to the EIJ, the cervical pattern is of Type 1b laterally and Type B ventrally and is similar in males and females. The tapering pattern laterally is complex, and ridge-pairs have 2 distinct points of origination. Three pairs of short discontinuous ridges originate along the lateral-most ridge and arch around the CP prior to termination. Additional pairs initiate symmetrically in the sublateral fields, and they converge and terminate on the lateral-most ridge in the posterior region of the cervical zone. Overall, 4–5 pairs of ridges terminate along the lateral-most ridge in the cervical region, and the tapering pattern extends posterior to the EIJ. Continuous subventral and sublateral ridges in the cervical region are present; 4–5 narrowly spaced ridges are present in each lateral field. The synlophe begins with about 20 ridges at the base of the cephalic expansion, and the number of ridges

increase posteriad from the cervical zone, attaining a maximum near the midbody. At the EIJ in males, there are about 39 ridges and in females 38–43; in the first quarter 40 and 42; at the midbody 42–43 and 39–40; and in the third quarter 32–34 in males. In males, the synlophe terminates ventrally near 350–400 µm and dorsally near 250 µm anterior to the PBP; about 8–10 ridges are retained in left and right lateral fields extending to the PBP. In females, the synlophe becomes discontinuous and irregular, and bilateral cuticular inflations are present at the level of the vulva; the synlophe extends to the level of the anus in lateral fields.

Ortlepp (1939) in the original description of *L. schrenki* reported 30–50 “longitudinal lines” increasing in number posteriad. Gibbons (1977) in a redescription reported 40–47 ridges in males and 37–49 in females at the midbody.

Synlophe of *Longistrongylus thalae* (Figs. 3, 9)

Anterior to the EIJ, the cervical pattern is of Type 1b laterally and Type B ventrally and is similar in males and females. Ridges initiate primarily in the sublateral fields and converge on the lateral-most ridge in the left and right fields. The lateral fields demonstrate substantial tapering with 3–5 pairs of ridges terminating along the lateral-most ridge within the cervical zone. The tapering pattern extends posterior to the EIJ; 4–5 narrowly spaced ridges are present in each lateral field. Continuous subventral and sublateral ridges in the cervical region are present. The synlophe begins with about 20–28 ridges at the base of the cephalic expansion, and numbers of ridges increase posteriad from the cervical zone attaining a maximum near the midbody and into the third quarter. At the EIJ in males, there are about 42–46 ridges; in the first quarter 45; at the midbody 42–45; and in the third quarter 45–48. In males, the synlophe initially terminates ventrally and later dorsally anterior to the PBP; about 6–10 ridges in total are retained in left and right lateral fields extending to the PBP. Data based on transverse sections from females are not available.

Boomker and Durette-Desset (1997) in a redescription of *L. thalae* reported 44–51 and 42–45 ridges at the midbody of males and females. In the lateral fields, 4 ridges are narrowly spaced and

smaller than those in dorsal and ventral fields (based on sections at the midbody). A right lateral view of the cervical region shows 3 lateral most and narrowly spaced ridges; all other ridges are parallel depicting what could be described as a Type 2 pattern. Notably, however, the figure shown by Boomker and Durette-Desset (1997) illustrates only the lateral field anterior to the cervical papillae, which accounts for this apparent discrepancy relative to the current study.

Prior studies in the genus

Considering those species examined in the current study, Gibbons (1977) reported numbers of ridges (some for unspecified levels of the body) based on counts from whole-mounted specimens and transverse sections. In prior evaluations, cross sections were prepared for males of 6 species (*L. meyeri*, *L. sabie*, *L. curvispiculum*, *L. schrenki*, *L. thalae*, and *L. banagiense*), and figures depict ridges at the level of the midbody (Gibbons, 1977; Boomker and Durette-Desset, 1997) (Table II).

Data for *L. albifrontis* and *L. namaquensis* were based on counts determined from whole-mounted specimens. In the original description of *L. albifrontis*, Mönnig (1931) reported 24 longitudinal striations in males and females; Gibbons (1977) reported 27–30 ridges in males. In the original description of *L. namaquensis*, Ortlepp (1963) stated that “very faint longitudinal cuticular striations cover the whole body,” and in some worms about 20 were very prominent; Gibbons (1977) reported 26–27 ridges in males. Among 5 of 6 species examined (excluding *L. meyeri*) in the current study, the numbers of ridges in males was equal to or exceeded that observed in females, consistent with *L. thalae* according to Boomker and Durette-Desset (1997) (Table II). Cervical patterns had not been defined for any species except a partial view of the lateral system in *L. thalae* (see Boomker and Durette-Desset, 1997).

DISCUSSION

Synlophe among the ostertagiines

The global ostertagiine fauna currently encompasses 15 genera (Hoberg, Abrams, and Pilitt, 2009). Among the ostertagiines, 8 genera are characterized by males in which the lateral rays of the copulatory bursa describe a 2-2-1 pattern (defined in Durette-Desset, 1983, 1985). Specifically, these include *Africanastrongylus* Hoberg, Abrams, and Ezenwa, 2008, *Cervicaprastrongylus* Gibbons and Khalil, 1982, *Hamulonema* Hoberg and Abrams, 2008, *Hyostrongylus* Hall, 1921, *Mazamastrongylus* Cameron, 1935, *Sarwaria* Drózdź, 1965, *Spiculoptera* (Orloff, 1933), and *Teladorsagia* Andreeva and Satubaldin, 1954 (e.g., Gibbons and Khalil, 1982; Durette-Desset, 1983; Hoberg and Abrams, 2008; Hoberg et al., 2008). Among 7 remaining genera, a 2-1-2 bursal pattern is characteristic, being represented in species of *Camelostongylus* Orloff, 1933, *Longistongylus* LeRoux, 1931, *Marshallagia* (Orloff, 1933), *Orloffia* Drózdź, 1965, *Ostertagia* Ransom, 1907, *Pseudommarshallagia* (Roetti, 1941), and *Robustostongylus* Hoberg, Abrams, and Pilitt, 2009. Patterns for the cervical synlophe have now been defined completely, or in part, for 14 genera, including *Longistongylus*; ridge systems have not been explored in *Pseudommarshallagia*.

Considering lateral cervical systems, 3 basic patterns have been delineated among the ostertagiines (Lichtenfels et al., 1988; Lichtenfels and Pilitt, 1991; Lichtenfels et al., 1993), although the degree to which different components may be homologous has not been determined. Tapering systems (Type 1) are typified by those where ridges converge weakly on a lateral-most ridge anterior to the EIJ (Type 1a: some species of *Ostertagia*, *Camelostongylus*, and *Longistongylus*) or are strongly convergent (Type 1b: species of *Africanastrongylus*, *Camelostongylus*, some *Longistongylus*, and some *Marshallagia*, *Orloffia*, *Sarwaria*, *Teladorsagia*). Parallel lateral systems (Type 2) are seen in species of *Cervicaprastrongylus*, *Hamulonema*, *Hyostrongylus*, *L. meyeri*, some *Marshallagia*, and some *Ostertagia* and *Robustostongylus*. Ventral systems exhibit 2 basic forms where the ventral-most ridge is paralleled by 2 continuous ridges (Type A species of *Camelostongylus*, *Hyostrongylus*, some *Longistongylus*, and some *Marshallagia*, *Ostertagia*, *Orloffia*, *Robustostongylus*, and *Sarwaria*) or where the ventral-most ridge is single (Type B species of *Africanastrongylus*, some *Longistongylus*, and some *Marshallagia* and *Teladorsagia*); ventral systems are not yet defined in species of *Cervicaprastrongylus* and *Hamulonema*. Ridge systems in species of *Mazamastrongylus* and *Spiculoptera* are distinct and represent a third pattern where lateral fields are strongly tapering, continuous sublateral and subventral ridges are absent, and ventral fields possess characteristic “hood-ridges” that are disposed laterally to the lip-like excretory pore (Lichtenfels et al., 1993; Hoberg, 1996; Hoberg and Khrustalev, 1996). Specific patterns of the synlophe do not appear to correspond to either the 2-1-2 or 2-2-1 bursal structure, although the unique systems in species of *Mazamastrongylus* and *Spiculoptera* may represent a synapomorphy that diagnoses relationship for these genera.

Variation in the cervical synlophe for species in a particular genus has been recognized in *Ostertagia* and *Marshallagia*, where congeners may exhibit either tapering or parallel lateral patterns (Lichtenfels et al., 1988; Lichtenfels and Pilitt, 1989; Lichtenfels et al., 1990; Lichtenfels and Hoberg, 1993; Hoberg et al., 1993c). Less common is intraspecific variation as seen in specimens of *Camelostongylus mentulatus* (Railliet and Henry, 1909), which may have strongly tapering to essentially parallel lateral systems, but exhibit only slight variation in the numbers of ridges (E. P. Hoberg, A. Abrams, and P. Pilitt, unpubl. obs.). In contrast, uniformity for general structure of the cervical synlophe for congeners, or conspecifics, or both, has been observed among species of *Africanastrongylus*, *Mazamastrongylus*, *Robustostongylus*, *Sarwaria*, *Spiculoptera*, *Teladorsagia*, and possibly *Hamulonema* and *Orloffia* (Lichtenfels et al., 1988; Lichtenfels and Pilitt, 1989; Lichtenfels et al., 1993; Hoberg 1996, Hoberg and Khrustalev, 1996; Lichtenfels et al., 1996; Hoberg et al., 1999; Hoberg and Abrams, 2001, 2007, 2008; Hoberg et al., 2008; Hoberg, Abrams, and Pilitt, 2009; E. Hoberg, A. Abrams, and P. Pilitt, unpubl. obs.). The degree of similarity among congeners within *Hyostrongylus* and *Cervicaprastrongylus* or conspecifics within *Pseudommarshallagia elongata* (Roetti, 1941) remains to be established because all species have yet to be examined (Hoberg et al., 1993b).

It has been recognized that the pattern of the cervical synlophe can be identical in related congeneric species of ostertagiines as demonstrated respectively for species of *Mazamastrongylus*, and some *Ostertagia* and *Teladorsagia* (Hoberg et al., 1993c, 1999;

Lichtenfels et al., 1993). In these situations the numbers of ridges have been shown to differ in a definable manner and discrete, non-overlapping ranges are generally observed (e.g., Hoberg, 1996; Hoberg and Khrustalev, 1996). For example, at the midbody in males of *T. circumcincta* (Stadelman, 1894), there are 26–29 ridges in contrast to 39–46 in *T. boreoarcticus* Hoberg, Monsen, Kutz and Blouin, 1999, although differentiation between these congeners is not possible based solely on the pattern of the cervical synlophe.

Irregular and asymmetrical cuticular inflations at the level of the vulva are known among species in 5 genera of the Ostertagiinae, including *Camelostrongylus*, *Hyostrongylus*, *Longistrongylus*, *Mazamastrongylus*, and *Teladorsagia* (e.g., Hoberg and Lichtenfels, 1992; Hoberg et al., 1993a, 1993b, 1999). Consistent with prior observations for specimens of *L. sabie*, inflations seen among other species of *Longistrongylus* are not supported by enlarged cuticular struts (Hoberg et al., 1993a) and the synlophe ridges are often superficial; further, the synlophe is discontinuous at the level of the vulva in all species of *Longistrongylus* where inflations are known. In species of *Mazamastrongylus* and *Teladorsagia*, struts and ridges making up the synlophe do not provide structural support for inflations at the level of the vulva. In contrast, enlarged but irregular struts are typical as the foundations of inflations seen in species of *Camelostrongylus* and *Hyostrongylus*. This may suggest that hypertrophied regions of the cuticle at the level of the vulva are not homologous across the genera where these structures occur in the subfamily (Hoberg and Lichtenfels, 1992; Hoberg et al., 1993b).

Synlophe in species of *Longistrongylus*

Species of *Longistrongylus* each appear to have a characteristic tapering pattern (Type 1) laterally in the cervical zone, which is largely consistent among multiple male and female specimens (Figs. 1–6; Tables I, II). The only exception is seen in specimens of *L. meyeri*, including the cotypes and vouchers in multiple host species, where a distinctly parallel Type 2 system has been identified. Ventral systems (Type A or Type B) do not exhibit intraspecific variation, except in *L. curvispiculum* where 2 patterns were identified. Species-specific patterns in conjunction with the numbers of ridges may serve to augment an array of diagnostic characters for species of *Longistrongylus* and contribute to increasingly accurate identification of female specimens (Gibbons, 1977). A caveat is warranted, however, given the relatively minimal number of specimens examined for each species in the current study and the degree to which the African fauna remains to be defined (e.g., Hoberg et al., 2008).

Differences demonstrated in the lateral and ventral synlophes do not correspond to former taxonomic proposals that partitioned generic diversity and recognized *Kobusinema* Ortlepp, 1963 (for *L. schrenki* and *L. banagiense*), *Bigalkenema* Ortlepp 1963 (for *L. curvispiculum*, *L. namaquensis*, and *L. sabie*), and *Longistrongylus* (for *L. meyeri*, *L. albifrontis*, and *L. thalae*). For example, *L. schrenki* is characterized by a strongly tapering Type 1b lateral and Type B ventral synlophe (Fig. 5), whereas *L. banagiense* has a weakly tapering Type 1a and a parallel Type A system (Fig. 2). In contrast to species among all other genera of ostertagiines, except *Africanaststrongylus buceros* Hoberg, Abrams

and Ezenwa, 2008, the numbers of ridges in males examined in the current study generally exceeded that seen in females, although the latter are always substantially greater in diameter (Boomker and Durette-Desset, 1997; Hoberg et al., 2008). The differential numbers of ridges in males and females may represent another character among the suite of attributes, which in part diagnose the genus *Longistrongylus* among the ostertagiines (Hoberg et al., 2008; Hoberg, Abrams, and Pilitt, 2009). Observations for these species of *Longistrongylus* further confirm the general utility of cuticular ridge systems as diagnostic characters at the species level among the ostertagiines (Lichtenfels et al., 1988).

Intraspecific variation in the numbers of ridges in both male and female specimens among species of *Longistrongylus* is evident (Table II). The range in numbers of ridges for multiple conspecific specimens in specific regions of the body is typically narrow and rarely exceeds 5–10. Apparent differences relative to prior reports for respective species may further reflect counts based on whole mounts rather than sections; this is particularly the case for counts reported in many early original descriptions (e.g., Le Roux, 1931; Mönnig, 1931, 1933; Ortlepp, 1939, 1963). In the former, it is a particular challenge to accurately count the number of ridges along the margins of the body, and such may result in underestimates; in these instances, counts should be based on drawings and reconstructions. Additionally, with transverse sections, differences in counts (usually in the range of 1–3 ridges) can result when tapering patterns are involved, and numbers at any particular level of the body may reflect where ridges either originate or terminate.

Assuming the pattern for ridge counts for species of *Longistrongylus* follows that observed among other ostertagiines, where it is independent of length or diameter for either male or female specimens, it is possible that extreme or extensive ranges in the minimum and maximum numbers of ridges may reflect the presence of cryptic species diversity within the genus (e.g., Hoberg, Abrams, and Pilitt, 1999). For example, a more detailed examination of specimens across a broad range of ungulate hosts may be warranted (e.g., Hoberg et al., 2009) (Table II). An evaluation of this hypothesis is currently not possible, however, because of the limited numbers of specimens representing species of *Longistrongylus* that are held in museum collections globally. Suitable materials are also lacking as a basis for comprehensive or integrated morphological/molecular-level comparisons and analyses. Although there is an extensive history for parasitological collections from ungulate hosts in sub-Saharan Africa, relatively few specimens have survived as either types or vouchers in archival museum collections (Hoberg et al., 2008). Again, this highlights the continued need for synoptic survey and inventory and direct linkage to archival collections and informatics resources as a basis to understand the diversity, history, and distribution of complex parasite faunas (Brooks and Hoberg, 2000, 2006; Hoberg, Pilitt, and Galbreath, 2009).

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