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Eric P. Hoberg

United States Department of Agriculture, eric.hoberg@ars.usda.gov

Arthur Abrams

United States Department of Agriculture

Patricia A. Pilitt

United States Department of Agriculture

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ROBUSTOSTRONGYLUS AFERENSIS GEN. NOV. ET SP. NOV. (NEMATODA: TRICHOSTRONGYLOIDEA) IN KOB (*KOBUS KOB*) AND HARTEBEEST (*ALCELAPHUS BUSELAPHUS JACKSONI*) (ARTIODACTYLA) FROM SUB-SAHARAN AFRICA, WITH FURTHER RUMINATIONS ON THE OSTERTAGIINAE

Eric P. Hoberg, Arthur Abrams, and Patricia A. Pillitt

United States National Parasite Collection and Animal Parasitic Disease Laboratory, United States Department of Agriculture, Agricultural Research Service, BARC East, Building 1180, 10300 Baltimore Avenue, Beltsville, Maryland 20705. e-mail: eric.hoberg@ars.usda.gov

ABSTRACT: Abomasal nematodes (Ostertagiinae: Trichostrongyloidea), representing a previously unrecognized genus and species, were discovered in kob (*Kobus kob*) and kongoni (hartebeest) (*Alcelaphus buselaphus jacksoni*) from Uganda during surveys of ungulate parasites in the 1960s. *Robustostrongylus aferensis* gen. nov. et sp. nov. is characterized by a ventriculus-like, bilobed valve at the junction of the esophagus and intestine, a synlophes with unusually robust ridges, cervical papillae and excretory pore situated posterior to the mid-length of the esophagus, a unique body form and large diameter in males and females, a relatively anterior position for the vulva, and strongly convoluted and spiraled ovarian tracks in females. Bursal structure is 2-1-2, with subequal Rays 2/3, strongly reduced and robust Rays 8, and relatively narrow Rays 9/10 contained within a reduced, laterally inflated dorsal lobe. Spicules are filamentous and tripartite; the gubernaculum is cryptic, alate, and heart-shaped in the anterior. *Robustostrongylus aferensis*, with narrow filamentous spicules that trifurcate distally near 80%, paired arcuate “0” papillae that terminate in bulbous expansions, and a reduced dorsal lobe and ray most closely resembles species of *Longistrongylus*. A suite of unique characters, consistent in males and females, however, unequivocally distinguishes specimens of *R. aferensis* from all ostertagiines with either a 2-1-2 or 2-2-1 bursal pattern. Among 15 genera of the Ostertagiinae in the global fauna, 5 are entirely limited in distribution to Africa, including *Africanaststrongylus*, *Hamulonema*, *Longistrongylus*, *Pseudomarsallagia*, and *Robustostrongylus* gen. nov.; species among 5 additional genera, including *Cervicaprastrongylus*, *Hyostrongylus*, *Marsallagia*, *Ostertagia*, and *Teladorsagia*, also occur in Africa, but they are represented as mosaics, with diversity centered in Eurasia or the Holarctic.

Medium stomach worms in ungulates, usually referred to the Ostertagiinae (Trichostrongyloidea), remain economically important parasites among domestic and free-ranging livestock throughout the world. Diversity for this abomasal parasite fauna is relatively well defined for those nematodes occurring globally in cattle, sheep, goats, and some farmed cervids (Hoberg et al., 2001; Haigh et al., 2002), although accurate taxonomy continues to be hindered by confusion over the application of polymorphism among males representing single species (Drózdź, 1995; Hoberg et al., 1999). Concepts for species-limits have also been changing in this group as a consequence of cryptic diversity revealed through molecular systematics combined with detailed comparative morphology (Criscione et al., 2005). Such is best exemplified within *Teladorsagia* Andreeva and Satubaldin, 1954 in which *T. circumcincta* (Stadelman, 1894) has been shown to include an array of cryptic species in domestic and free-ranging artiodactyls (Hoberg et al., 1999; Leignel et al., 2002; Grillo et al., 2007); the occurrence of species complexes is predicted to be a generality across other related genera among the ostertagiines but remains to be evaluated. An accurate definition of diversity, including reliable taxonomy encompassing morphological and molecular criteria extending to population genetics, in conjunction with comprehensive data for host and geographic distributions, are the cornerstones for understanding epizootiology and patterns of emerging disease across a mosaic of rapidly changing environments and for development of efficient and robust measures for control of parasitism in ungulates (Hoberg, 1997; Brooks and Hoberg, 2000, 2006, 2007; Hoberg, Polley et al., 2008).

Although the global fauna and its intricate structure of endemic and introduced species in most biogeographic regions is

becoming understood (Hoberg et al., 2004; Hoberg, Polley et al., 2008), previously unrecognized genera and species continue to be discovered, particularly in Africa (Hoberg and Abrams, 2008; Hoberg, Abrams, and Ezenwa, 2008). One third of known genera of ostertagiines are endemic to Africa; yet, comprehensive surveys for many species of ungulates have not been conducted, and parasitological examinations have often been based on relatively few hosts or have focused on relatively restricted geographic zones. Over the last century, however, considerable details of the African ostertagiine and trichostrongyloid fauna in both domestic and free-ranging ungulates have been revealed (e.g., Le Roux, 1931; Mönnig, 1932; Round, 1962, 1968; Sachs and Sachs, 1968; Gibbons, 1974, 1977); notable here are the substantial body of surveys and articles addressing parasite faunas among domestic and free-ranging ungulates from South Africa by J. Boomker, I. G. Horak, and their colleagues and from eastern Africa by L. M. Gibbons and L. F. Khalil (summarized in Hoberg, Abrams, and Ezenwa, 2008).

The global ostertagiine fauna currently encompasses 14 genera (Hoberg and Abrams, 2008); aspects of this proposed generic taxonomy adopt components of a diversity of opinions presented for these nematodes over the past 70 yr (e.g., Travassos, 1937; Skrjabin et al., 1954; Andreeva, 1956; Drózdź, 1965; Durette-Desset and Chabaud, 1981; Durette-Desset, 1982, 1983, 1989; Gibbons and Khalil, 1982; Jansen, 1989; Durette-Desset et al., 1999). 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 by Durette-Desset and Chabaud, 1981; Durette-Desset, 1983). Specifically, these include *Africanaststrongylus* Hoberg, Abrams and Ezenwa, 2008, *Cervicaprastrongylus* Gibbons and Khalil, 1982, *Hamulonema* Hoberg and Abrams, 2008, *Hyostrongylus* Hall, 1921, *Mazamastrongylus* Cameron, 1935, *Sarwaria* Drózdź, 1965, *Spiculopteragia* (Orloff, 1933), and *Teladorsagia* (e.g., Durette-Desset, 1983; Gibbons and Khalil, 1982; Hoberg, Abrams, and

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TABLE I. Specimens of *Robustostromylus aferensis* gen. nov. et sp. nov. and species of *Longistromylus* and *Pseudomarsallagia* examined from Africa.

Accession*	Field†	Species	Host	Locality	♂‡	♀‡
USNPC 10000§	BND-409	<i>R. aferensis</i>	<i>Kobus kob</i>	Uganda	1	—
USNPC 100001§	BND-409	<i>R. aferensis</i>	<i>K. kob</i>	Uganda	—	1
USNPC 66320	BND-409	<i>R. aferensis</i>	<i>K. kob</i>	Uganda	8	8
USNPC 100002#	BND-409	<i>R. aferensis</i>	<i>K. kob</i>	Uganda	1	—
USNPC 66321	BND-62	<i>R. aferensis</i>	<i>Alcelaphus buselaphus jacksoni</i>	Uganda	—	2
OHC T2032	—	<i>Longistromylus albifrontis</i> ¶	<i>Damaliscus albifrons</i>	South Africa	4	—
OHC (type series)	—	<i>L. albifrontis</i> ¶	<i>D. albifrons</i>	South Africa	—	3
RVC 1586	—	<i>L. banagiense</i>	<i>Damaliscus korrigum</i>	Tanzania	3	—
USNPC 81213	—	<i>L. curvispiculum</i> **	<i>Ovis aries</i>	Texas, USA	2	—
BMNH 1998.11.20.312-317 (cotypes)		<i>L. meyeri</i>	<i>Alcelaphus caama</i>	South Africa	1	3
RVC 1673		<i>L. meyeri</i>	<i>Gazella thomsonii</i>	Kenya	5	4
OHC (type series)		<i>L. namaquensis</i> ¶	<i>O. aries</i>	South Africa	14	—
USNPC 77484	—	<i>L. sabie</i> ††	<i>Aepyceros melampus</i>	South Africa	4	—
OHC T2465	—	<i>L. sabie</i> ¶	<i>A. melampus</i>	South Africa	2	4
USNPC 66325	—	<i>L. schrenki</i> ‡‡	<i>Ourebia ourebi</i>	Uganda	4	—
USNPC 66323	—	<i>L. schrenki</i> ‡‡	<i>K. kob</i>	Uganda	2	—
OHC (type series)	—	<i>L. schrenki</i> ¶	<i>Kobus ellipsiprymnus</i>	South Africa	1	2
USNPC 66324	—	<i>L. thalae</i> §§	<i>A. b. jacksoni</i>	Uganda	5	—
USNPC 66327	—	<i>L. thalae</i> §§	<i>Redunca redunca</i>	Uganda	2	—
CIH 3358	—	<i>Pseudomarsallagia elongata</i>	<i>O. aries</i>	Ethiopia	1	1

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

† Field number at time of original collection.

‡ Number of male and female specimens examined.

§ Holotype male and allotype female. Originally from collections by J. Bindernagle.

|| Paratypes. Originally from collections by J. Bindernagle.

Voucher specimen.

¶ Morphological data and line drawings from the type specimens examined by W. W. Becklund and M. L. Walker (U.S. National Parasite Collection, unpublished documents). Numbers of specimens examined by WWB and MLW could not be reliably determined.

** *Longistromylus curvispiculum* represents a species previously referred to *Bigalakenema*; material examined represent vouchers from an introduced population in western Texas (Craig, 1993) and was from an experimental infection in domestic sheep based on larvae recovered from *Oryx biesia*.

†† *Longistromylus sabie* are vouchers and represent a species previously referred to *Bigalakenema*.

‡‡ *Longistromylus schrenki* represents a species previously referred to *Kobusinema*. Specimens are vouchers from collections by J. Bindernagle.

§§ *Longistromylus thalae* represent voucher specimens from collections by J. Bindernagle.

||| Voucher specimens are represented by 4 permanent slides deposited by M. Graber and include a male specimen with detached bursa, dissected spicules, and 2 slides of cross sections showing the synlophes.

Ezenwa, 2008; Hoberg and Abrams, 2008). Among 6 remaining genera, a 2-1-2 bursal pattern is characteristic, being represented in species of *Camelostromylus* Orloff, 1933, *Longistromylus* Le Roux, 1931, *Marshallagia* (Orloff, 1933), *Orloffia* Drózdź, 1965, *Ostertagia* Ransom, 1907, and *Pseudomarsallagia* (Roetti, 1941).

In the current study, we propose establishment of a new genus among the ostertagiines to accommodate unique nematodes in ungulates from eastern Africa originally collected by Dr. John Bindernagle during the 1960s. These specimens were initially examined by W. W. Becklund and M. L. Walker at the U.S. National Parasite Collection in the late 1960s and early 1970s, but definitive taxonomic decisions were not developed. Studies of materials in the Bindernagle Collections were reinitiated during broader investigations of the ostertagiines, which led to proposals for *Africanastromylus* and *Hamulonema* (Hoberg and Abrams, 2008; Hoberg, Abrams, and Ezenwa, 2008). Here, we diagnose the remaining new generic-level taxon evident in these collections, and explore aspects of the history and distribution for ostertagiines in the African and global faunas.

MATERIALS AND METHODS

Specimens of a previously undescribed ostertagiine nematode included 10 males and 9 females in a kob, *Kobus kob* (Erleben), and 2 females in a kongoni (hartebeest), *Alcelaphus buselaphus jacksoni* (Pallas), from Uganda collected by J. Bindernagle in 1964. All materials representing this unrecognized species and new genus are held in the U.S. National Parasite Collection, U.S. Department of Agriculture, Beltsville, Maryland (USNPC); specimens are held in vials in a solution of 70% ethanol with 4% formalin by volume.

As a basis for comparisons within the Ostertagiinae, specimens of *Longistromylus banagiense* (Gibbons, 1972), *L. curvispiculum* (Gibbons, 1973), *L. meyeri* Le Roux, 1931, *L. sabie* (Mönnig, 1932), *L. schrenki* (Ortlepp, 1939), and *L. thalae* (Troncy and Graber, 1973) were examined. Observations, notes, and line drawings from morphological studies of the type specimens for *L. albifrontis* (Mönnig, 1931), *L. namaquensis* (Ortlepp, 1963), *L. sabie*, and *L. schrenki* by W. W. Becklund and M. L. Walker (U.S. National Parasite Collection, unpublished documents) were also used in our current evaluations. A male specimen of *Pseudomarsallagia elongata* (Roetti, 1941), permanently mounted in glycerine jelly; transverse sections; and dissected spicules were examined. Redescriptions of *P. elongata* Roetti, 1941 by Graber and Delavenay (1978), Gibbons (1981a), and Gibbons and Khalil (1982) were also used for comparisons because of the unavailability of the type specimens or larger series of vouchers for evaluation. Specimens and

sources for species of ostertagiine nematodes used in comparative morphological studies are listed (Table I). Specimens of *Haemonchinae* from the USNPC used in the current study are listed in Hoberg et al. (2004). Additionally, multiple lots of *Graphidium strigosum* (Dujardin, 1845) from leporid hosts included USNPC 16895, 18065, and 66335. These latter specimens were necessary to establish the context for certain morphological attributes among the Ostertagiinae.

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 studied in whole mounts, with particular attention to the pattern of ridge systems in the cervical zone and their extent posteriorly in males and females consistent with prior studies among the ostertagiines (Lichtenfels et al., 1988; Hoberg et al., 1999). Transverse sections were hand cut with a cataract knife and mounted in glycerin jelly. Sections were used to examine structure and to count the number of ridges in a single male and female at the esophageal-intestinal junction (EIJ), one fourth, midbody, and three fourths of total body length as determined from the anterior. Sectioning was restricted to 2 specimens because of the limited number of worms that had been collected. Additional counts of ridges were based on reconstructions from whole-mounted specimens.

The male specimens were evaluated on the basis of the copulatory bursa, spicules, and genital cone. Bursal ray patterns were determined and described using the system of Durette-Desset and Chabaud (1981) and Durette-Desset (1983). Papillae of the genital cone and rays of the bursa followed the numbering system of Chabaud et al. (1970). The structure of the ovejectors was evaluated based on recent definitions and descriptions among related nematodes (Lichtenfels et al., 2003). Owing to the difficulty in consistently discerning the division of the sphincter region S2 from the vestibule, the anterior and posterior portions of the vestibule, relative to the vulva, and adjacent portions of the sphincters (S1 and S2), were measured as a single unit. All measurements are given in micrometers, unless specified otherwise. In the description and tables the sample size ($n =$) is followed by the range and mean ± 1 SD in parentheses.

Taxonomy for hosts follows Wilson and Reeder (1993) in all text and tables. Host listings have been modified from those reported in the original literature to reflect current use and understanding of ungulate taxonomy.

RESULTS

Field collections for survey of helminth diversity in ungulates from eastern Africa revealed the occurrence of abomasal nematodes. Kob, and kongoni from the West Acholi District of Uganda, were found to be naturally infected with nematodes representing a previously undiagnosed genus and undescribed species of ostertagiine with a 2-1-2 bursal form.

MORPHOLOGICAL DIAGNOSIS AND DESCRIPTION

Robustostromylus gen. nov.

Diagnosis: Ostertagiinae: Trichostrongyloidea. Small uncoiled nematodes with robust, stout body of large diameter, tapering bluntly in the cephalic and caudal extremities. Cephalic vesicle well developed. Synlophe bilaterally symmetric, with robust, knob-like ridges, parallel to slightly tapering in cervical region, extending to caudal extremity. Cervical papillae miniscule, thorn-like; along with excretory pore situated in posterior half of esophagus. Esophageal-intestinal valve prominent, bilobed, with constricted, muscularized ventriculus-like base. Males monomorphic. Bursal structure 2-1-2, symmetrical, membrane lacking cuticular bosses. Rays 2/3 parallel throughout length, Rays 3 massive with inflated tip relative to Rays 2; thickness of Rays 3 equal to or exceeding that of Rays 4. Rays 5/6 narrow, divergent distally. Accessory bursal membrane reduced containing widely spaced, divergent papillae "7." Rays 8 with massive bases, with distal tips curved medially. Dorsal lobe laterally inflated, disposed ventrally to Rays 8, containing reduced, narrow dorsal ray with distal bifurcation; branches terminating in Rays 9/10. Females amphidelphic with transverse vulva near 70% of

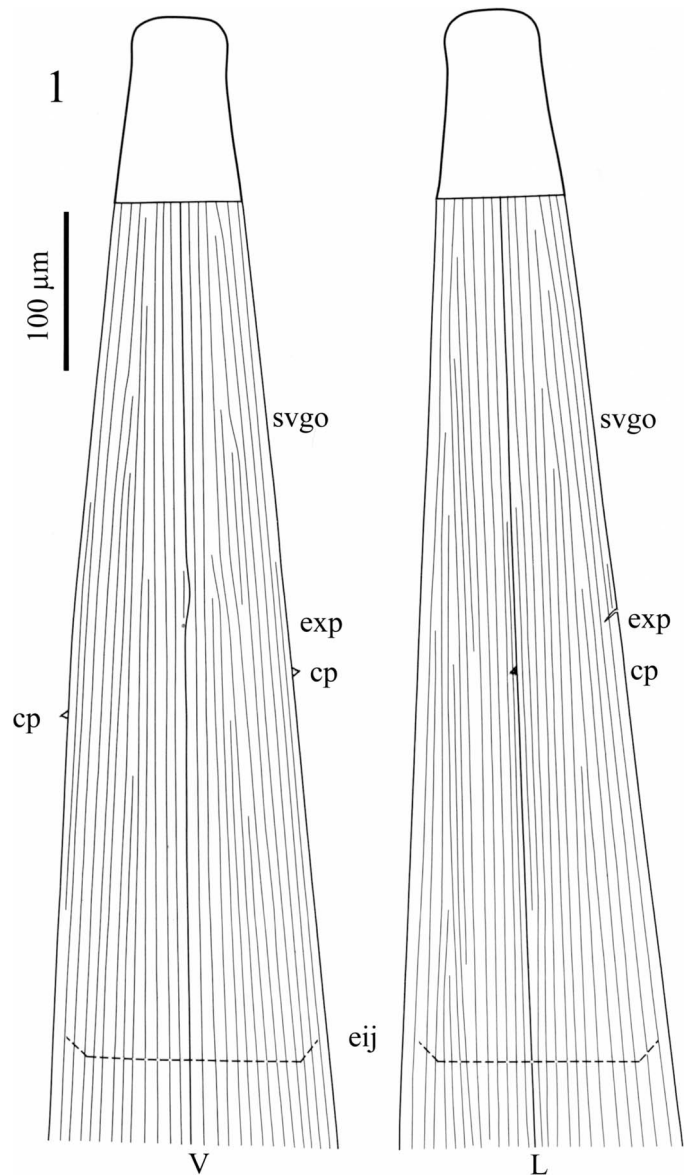


FIGURE 1. *Robustostromylus aferensis* gen. nov. et sp. nov., showing structure of synlophe in ventral (V) and lateral (L) views based on line drawings from a female paratype. Note parallel to weakly tapering pattern laterally, and positions of the orifices of the subventral glands (svgo), excretory pore (exp), cervical papillae (cp), and esophageal-intestinal junction (eij).

body length from anterior, lacking cuticular fans or inflations; ovarian tracts highly convoluted, spiraled around intestine.

Taxonomic summary

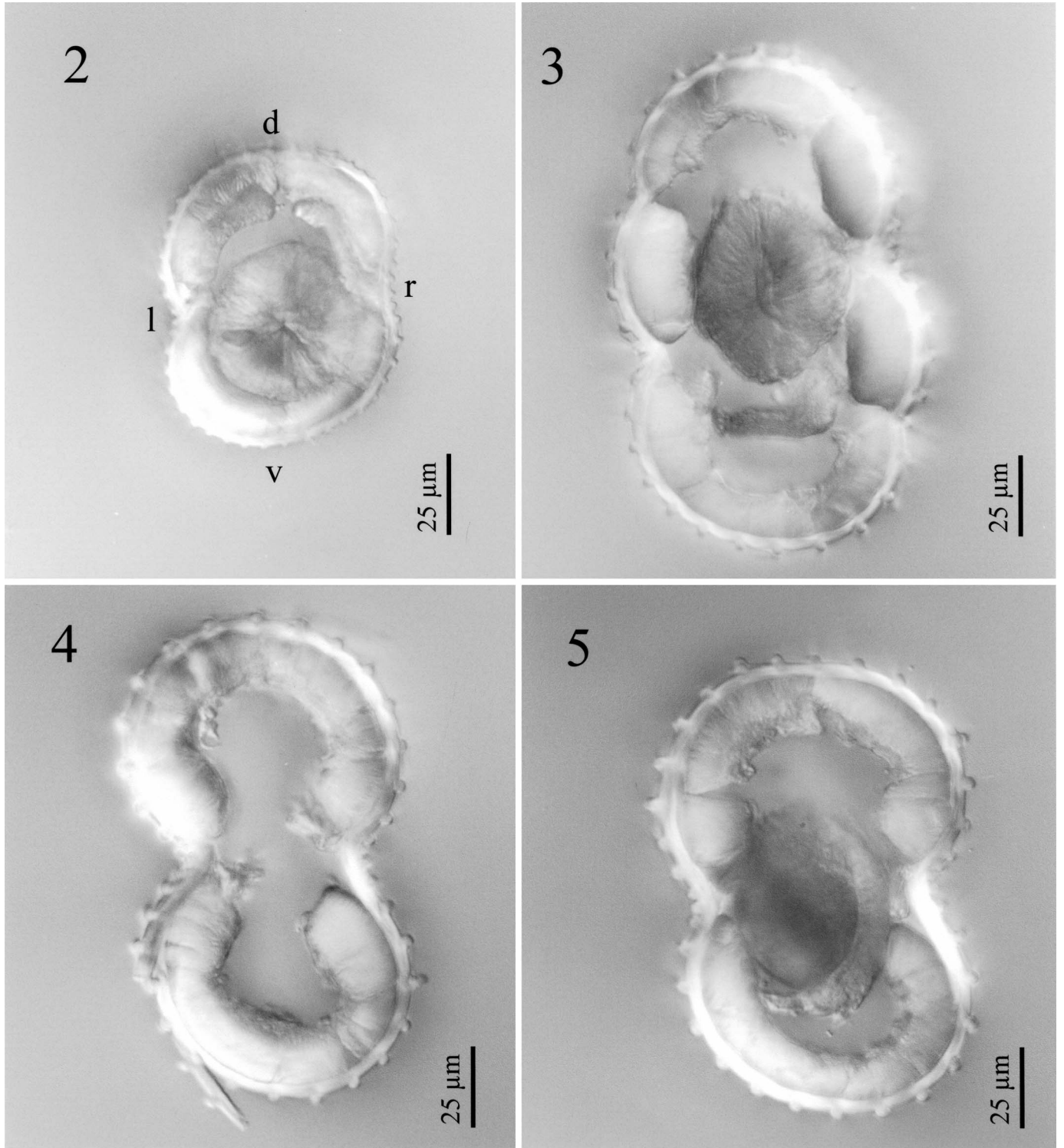
Type species: *Robustostromylus aferensis* gen. nov. et sp. nov.

Hosts: *Kobus kob* (Erxleben) (type) and kongoni or hartebeest, *Alcelaphus buselaphus jacksoni* (Pallas).

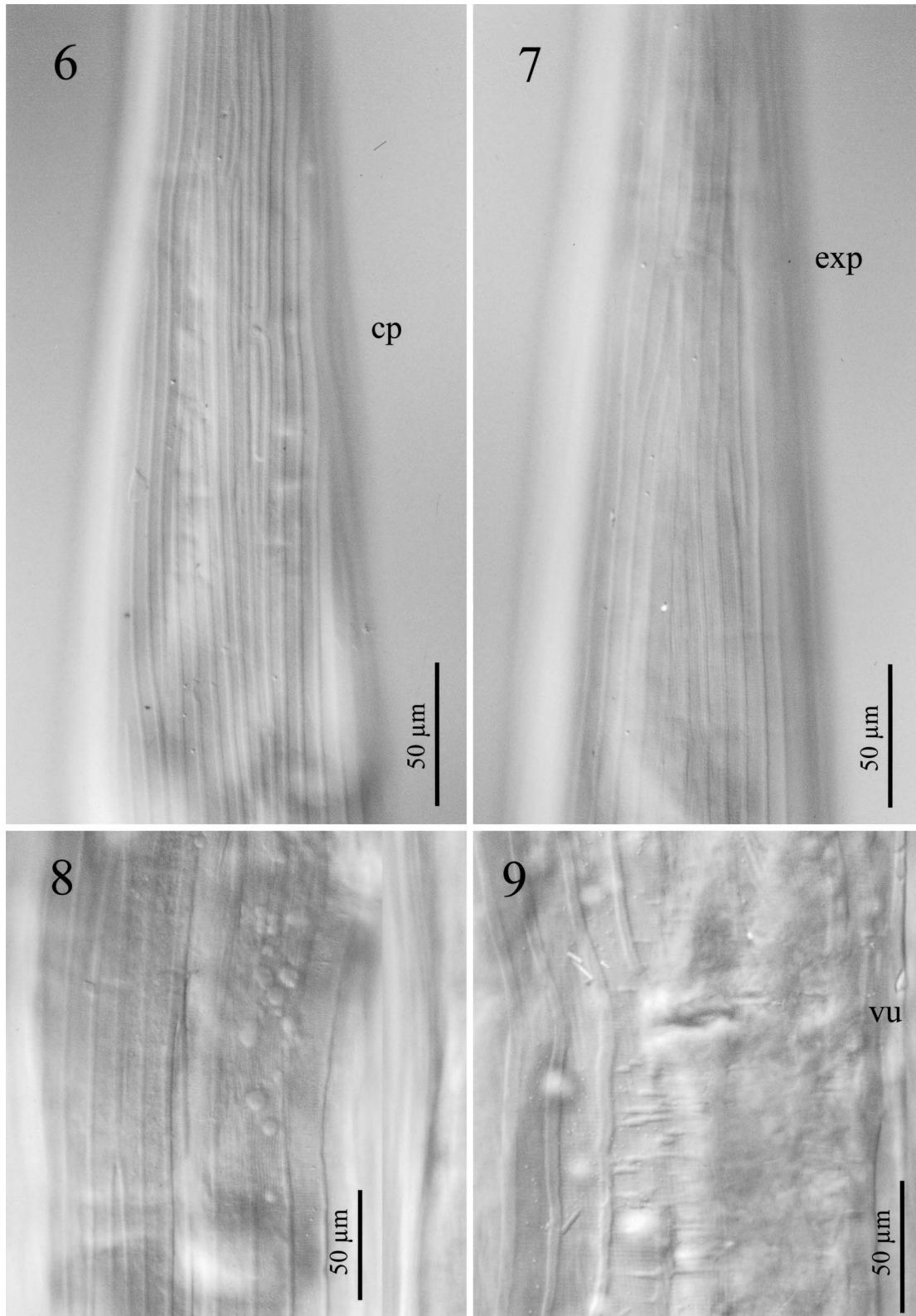
Robustostromylus aferensis sp. nov.

(Figs. 1–35)

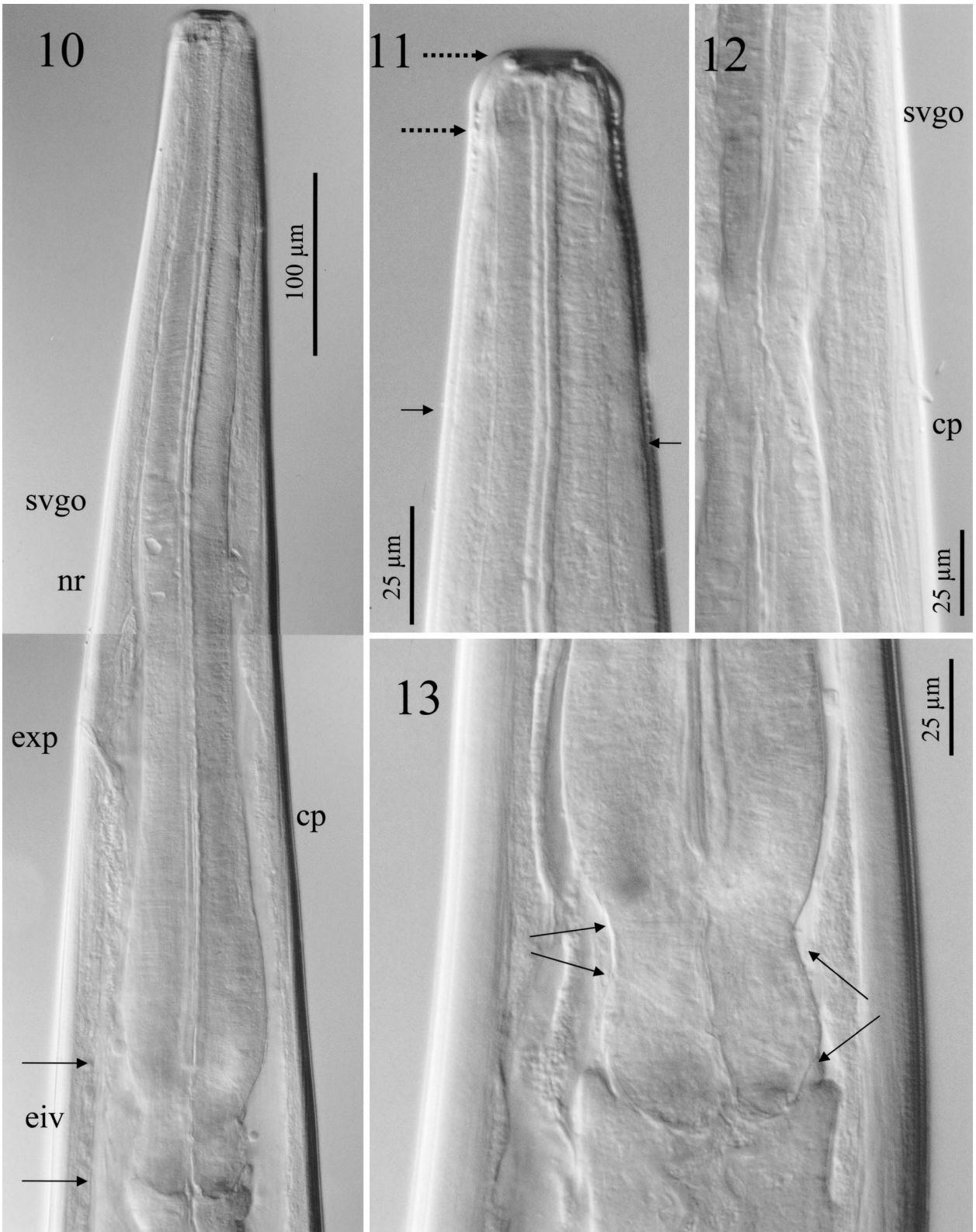
General description: Trichostrongyloidea, uncoiled, straight, maximum diameter near midbody, 220 in males and 295 in females. Cephalic vesicle present as bipartite expansion; anterior-most portion strongly annulated. Cuticle with well-developed synlophe, lacking gradient, with perpendicular orientation; maximum number of ridges, 54, at esopha-



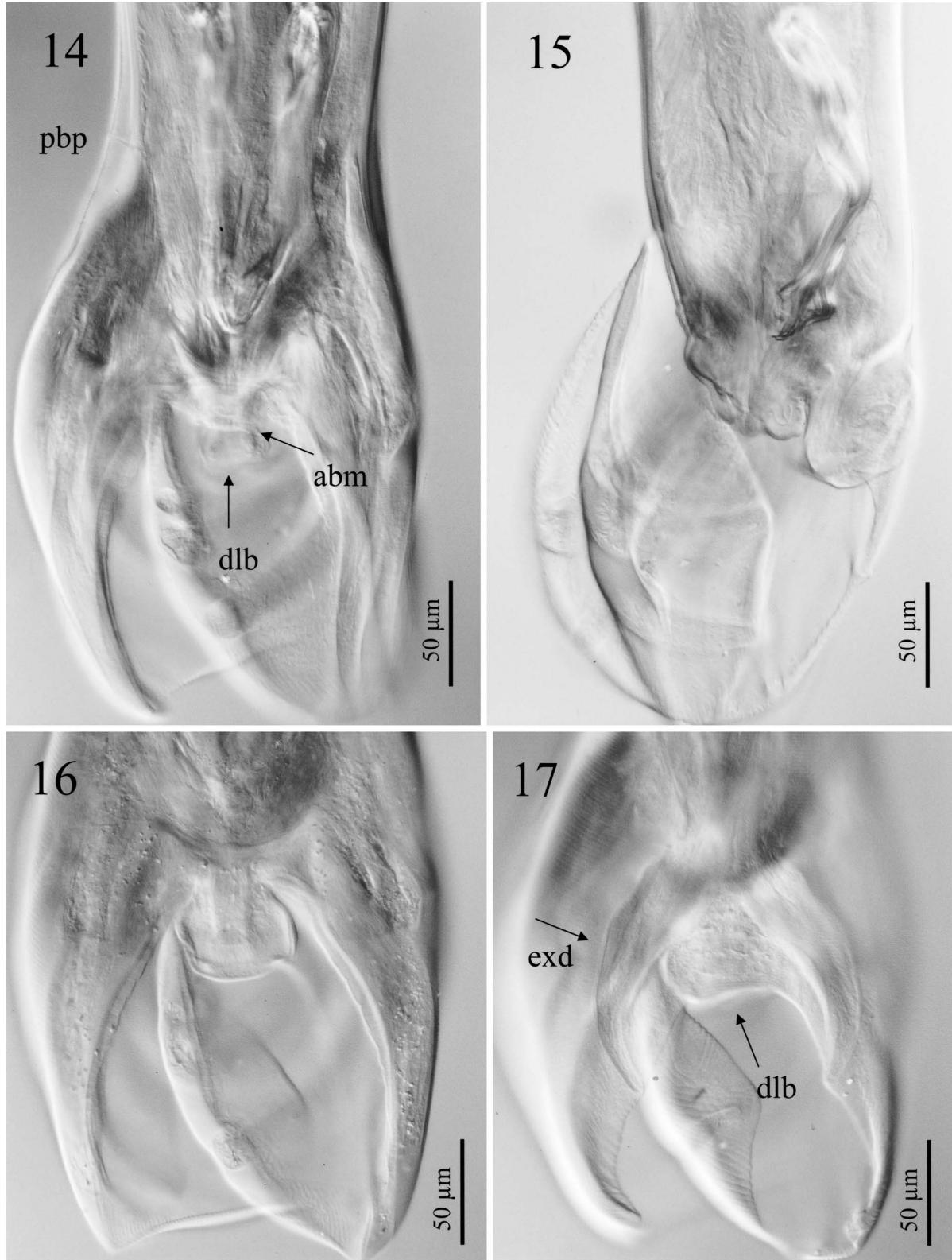
FIGURES 2–5. *Robustostrongylus aferensis* gen. nov. et sp. nov., showing structure of robust and knob-like synlophe based on photomicrographs of transverse sections of a male paratype; orientation is indicated as dorsal = d, ventral = v, left = l, and right = r. (2) Synlophe at level of esophageal-intestinal junction showing 46 ridges. (3) Synlophe near termination of first quarter of body from anterior showing 38 ridges. (4) Synlophe at midbody showing 37 ridges. (5) Synlophe in posterior third quarter of body showing 36 ridges.



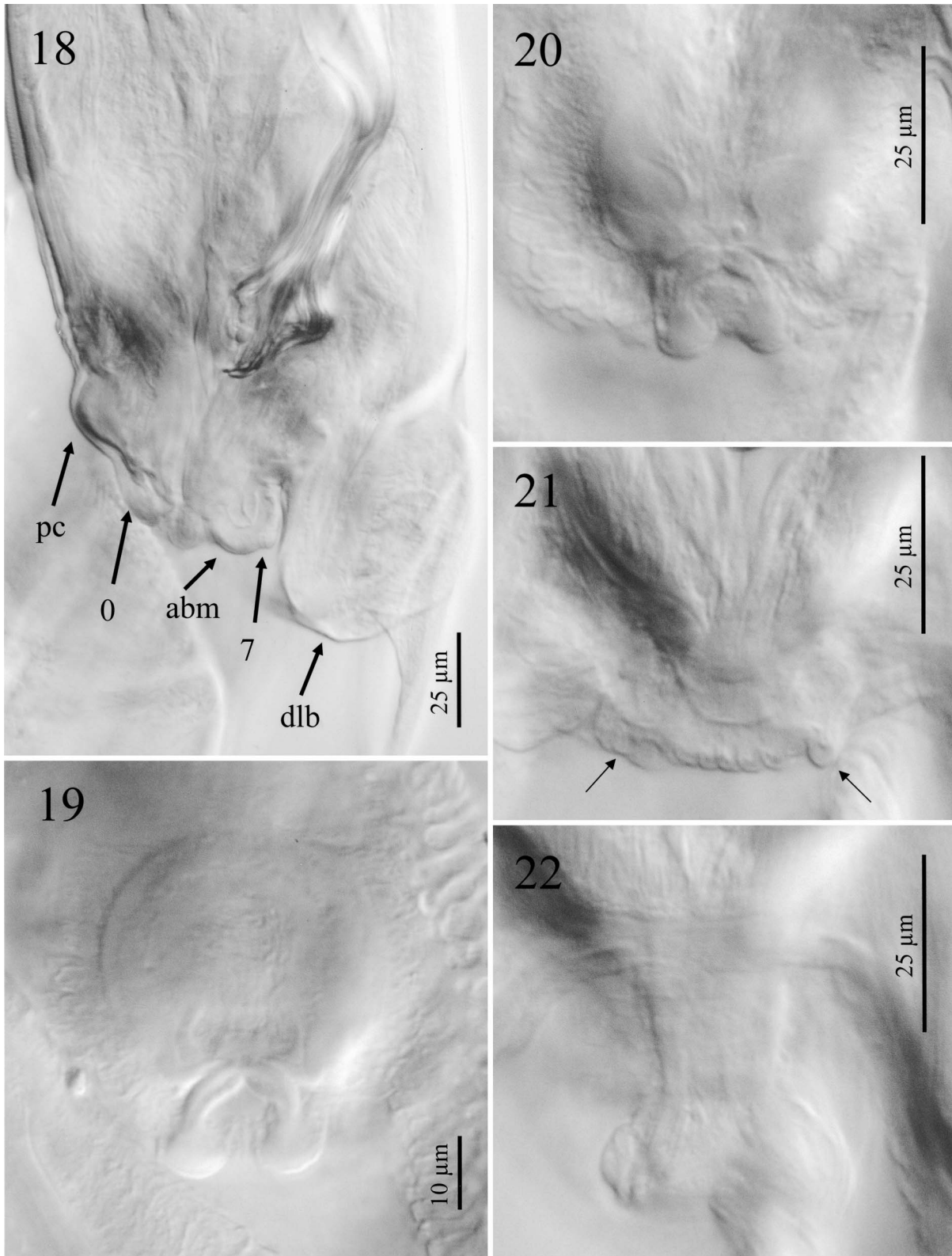
FIGURES 6–9. *Robustostromylus aferensis* gen. nov. et sp. nov. showing structure of synlophe based on photomicrographs from entire specimens. (6) Cervical zone in right lateral view of female paratype showing parallel to weakly tapering pattern and position of the cervical papilla (cp). (7) Cervical zone in ventral view of male paratype showing position of excretory pore (exp) and crossover pattern in ventral ridges. (8) Synlophe in female paratype, right lateral view, showing robust structure of ridges in region posterior to vulva. (9) Transverse vulva (vu) in ventral view showing rugose cuticle and plate-like structure of synlophe.



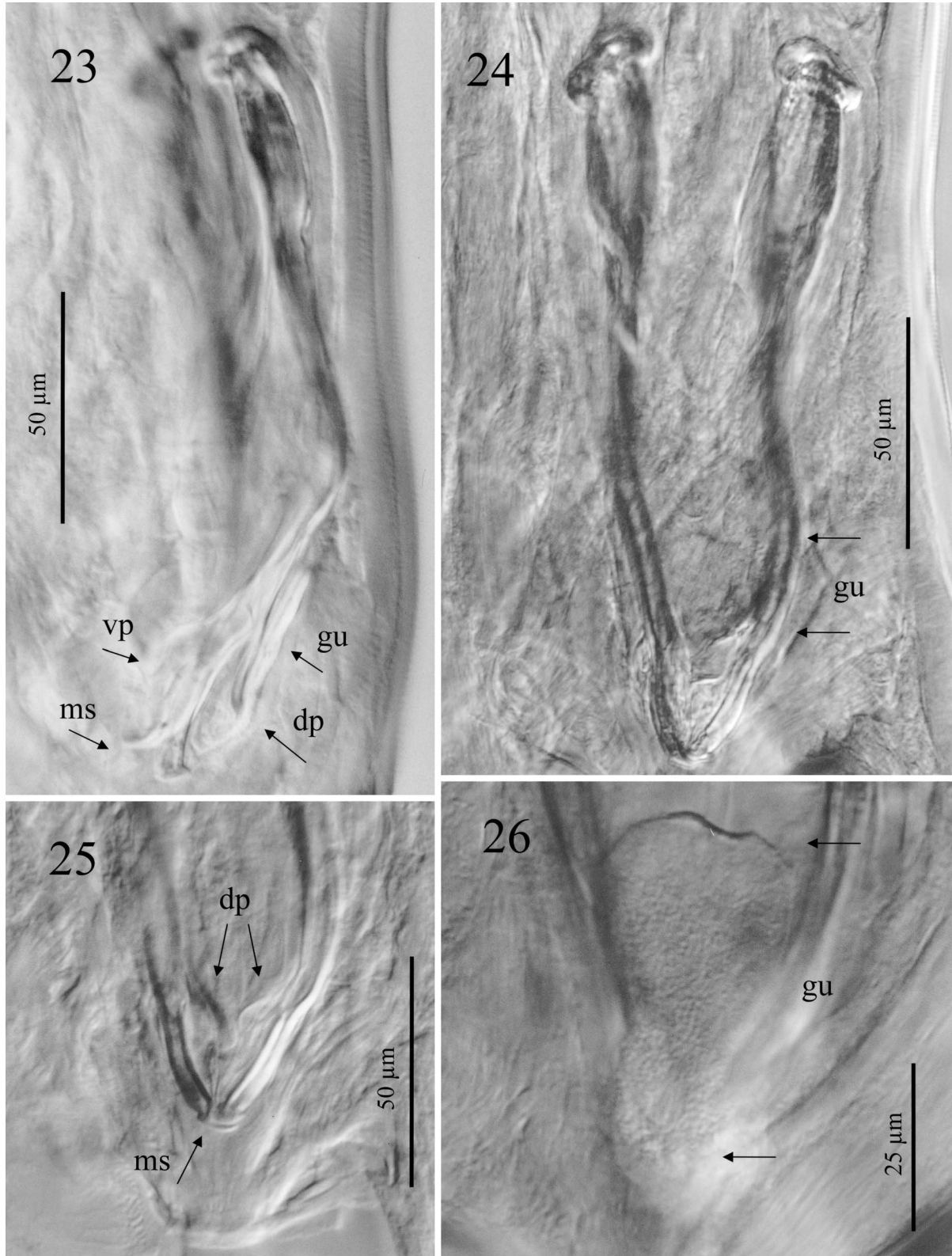
FIGURES 10–13. *Robustostromylus aferensis* gen. nov. et sp. nov., cephalic and cervical structures based on photomicrographs as seen in male and female paratypes. (10) Anterior region of body in left lateral view of female, based on a composite of 2 micrographs, showing structure of esophagus, and positions of the orifices of the subventral glands (svgo), nerve ring (nr), excretory pore (exp), cervical papillae (cp) and constricted, bilobed esophageal-intestinal valve (eiv). (11) Cephalic extremity in left lateral view of male showing cephalic capsule (between dotted arrows) and asymmetrical extent of cephalic expansion (black arrows). (12) Cervical zone of male in ventral view showing miniscule, thorn-like cervical papilla (cp) and relative position of SVGO. (13) Basal esophagus of male in left lateral view showing constricted esophageal-intestinal valve and a band of strongly developed oblique musculature (arrows).



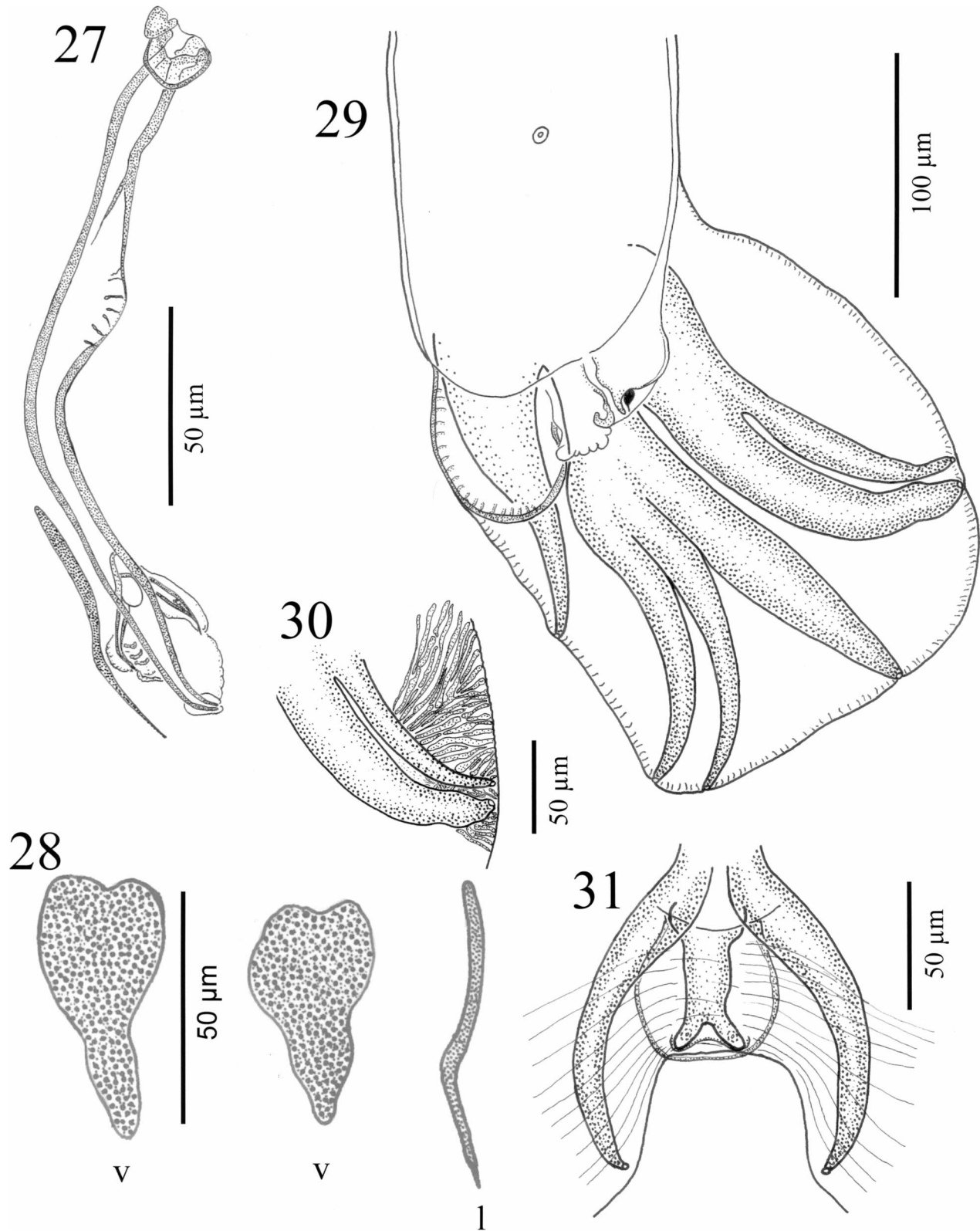
FIGURES 14–17. *Robustostrongylus aferensis* gen. nov. et sp. nov., showing structure of copulatory bursa in a male paratype based on photomicrographs. (14) Bursa in dorsal view, showing positions for prebursal papillae (pbp), accessory bursal membrane (abm), and dorsal lobe (dlb). (15) Bursa in left lateral view showing rounded and elongate bursal membrane, spicules with characteristic bend, genital cone and inflated dorsal lobe. (16) Dorsal lobe and narrow dorsal ray in dorsal view. (17) Dorsal lobe (dlb) showing rounded, inflated structure and position ventral to curved externodorsal rays (exd) or Rays 8.



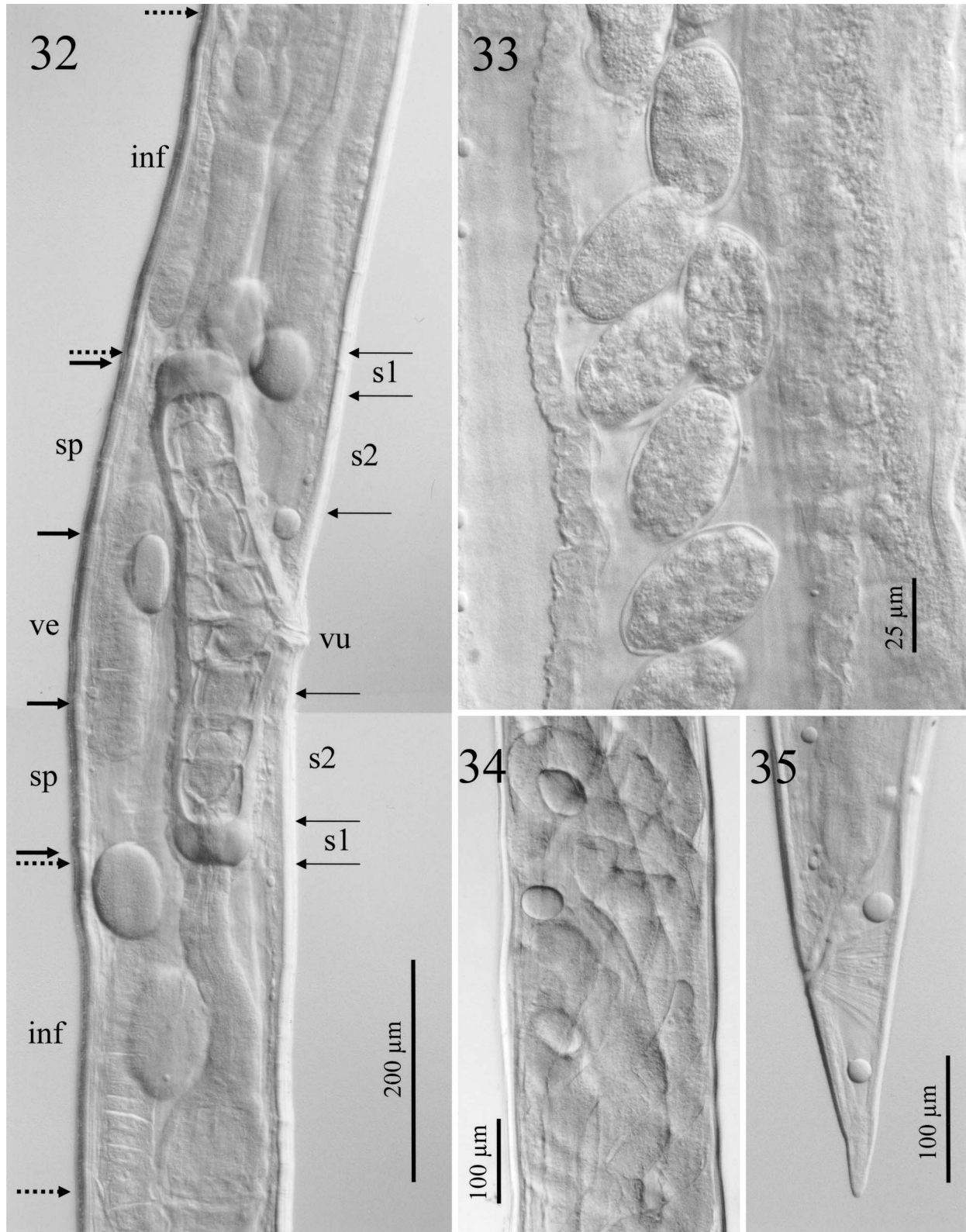
FIGURES 18–22. *Robustostrongylus aferensis* gen. nov. et sp. nov., showing structure of genital cone in male paratypes based on photomicrographs. (18) Genital cone in left lateral view showing weakly developed proconus (pc); “0” papillae (0); reduced, membranous accessory bursal membrane (abm); position of the 7 papillae (7) on the posterior margin of the abm; and an inflated dorsal lobe (dl). (19) Paired, arcuate “0” papillae terminating in bulbous expansions shown in ventral view; note plate-like structure of telmon supporting the cloaca. (20–22) Sequential views, from ventral to dorsal through genital cone, showing (20) position of arcuate “0” papillae; (21) structure of reduced and laterally expanded accessory bursal membrane and widely divergent 7 papillae (arrows); and (22) dorsal lobe, laterally inflated, containing relatively narrow dorsal ray or Rays 9/10.



FIGURES 23–26. *Robustostromylus aferensis* gen. nov. et sp. nov., showing structure of spicules and gubernaculum in male paratypes based on photomicrographs. (23) Spicules in left lateral view showing characteristic kinked or curved form, and positions and structure of the ventral process (vp), dorsal process (dp), and main shaft (ms); note the position and form of the weakly curved gubernaculum (gu) located dorsal to the spicules. (24) Spicules in dorsal view; note relative position for the head of the granular gubernaculum (gu, between arrows). (25) Spicule tips in dorsal view showing spatulate dorsal process (dp) and main shaft (ms) with hyaline foot. (26) Gubernaculum (gu) in dorsal view showing plate-like and weakly heart-shaped head (between arrows), and cryptic granular consistency.



FIGURES 27–31. *Robustostrongylus aferensis* gen. nov. et sp. nov., showing structure of bursa, spicules, and gubernaculum in male holotype and paratypes based on line drawings. (27) Spicule and gubernaculum in paratype specimen, in right lateral view; note acutely pointed ventral and dorsal processes of equal length and series of membranes. (28) Gubernaculum in ventral (v) and lateral (l) views in holotype and paratype specimens. (29) Copulatory bursa of holotype in right lateral view showing left lobe and 2-1-2 pattern of lateral rays. Note robust Rays 3 with expanded tip attaining margin of bursal membrane, thick, elongate Rays 4, and ventral position of dorsal lobe. (30) Internal margin of bursal membrane (right lobe) at level of Rays 2 and Rays 3 showing vermicular ridges in holotype. (31) Dorsal lobe and ray in paratype specimen in dorsal view, showing relative positions and size of dorsal and externodorsal rays.



FIGURES 32–35. *Robustostrongylus aferensis* gen. nov. et sp. nov., showing characters of female allotype and paratype based on photomicrographs. (32) Ovejectors in allotype, composite image, in right lateral view showing structure of paired infundibula (inf), sphincters (sp) with bulb-like sphincter 1 (s1) and tubular sphincter 2 (s2), vestibule (ve), and simple ventral vulva lacking inflations or ornamentation. (33) Eggs in utero, paratype. (34) Ovary in allotype, showing convoluted and spiraled structure in region anterior to midbody. (35) Tail in allotype showing robust and conical structure.

geal-intestinal-junction (EIJ). Nerve ring (NR) and orifices of the subventral glands (SVGO) adjacent, in anterior third of cervical region. Cervical papillae (CP) miniscule, thorn-like, situated posterior to level of excretory pore (EXP). Position of CP and EXP substantially distal to SVGO, in posterior half of esophagus. Cuticular ornamentation at level of EXP lacking. Esophagus well developed, maximum diameter attained in slightly broadened, bulb-like base; esophageal-intestinal valve (EIV) prominent, bilobed, constricted, ventriculus-like, with oblique musculature. Males and females monomorphic.

Synlophe: Bilaterally symmetrical synlophe similar in males and females. Ridges notably robust, blunt, knob-like in transverse sections of body. Cervical zone ($n = 6$) with 24–30 ridges extending to level of cephalic expansion increasing to ($n = 7$) 42–54 ridges at EIJ. Laterally, cervical synlophe parallel in appearance, overall consistent with Type II pattern; in 8 of 22 lateral fields examined in 14 specimens, 1 ridge pair or partial ridge pair terminates in cervical region. 3–5 ($n = 4$) ridges continuous in each sub-lateral/ventral field. CP adjacent to lateral-most ridge in right and left fields. Ventral/dorsal ridge systems parallel, consistent with Type A pattern; crossovers of ventral ridges present or absent. Lateral ridges ($n = 6$) and 5 of 6 dorsal-most ridges extend anterior to level of cephalic expansion. In males and females, in anterior half of body posterior to cervical zone, ridges in lateral fields initially terminate sequentially adjacent to single lateral-most ridge ($n = 5$) 46–54% ($48 \pm 3\%$) and 29–38% ($33 \pm 4\%$) of total length from anterior respectively. In midbody transverse sections (1 male and 1 female, respectively) 36 and 37 ridges; in third quarter, 36. In females synlophe extends to anus dorsal/ventrally, may extend beyond anus laterally. In males ridges terminate laterally at the prebursal papillae (PBP); dorsal/ventrally at 38–75 anterior to the PBP.

Male: Small nematodes with prominent copulatory bursa; discrete fields of bursal bosses lacking. Total length ($n = 10$) 6,438–7,560 ($6,957 \pm 368$); maximum width ($n = 10$) 165–220 (194 ± 16) attained at 34–69% of body length measured from anterior; ratio of total body length: maximum width 1:34–39. Esophagus ($n = 10$) 570–660 (616 ± 28) long; 8.1–9.9% of total body length. Valve at EIJ cylindrical, bilobed, ventriculus-like, longer than wide, ($n = 10$) 68–75 (70 ± 2) in length by ($n = 10$) 52–65 (58 ± 4) in maximum width. Cephalic vesicle ($n = 8$) 72–108 (91 ± 10). SVGO ($n = 10$) 215–330 (264 ± 33), NR ($n = 10$) 232–298 (280 ± 20), EXP ($n = 10$) 295–362 (343 ± 21), and CP ($n = 10$) 325–402 (376 ± 21) from cephalic extremity; position of EXP at 53–60% and CP at 55–65% of esophageal length from anterior. Copulatory bursa symmetrical, of type 2-1-2; lacking bosses, complex vermicular-ridges along margin on inner surface of bursal membrane. Rays 2/3 curved, congruent along entire length, extending to margin of bursal membrane; Rays 3 massive relative to Rays 2, thickness of Rays 3, with expanded distal tip, equal to or exceeding that of Rays 4. Rays 5/6 narrow, parallel throughout length, gradually divergent distally. Rays 8, slight, curved dorsally, extending to margin of bursa. Dorsal ray narrow with parallel margins, relatively short ($n = 8$) 42–48 (44 ± 2) with initial bifurcation ($n = 7$) 67–76 % of total length from base. Papillae “9/10” on bifurcate distal tips of dorsal ray. Dorsal lobe reduced, laterally inflated, substantially exceeds width of dorsal ray; disposed ventrally to Rays 8. Genital cone with weakly developed proconus; prominent, arcuate, paired “0” papillae with bulbous distal expansions positioned posterior to proconus on ventral aspect of cloaca. Accessory bursal membrane (ABM) inconspicuous in dorso-ventral view; reduced in length, laterally expanded with delicate papilliform margin and widely divergent, filamentous papillae “7.” Cloaca with telamon and cuticularized support structures surrounding orifice. Spicules equal in length ($n = 10$) 162–178 (171 ± 5) with trifurcation 78–82% of total length from anterior. In lateral view, spicules narrow and filamentous, strongly curved, with bend at mid-length. Dorsal and ventral processes of spicules near equal length; dorsal process simple, spatulate in dorso-ventral view, weakly curved in lateral view, tapering to acute point; ventral process straight, with bend near acutely pointed, narrow, distal tip; main shaft tapering to blunt point, with weakly developed hyaline foot. Well-developed membranes envelop all processes of spicules. Gubernaculum cryptic, shield-like, weakly heart-shaped, strongly granular in dorsal/ventral view, tapering distally, maximum width ($n = 5$) 25–26 (25 ± 0.4); laterally with pronounced bend anterior to distal tip, total length ($n = 5$) 50–61 (52 ± 2).

Female: Small nematodes lacking prominent cuticular ornamentation other than synlophe. Total length ($n = 10$) 8,585–11,107 ($9,969 \pm 748$);

maximum width ($n = 10$) 248–295 (275 ± 14) attained 29–67% of body length measured from anterior; ratio of total body length: maximum width 1:32–40. Cephalic vesicle ($n = 10$) 82–112 (100 ± 11). Esophagus ($n = 10$) 595–750 (672 ± 45) long; 6.1–7.5% (6.8 ± 0.5) of total body length. Valve at EIJ, ventriculus-like, bilobed, ($n = 11$) 70–82 (77 ± 3) long, ($n = 11$) 62–72 (68 ± 3) in maximum width. SVGO ($n = 8$) 258–308 (282 ± 16), NR ($n = 10$) 258–338 (301 ± 21), EXP ($n = 9$) 342–392 (371 ± 16), and CP ($n = 10$) 358–442 (404 ± 26) from cephalic extremity; position of EXP at 51–60% and CP at 54–68% of esophageal length from anterior. Ovaries didelphic, amphidelphic, strongly convoluted, spiraled around intestine. Vulva opens as ventral transverse slit ($n = 10$) 68–75% (72 ± 2.0) of body length from anterior; cuticular inflations and fans absent; synlophe modified as plate-like structures posterior to vulva. Perivulvar pores bilateral, located postero-lateral to vulva in subventral fields. Anterior infundibulum ($n = 11$) 262–345 (299 ± 27), anterior sphincter and vestibule, including S1 and S2, ($n = 11$) 170–300 (238 ± 38). Posterior infundibulum ($n = 11$) 250–302 (282 ± 18), posterior sphincter and vestibule, including S1 and S2, ($n = 11$) 180–248 (216 ± 21); length of anterior vestibule > posterior vestibule. Total ovejector length ($n = 11$) 938–1,137 ($1,036 \pm 67$). Eggs ovoid, with thin shell, ($n = 60$ in 6 specimens) 51–80 (62 ± 12) long by 30–42 (36 ± 7) wide; oriented in single or double rows in anterior and posterior uterine limbs. Tail conical ($n = 11$) 132–218 (172 ± 21), bluntly rounded at caudal extremity, with weak annulations present distal to synlophe termination.

Taxonomic summary

Host: *Kobus kob* (Erxleben), type host. Other recognized hosts include kongoni or hartebeest, *Alcelaphus buselaphus jacksoni* (Pallas).

Locality: Type locality: In type host from West Acholi District, Uganda; ca. 02°45'N, 032°10'E. Currently unknown from other localities.

Specimens: Holotype male, USNPC 100,000 and allotype female, USNPC 100,001 in type host from type locality. Paratypes from type locality include (1) USNPC 66320, 8 males and 8 females in *K. kob*; and (2) USNPC 66321, 2 female nematodes in *A. b. jacksoni*. One male voucher in *K. kob* was excluded from the type series because it was damaged; originally under USNPC 66320, it is now under USNPC 100,002.

Etymology: *Robustostrongylus* is a compound name derived from the Latin “robustus” for strong or robust and the Greek “strongylus” denoting a roundworm. The species “aferensis” is derived from the Latin “afer” for African. Thus, *R. aferensis* for a robust, cigar-like nematode from Africa.

Remarks

Affiliation of *Robustostrongylus* gen. nov. within the Ostertagiinae, is based on putative synapomorphies for the subfamily. Attributes which diagnose a relationship within the ostertagiines include trifurcate spicules with a characteristic ostertagiine window (Figs. 15, 23, 24, 27), paired “0” papillae (Figs. 19, 20), a simple accessory bursal membrane (Figs. 18, 21, 29), and a prominent, elongate, esophageal valve (Figs. 10, 13) (Hoberg and Abrams, 2007; Hoberg, Abrams, and Ezenwa, 2008). Although the ABM and EIV are modified in *Robustostrongylus*, these attributes remain consistent with the general structure seen among other ostertagiines. These putative synapomorphies for the ostertagiines are established relative to sister-taxa represented by the Haemonchinae (e.g., species of *Haemonchus* Cobb, 1898, *Mecistocirrus* Railliet et Henry, 1912, *Ashworthius* Le Roux, 1930) and species of *Graphidium* Railliet et Henry, 1909 as identified in prior analyses (Hoberg and Lichtenfels, 1994; Durette Desset et al., 1999).

A suite of unique characters for *R. aferensis* gen. nov. et sp. nov. relative to all ostertagiine genera is demonstrated in males and females by a posterior position for the EXP and CP (in the posterior 50% of esophageal length from the anterior and substantially distal to the SVGO) (Figs. 1, 10), a ventriculus-like, constricted and bilobed EIV with prominent oblique musculature (Figs. 10, 13), robust, domed or knob-like ridges comprising the synlophe (Figs. 2–9), a maximum number of ridges attained near the EIJ, the exceptionally large midbody diameter relative to length (e.g., in females, length:width = 1:32–40), and in females, the anterior position of the vulva (near 70% from the anterior extremity) and absence of cuticular inflations adjacent to the vulva (Figs. 8, 9, 32). Among all other ostertagiines across 14 genera,

the CP and EXP are always near the SVG0 and in the anterior half of the esophagus; the valve at the EIJ is cylindrical, never bilobed or constricted and lacks strongly developed oblique musculature; the synlophe is composed of narrow acutely pointed ridges, and where known, the numbers of ridges increase posteriorly to the EIJ usually attaining a maximum near the middle third of body length, the midbody is narrow and not strongly inflated (in females, length:width = 1:58–107), the position of the vulva is always >80% of body length from the anterior, and cuticular inflations at the vulva are present in species of some genera. Based on these criteria, specimens of *Robustostromylus* are unequivocally distinct from nematodes representing all known genera of the subfamily.

Specimens of *Robustostromylus* further contrast with the haemonchines, the putative sister-group for the Ostertagiinae, and closely related species of *Graphidium* with respect to the synlophe, cephalic, esophageal and cervical characters and in the position of the vulva and structure of the “0” papillae (Figs. 1–13, 18–20, 32). Among haemonchines, the EXP and CP are situated in the anterior half of the esophagus, a prominent valve is lacking at the junction with the intestine, and the vulva is located near 80% of body length from the anterior and there is a single “0” papilla. Relative to *Robustostromylus*, the ridges of the synlophe are acutely pointed with patterns and distribution differing considerably in the Haemonchinae (Lichtenfels and Pilitt, 2000; Hoberg et al., 2002). Among species of *Graphidium*, although the CP and EXP are positioned from mid-length into the posterior region of the esophagus, a weakly developed, ovoid valve joins the esophagus and intestine, the synlophe ridges are acutely pointed, the vulva (often with a copulatory plug) is situated near 74–85% of body length, and there is a single “0” papilla. Midbody diameter for haemonchines (length:width ratio = 1:30–54, mean = 1:45 among 6 species) and *Graphidium strigosum* (1:28–44) overlaps with that for *Robustostromylus* but not with other taxa within the Ostertagiinae.

Among the ostertagiines, specimens of *R. aferensis* are immediately distinguished from nematodes in 8 genera where the lateral rays of the bursa are disposed in the 2–2–1 pattern (Fig. 29) (*Africanastromylus*, *Cervicaprastromylus*, *Hamulonema*, *Hyostrongylus*, *Mazamastrongylus*, *Sarwaria*, *Spiculopteragia*, and *Teladorsagia*) (Durette-Desset, 1983; Hoberg, Abrams, and Ezenwa, 2008; Hoberg and Abrams, 2008). Among 6 remaining genera in which a 2–1–2 bursal pattern is characteristic (*Camelostromylus*, *Longistromylus*, *Marshallagia*, *Orloffia*, *Ostertagia*, and *Pseudommarshallagia*), specimens of *R. aferensis* are distinguished, respectively, among these taxa by a broader suite of structural characters in addition to those previously outlined (Figs. 1–35).

Polymorphism for males is apparently not demonstrated in *Robustostromylus*, *Camelostromylus*, *Longistromylus*, and *Pseudommarshallagia*; this conclusion is based on prior examinations of ostertagiine diversity (Hoberg and Abrams, 2008; Hoberg, Abrams, and Ezenwa, 2008). Specimens of *R. aferensis* contrast with those of the monotypic *C. mentulatus* (Railliet and Henry, 1909) (Figs. 1–5, 18, 21, 23–27) in which males of the latter are characterized by the extreme length and unique ornamented structure of the spicules, strongly cuticularized gubernaculum, absence of a proconus, fused “7” papillae that diverge distally, a membranous ABM, and a dorsal lobe positioned dorsally to Rays 8.

Only 1 male of *P. elongata* was available for study. Based on this specimen and on the redescription (Graber and Delavenay, 1978; Gibbons, 1981a) and as illustrated by Gibbons and Khalil (1982), in *P. elongata* the spicules are broad and thick in dorso-ventral view, and the alate main shaft is trifurcate near the distal end with the tips enveloped in a series of complex membranes. The dorsal ray and lobe are inflated and broad proximally, with a pronounced taper towards the distal end; the robust but reduced dorsal lobe is situated in a position dorsal to the externodorsal rays or Rays 8. These characters serve to distinguish male specimens of *R. aferensis* from the monotypic *P. elongata*.

Robustostromylus aferensis contrasts with *Marshallagia*, *Orloffia*, and *Ostertagia* in the absence of polymorphism among males; comparisons outlined here are in the context of major morphotypes for the 3 latter genera (see Drózdź, 1995). *Robustostromylus* further differs from *Marshallagia* based on the exceptionally long dorsal ray, filamentous “0” papillae, elongate filamentous “7” papillae contained in a delicate ABM, relatively massive spicules, and absence of a gubernaculum and proconus among males and the large dimensions for eggs among females that characterize species of the latter genus. A reduced and inflated

dorsal lobe and ray disposed ventrally to Rays 8 (Figs. 14–17, 31), reduced and laterally expanded ABM (Figs. 14, 21), arcuate structure of the “0” papillae (Figs. 19, 20), strongly curved or kinked spicules and a granular gubernaculum (Figs. 23, 26–28) distinguish *R. aferensis* from species of both *Orloffia* and *Ostertagia*; in addition, a proconus is lacking in species of *Orloffia*.

Robustostromylus aferensis seems most similar to species of *Longistromylus* based on the reduced ABM; inflated dorsal lobe containing a relatively narrow dorsal ray, which bifurcates distally; the arcuate “0” papillae that terminate in bulbous expansions; and thin, narrow spicules that in some species have a characteristic bend near mid-length (Figs. 14–27) (E. P. Hoberg and A. Abrams, unpubl. obs.). The original description of *L. meyeri* (type species) and diagnosis of the genus *Longistromylus* was based on male and female specimens of large dimensions (Le Roux, 1931). Maximum width of females for *L. meyeri* is reported as 437 μm ; however, the length:width ratio (1:58–64) calculated from measurements for individual females in the original description (and from specimens attributed to this species and examined during the current study) is typical but at the lower range of variation among other ostertagiines; the CP and EXP are both in the anterior half of the esophagus. Le Roux (1931) described males and females as “rather long and thin,” which differs substantially from the robust body form seen in specimens of *R. aferensis*. The valve at the EIJ for *L. meyeri* was described as “not well developed,” and the figure of the cervical region showed the esophagus lacking any basal constriction, a character consistent among all species of *Longistromylus* (Le Roux, 1931; Yeh, 1956; Gibbons, 1977; E. P. Hoberg and A. Abrams, unpubl. obs.). Females were described as having ovarian tracks that spiraled around the intestine in a manner similar to that typical for some haemonchines. This pattern does not seem usual among other species now relegated to *Longistromylus*. In type and voucher specimens attributed to *L. meyeri* that were examined during the present study (E. P. Hoberg and A. Abrams, unpubl. obs.), the ovarian tracks were weakly spiraled around the intestine, but not strongly convoluted; the disposition of the ovarian tracks was not addressed in redescription by Yeh (1956) or Gibbons (1977). Specimens of *R. aferensis* further differ from *L. meyeri* in the details of the spicules and copulatory bursa, presence of a proconus, position of Rays 8, the terminal bifurcation of the dorsal ray, and genital cone including structure and position of papillae “7” and the ABM (Le Roux, 1931; Gibbons, 1977). Finally, in all species of *Longistromylus* the dorsal lobe remains dorsal to Rays 8, the bursa contains numerous and discrete fields of bosses, and irregular cuticular inflations occur at the level of the vulva (Gibbons, 1977; Hoberg et al., 1993; Hoberg, Abrams, and Ezenwa, 2008).

These attributes are in addition to the suite of characters that are distinct at the generic level among the ostertagiines, and as a consequence *Longistromylus* cannot be simply emended to accommodate *Robustostromylus*. Resurrection of either *Kobusinema* Ortlepp, 1963 or *Bigalkenema* Ortlepp, 1963 for *R. aferensis*, both correctly reduced as synonyms of *Longistromylus* by Gibbons (1977), also is not supported. Although *R. aferensis* can be readily distinguished from all species of *Longistromylus*, it is apparent that these genera are likely to be closely related and may be sister-groups.

Gibbons (1977) noted broad morphological variation among specimens attributed to *L. schrenki* in species of *Kobus* from Uganda and Tanzania. These included some female nematodes in which the maximum width attained 288 (males at 216), and in which the EXP and CP were situated in the posterior half of the esophagus. Additionally, the position of the vulva in some specimens (e.g., in *Kobus kob* from Uganda) is at 68–72% of body length from the anterior extremity. The ratio of total body length:maximum width could not be accurately calculated for these specimens, and there are no data for the structure of the synlophe, esophageal valve, or ovarian tracks. In contrast, for specimens representing *L. schrenki*, otherwise consistent with descriptions and redescriptions for this species (and other species of *Longistromylus* available to us during the current study) (Table I), the CP and EXP were in the anterior half of the esophagus, the length-to-width ratio ranged from 1:58–104, and the vulva was located between 82 and 85% of body length from the anterior. Consequently, it seems possible that some specimens relegated to *L. schrenki* in the revision by Gibbons (1977) may be attributable to *Robustostromylus* and that the redescription of this species may have been a composite. At a minimum, this may include some female and male specimens in *Kobus kob* from Uganda,

and male specimens in *Kobus* sp. and *Kobus vardonii* (Livingstone) from Tanzania (see Gibbons, 1977 for critical meristic data).

DISCUSSION

Robustostrongylus aferensis gen. nov. et sp. nov. represents a new ostertagiine, among those with a 2-1-2 bursal pattern, in which males are monomorphic. Assessment of distribution, diversity, and records of occurrence for ostertagiines across Africa (summarized in Hoberg and Abrams, 2008; Hoberg, Abrams, and Ezenwa, 2008) suggests the absence of polymorphism among males of *R. aferensis* as defined for this subfamily (e.g., Drózdź, 1995). Across the global ostertagiine fauna, monomorphic males are known from 4 of 7 genera where a 2-1-2 bursal pattern is characteristic (*Camelostrongylus*, *Longistrongylus*, *Pseudommarshallagia*, and *Robustostrongylus*) and from 6 of 8 genera defined by a 2-2-1 bursal formula (*Africanaststrongylus*, *Cervicaprastrongylus*, *Hamulonema*, *Hyostrongylus*, *Mazamastrongylus*, and *Sarwaria*) (Hoberg and Abrams, 2008). Interestingly, polymorphism seems to be most often manifested among ostertagiines with distributions in the Palearctic and across the Holarctic, i.e., *Marshallagia*, *Orloffia*, *Ostertagia*, *Spiculoptera*, and *Teladorsagia*. Perhaps this reflects an environmental component (temperature or humidity) in the origins and drivers that serve to maintain the balanced polymorphism for structurally discrete males among species that characterize these primarily northern or high-latitude genera (Hoberg and Abrams, 2008; Hoberg, Polley et al., 2008).

Globally, ostertagiine faunas and more generally those of gastrointestinal nematodes in ungulates are defined by an intricate mosaic structure composed of endemic and introduced species (Hoberg et al., 1999; Hoberg, Polley et al., 2008). Among ostertagiines, there are 15 genera in the global fauna, with 5 being endemic to Africa (*Africanaststrongylus*, *Hamulonema*, *Longistrongylus*, *Pseudommarshallagia*, and *Robustostrongylus*); although generic-level endemism is high, there are relatively few species limited solely to Africa (Hoberg, Abrams, and Ezenwa, 2008). There are 26 species partitioned in 10 genera that occur in African mammals and, among these, 22 species in 8 genera are endemic (Hoberg and Abrams, 2008; Hoberg, Abrams, and Ezenwa, 2008). Among those occurring in free-ranging ungulates, most genera are monotypic, but highly discrete morphologically, including *Africanaststrongylus* (1 species), *Hamulonema* (2), *Longistrongylus* (8), *Pseudommarshallagia* (1), and *Robustostrongylus* (1). Also, 9 endemic species are known among *Ostertagia* (5), *Cervicaprastrongylus* (2), and *Hyostrongylus* (2), and, for the latter 2 genera, distributions encompass some non-ungulate hosts such as lagomorphs and primates, respectively (Hoberg, Abrams, and Ezenwa, 2008). In contrast, non-endemics, primarily associated with introduced and domestic ungulates, represent species that are geographically widespread around the globe, including *Hyostrongylus* (1), *Marshallagia* (1), *Ostertagia* (1), and *Teladorsagia* (1). The center of diversity for the ostertagiines is outside of the African region, although this continent has been significant in the radiation of this nematode fauna (Daubney, 1933; Hoberg, Abrams, and Ezenwa, 2008).

Endemism in the contemporary fauna may be an indicator of the temporal duration and degree of isolation of ostertagiines and other gastrointestinal nematodes among African ungulates (Hoberg et al., 2004). Among the Cooperiinae, another related

subfamily among the trichostrongyloids, there are both a high number of endemic genera (5 of 8, including *Cooperioides* Daubney, 1933; *Impalaia* Mönning, 1923; *Megacooperia* Khalil and Gibbons, 1976; *Minutostrongylus* Le Roux, 1936; and *Ortleppstrongylus* Durette-Desset, 1970) and some taxa, particularly *Cooperia* Ranson, 1907, that contain numerous endemic species primarily associated with bovids as hosts (Gibbons 1978, 1981b; Gibbons and Khalil, 1982; Khalil and Gibbons, 1976; Durette-Desset, 1983; Hoberg and Lichtenfels, 1994; Durette-Desset et al., 1999). Haemonchinae (specifically *Ashworthius*, *Haemonchus*, and *Leiperiatus* Sandground, 1930) diversified in large part in association with ungulates in Africa (Gibbons, 1979; Hoberg et al., 2004) and collectively with Cooperiinae must be regarded as a strongly tropical-adapted fauna (Hoberg, Abrams, and Ezenwa, 2008).

Parallel radiations in Africa are postulated for some ostertagiines, cooperines, and haemonchines, although it is not clear whether periods of diversification across these disparate nematode taxa and their artiodactyl hosts were congruent on spatial and temporal scales (Hoberg et al., 2004; Marcot, 2007; Hoberg, Abrams, and Ezenwa, 2008). Diversification in *Haemonchus* was associated with successive waves or episodes of biotic expansion by ungulates from Eurasia into Africa and sequential host switching by nematodes extending since the Miocene (Hoberg et al., 2004). Radiation among parasite groups coincided with periods of ecological perturbation and variation in climate which influenced ecological structure for artiodactyl faunas in Africa during the late Tertiary (Vrba, 1985, 1995; Vrba and Schaller, 2000). Host switching beyond ungulates is also seen among the Cooperiinae (in Bathyergidae for *Ortleppstrongylus*; in Lagomorpha for some *Impalaia*) and also among Ostertagiinae (*Cervicaprastrongylus* in Lagomorpha; *Hyostrongylus* in Pongidae) in Africa. Such distributions are indicative of colonization events involving mammalian groups occupying habitat and in sympatry with artiodactyls, and ecological structure promoting host switching (Hoberg and Brooks, 2008).

Geographic and host colonization are emerging as primary mechanisms involved in diversification of complex host-parasite assemblages (Hoberg and Brooks, 2008). Ecological perturbation driven by episodic variation in climate was an important determinant for biotic expansion, isolation, and development of faunal associations across sub-Saharan Africa since the Miocene. These processes that have functioned in evolutionary time continue to be manifested in shallow ecological time where a breakdown in ecological isolation leads to expansion of invasive species and emergence of disease in contemporary systems involving both free-ranging and domestic ungulates (Hoberg, 1997; Brooks and Hoberg, 2006, 2007). Tropical-adapted faunas, including haemonchines, cooperiines, and some ostertagiines have been introduced or translocated with ungulate hosts around the world. In temperate to boreal latitudes, current regimes for global warming and alteration in precipitation are predicted to be associated with novel patterns of host and geographic associations for this fauna, potentially driving the emergence of disease (Hoberg, Polley et al., 2008). Thus, knowledge of biodiversity extending from species to population structure is critical, particularly when explored in the context of historical determinants that may either limit or serve to promote expansion by an array of pathogens into new geographic settings and host groups.

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