

AN EXPLORATION OF DIVERSITY AMONG THE OSTERTAGIINAE (NEMATODA: TRICHOSTRONGYLOIDEA) IN UNGULATES FROM SUB-SAHARAN AFRICA WITH A PROPOSAL FOR A NEW GENUS

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ABSTRACT: Abomasal nematodes (Ostertagiinae: Trichostrongyloidea) representing a previously unrecognized genus and species are reported in African buffalo (*Syncerus caffer caffer*) from Kenya, Uganda, and South Africa. *Africanaststrongylus buceros* gen. nov. et sp. nov. is characterized by a symmetrical tapering synlophe in the cervical region and a maximum of 60 ridges in males and females. Bursal structure is 2–2–1, with subequal Rays 4/5, massive Rays 8, and Rays 9/10, and a massive dorsal lobe that is reduced in length, laterally and dorsally inflated, and positioned ventral to externodorsal rays. Spicules are tripartite, and the gubernaculum is broadly alate in the anterior. A proconus is present. Among ostertagiines with a 2–2–1 bursa (*Cervicapraststrongylus*, *Hyostrongylus*, *Mazamastrongylus*, *Sarwaria*, *Spiculoptera*, and *Teladorsagia*) specimens of *Africanaststrongylus* are differentiated from respective genera based on the structure of the cervical synlophe, patterns of dorsal, externodorsal, lateral, and ventral rays, and configuration of the genital cone, gubernaculum, and spicules. Among 13 genera of the Ostertagiinae in the global fauna, 3 are entirely limited in distribution to Africa, including *Africanaststrongylus*, *Longiststrongylus*, and *Pseudomarsallagia*. Another 5 genera including *Cervicapraststrongylus*, *Hyostrongylus*, *Marshallagia*, *Ostertagia*, and *Teladorsagia* are represented as mosaics, with diversity centered in Eurasia or the Holarctic. Genera not represented in the African fauna include *Cameloststrongylus* among Caprinae and some Antelopinae from Eurasia, *Mazamastrongylus* and *Spiculoptera* in Cervidae from the Holarctic and Eurasia, respectively, *Orloffia* in Cervidae and Bovidae from the Holarctic, and *Sarwaria* among Tragulidae and Bovinae in southern Asia. The diverse nature of the ostertagiine fauna, with a disproportionate number of endemic genera relative to other regions of the northern hemisphere, may reflect the timing of episodic expansion events for artiodactyls into Africa from Eurasia during the Tertiary and Quaternary.

Ostertagiine nematodes represent a monophyletic group within the Trichostrongyloidea with a primary geographic distribution centered in Eurasia and the Holarctic Region (Durette-Desset, 1985; Lichtenfels and Hoberg, 1993; Hoberg and Lichtenfels 1994; Durette-Desset et al., 1999). Across Africa, diversity for species of Ostertagiinae, primarily abomasal nematodes among artiodactyls, appears relatively limited. Extensive survey and inventory over the past century among Bovinae, Antelopinae, and other pecoran artiodactyls have revealed relatively few endemic species, except for those in the genus *Longiststrongylus* Le Roux 1931, and among the otherwise geographically widespread *Ostertagia* Ransom, 1907 (e.g., Mönnig, 1932; Round, 1968; Gibbons, 1977; Gibbons and Khalil, 1980; Boonker and Durette-Desset, 2003).

Among the diverse ungulate fauna characteristic of sub-Saharan Africa, there are relatively few reports of ostertagiine or other abomasal parasites in African buffalo (*Syncerus caffer caffer* (Sparrman)). These have been limited to *Longiststrongylus meyeri* Le Roux, 1931; species of *Ostertagia* Ransom, 1907 from Uganda (Dinnik et al., 1963; Bwangamoi, 1968); *Ashworthius lerouxi* Diaouré, 1964 from Congo (Diaouré, 1964), *Haemonchus bedfordi* Le Roux, 1929 from Uganda (Dinnik et al., 1963) and South Africa (Le Roux, 1929; Ortlepp, 1961); *Haemonchus contortus* (Rudolphi, 1803) from Kenya and South Africa (Curson, 1928; Ezenwa, 2003); and *Haemonchus placei* Place, 1893 from Kenya (Ezenwa, 2003).

Surveys in the late 1960s and more recent collections of wild African buffalo, or Cape buffalo (*Syncerus caffer caffer* (Sparrman)) from Uganda, Kenya, and South Africa have now revealed a previously unrecognized genus and undescribed species of ostertagiine nematode. We provide a generic diagnosis and the first description of these ostertagiines. Concurrently, we

explore (1) the limits and criteria for genera within the Ostertagiinae (see also Hoberg and Abrams, 2007), and (2) aspects of the structure of the ostertagiine fauna among African ungulates. Faunal discovery, inventory, and characterization of biodiversity for complex faunas are cornerstones necessary for understanding, documenting, and predicting biotic responses to ecological perturbation under an expanding regime of global climate change (Brooks and Hoberg, 2000, 2006; Hoberg and Brooks, 2008).

MATERIALS AND METHODS

Specimens examined

Abomasal nematodes in African buffalo or Cape buffalo, *S. caffer caffer* (Sparrman), were collected from widely separated localities in Africa (Table I). Specimens in 2 hosts from localities in Uganda (Field 11 at Anaka Village, West Acholi District and 33 at Queen Elizabeth National Park, Toro District) were collected by J. Bindernagle during 1964–1967 and originally studied at the U.S. National Parasite Collection in the late 1960s by W. W. Becklund and M. L. Walker, who noted the distinctive morphology of these nematodes. Additional specimens were collected by 1 of us (V.E.), from 1 adult female host (Field BN1-200 on 2 February 2000) at the Mpala Ranch, Laikipia, Kenya and 2 subadult females (Field B13 on 29 May 2006; C72 on 30 May 2006) at Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa. All specimens were archived permanently at the U.S. National Parasite Collection and stored in a mixture of 70% ethanol, 5% glycerin, and 3% formalin.

Other specimens examined

Specimens and sources of other species of ostertagiine nematodes used in comparative morphological studies are listed (Table I).

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 studied in whole mounts with particular attention 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 (Lich-

Received 16 April 2007; revised 14 July 2007; accepted 17 July 2007.

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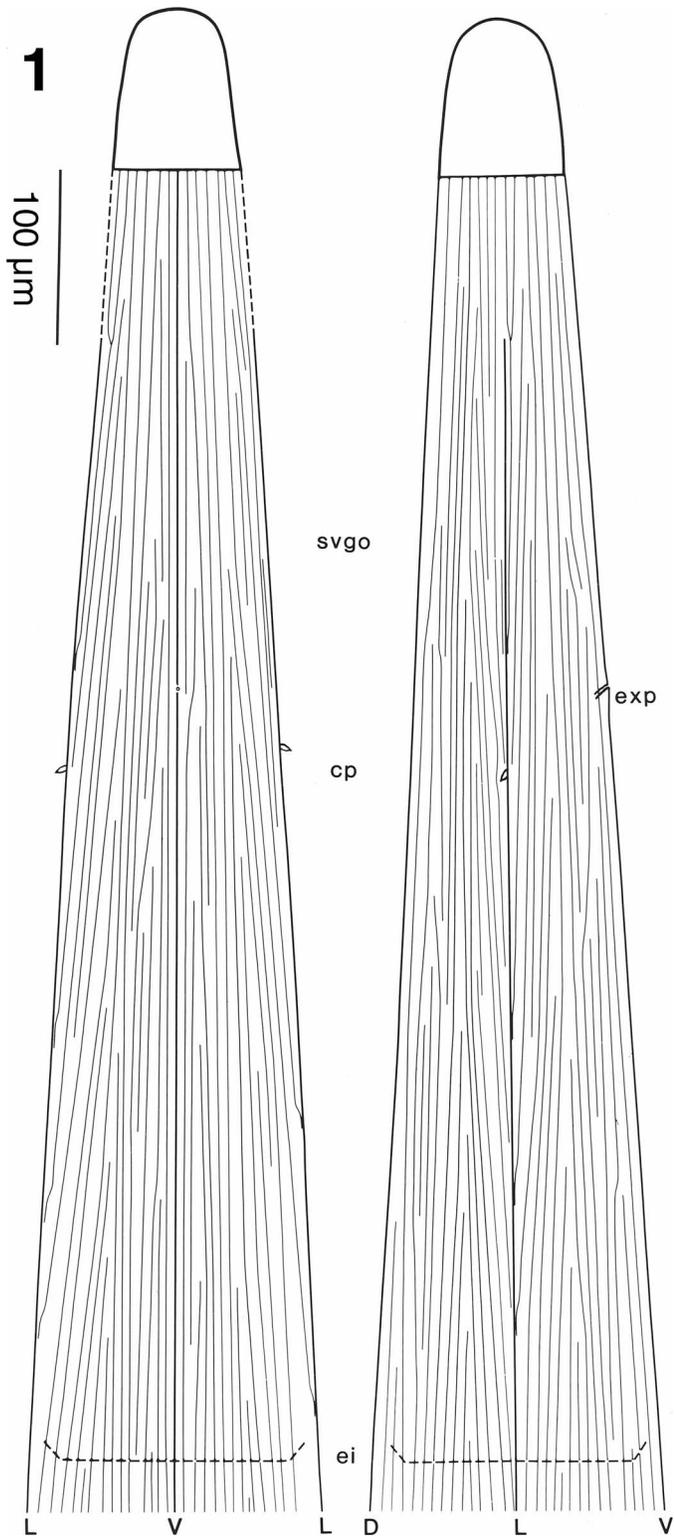


FIGURE 1. *Africanastrongylus buceros* gen. nov. et sp. nov., showing line drawings of the cervical synlophe in ventral and right lateral views of a female paratype (USNPC 66322). The excretory pore (exp) is on the ventralmost ridge consistent with a Type-B ventral pattern. Laterally the synlophe describes a Type-1 pattern; note relative positions for the subventral gland orifices (svgo), cervical papillae (cp), and esophageal-intestinal junction (ei). Orientation is indicated by v = ventral, d = dorsal, and l = lateral.

tenfels et al., 1988). Thick transverse sections were hand cut with a cataract knife and mounted in glycerin jelly; methods were based on those developed by Durette-Desset (1983). Sections were used to count the number of ridges in a single male and female at the esophageal-intestinal junction (EIJ), 1/4, midbody, and 3/4 of total body length as determined from the anterior. Sectioning was completed for only 2 specimens due to 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 under 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 ovjectors was evaluated in the context of recent definitions and descriptions among related nematodes (Lichtenfels et al., 2003). 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 \pm 1 SD in parentheses.

Host nomenclature

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

RESULTS

Field collections for survey of helminth diversity in ungulates from eastern and southern Africa revealed the occurrence of abomasal nematodes. Wild Cape buffalo from the West Acholi District of Uganda and the Queen Elizabeth National Park, Toro District, Uganda, Laikipia, Kenya and the Hluhluwe-iMfolozi Park in KwaZulu-Natal, South Africa were naturally infected with a previously undiagnosed genus and undescribed species of ostertagiine with a 2-2-1 bursal form.

DESCRIPTION

Africanastrongylus gen. nov.

Diagnosis: Trichostrongylidae. Small uncoiled nematodes with well-developed bilateral tapering synlophe, miniscule thornlike cervical papillae and prominent esophageal-intestinal valve in males and females. Males monomorphic. Bursal structure 2-2-1, symmetrical, membrane lacking discrete fields of bosses. Rays 2/3 curved, divergent through midlength, convergent distally; Rays 4/5 parallel throughout length, highly divergent distally at tips; relatively narrow, subequal with Rays 4 \leq Rays 5. Accessory bursal membrane simple, bilobed, containing filamentous papillae "7." Rays 8, massive curved mediad. Dorsal lobe massive, reduced in length, laterally and dorsally inflated, positioned ventral to externodorsal rays. Dorsal ray, or Rays 9/10, massive with stout base proximally, positioned ventral relative to Rays 8. Genital cone with weakly developed proconus; paired "0" papillae miniscule, positioned posterior to proconus on ventral aspect of cloaca. Cloaca with telamon and cuticularized support structures at orifice. Spicules alate, trifurcate, subequal. Gubernaculum present, proximally alate. Females amphidelphic with transverse vulva in posterior quarter lacking cuticular fans or inflations.

Taxonomic summary

Type species: *Africanastrongylus buceros* gen. nov. et sp. nov.

Host: African buffalo, *S. caffer* (Sparman).

Africanastrongylus buceros sp. nov.

(Figs. 1-42)

Diagnosis: Trichostrongylidae, uncoiled. Cuticle with well-developed synlophe, lacking gradient, with perpendicular orientation; maximum number of ridges, 60, in anterior quarter. Cervical papillae (CP) miniscule, triangular, thornlike near level of nerve ring, subventral gland

TABLE I. Specimens of *Africanastrongylus buceros* gen. nov. et sp. nov. and other ostertagiines examined.

Accession*	Field†	Species	Host	Locality	♂‡	♀‡
USNPC 99545§	11	<i>Africanastrongylus buceros</i>	<i>Syncerus caffer</i>	Uganda	1	—
USNPC 99546§	33	<i>A. buceros</i>	<i>S. caffer</i>	Uganda	—	1
USNPC 86939	33	<i>A. buceros</i>	<i>S. caffer</i>	Uganda	—	2
USNPC 99551	33	<i>A. buceros</i>	<i>S. caffer</i>	Uganda	5	2
USNPC 66322.02	11	<i>A. buceros</i>	<i>S. caffer</i>	Uganda	7	7
USNPC 99547	BN1-200	<i>A. buceros</i>	<i>S. caffer</i>	Kenya	—	5
USNPC 99548	B13	<i>A. buceros</i>	<i>S. caffer</i>	South Africa	2	1
USNPC 99549	C72	<i>A. buceros</i>	<i>S. caffer</i>	South Africa	—	2
Other species of ostertagiines						
OHC 2366§	—	<i>Teladorsagia hamata</i>	<i>Antidorcas marsupialis</i>	South Africa	Not available	—
UP T-2053#	—	<i>T. hamata</i>	<i>A. marsupialis</i>	South Africa	1	—
BNH 1998.10.26.22-26	—	<i>Ostertagia kenyensis</i>	<i>Gazella granti</i>	Kenya	2	2
			<i>Madoqua kirkii</i>	Kenya		
USNPC 81213	—	<i>Longistrongylus curvispiculum</i> ¶	<i>Ovis aries</i>	Texas, USA	2	—
USNPC 77484	—	<i>Longistrongylus sabie</i> **	<i>Aepyceros melampus</i>	South Africa	4	—
USNPC 66325	—	<i>Longistrongylus schrenki</i> ††	<i>Ourebia ourebi</i>	Uganda	4	—
USNPC 66323	—	<i>L. schrenki</i>	<i>Kobus kob</i>	Uganda	2	—

* Collection numbers from the U.S. National Parasite Collection (USNPC), Onderstepoort Helminthological Collection (OHC), the Natural History Museum, London (BNH), and University of Pretoria (UP).

† Field number at time of original collection.

‡ Number of male and female specimens examined.

§ Holotype male and allotype female.

|| Paratypes.

Syntype, from original collection by H. O. Mönnig, on 1 August 1931 at Houtkraal Farm, Karoo, Cape Province, derived from host following transport to Pretoria Zoo (Mönnig, 1932).

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

** *Longistrongylus sabie* represents a species previously referred to *Bigalakenema*.

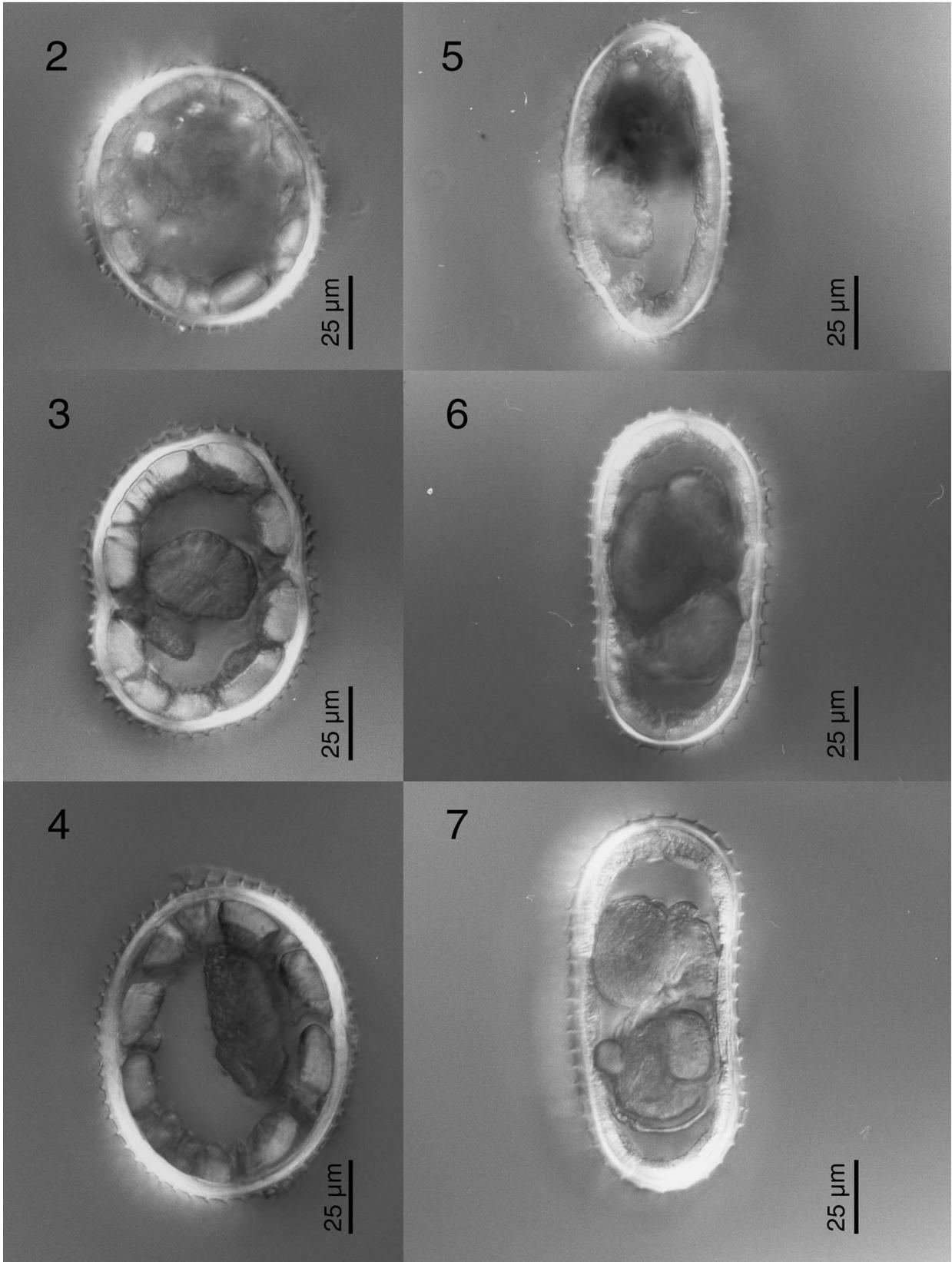
†† *Longistrongylus schrenki* represents the species previously referred to *Kobusinema*.

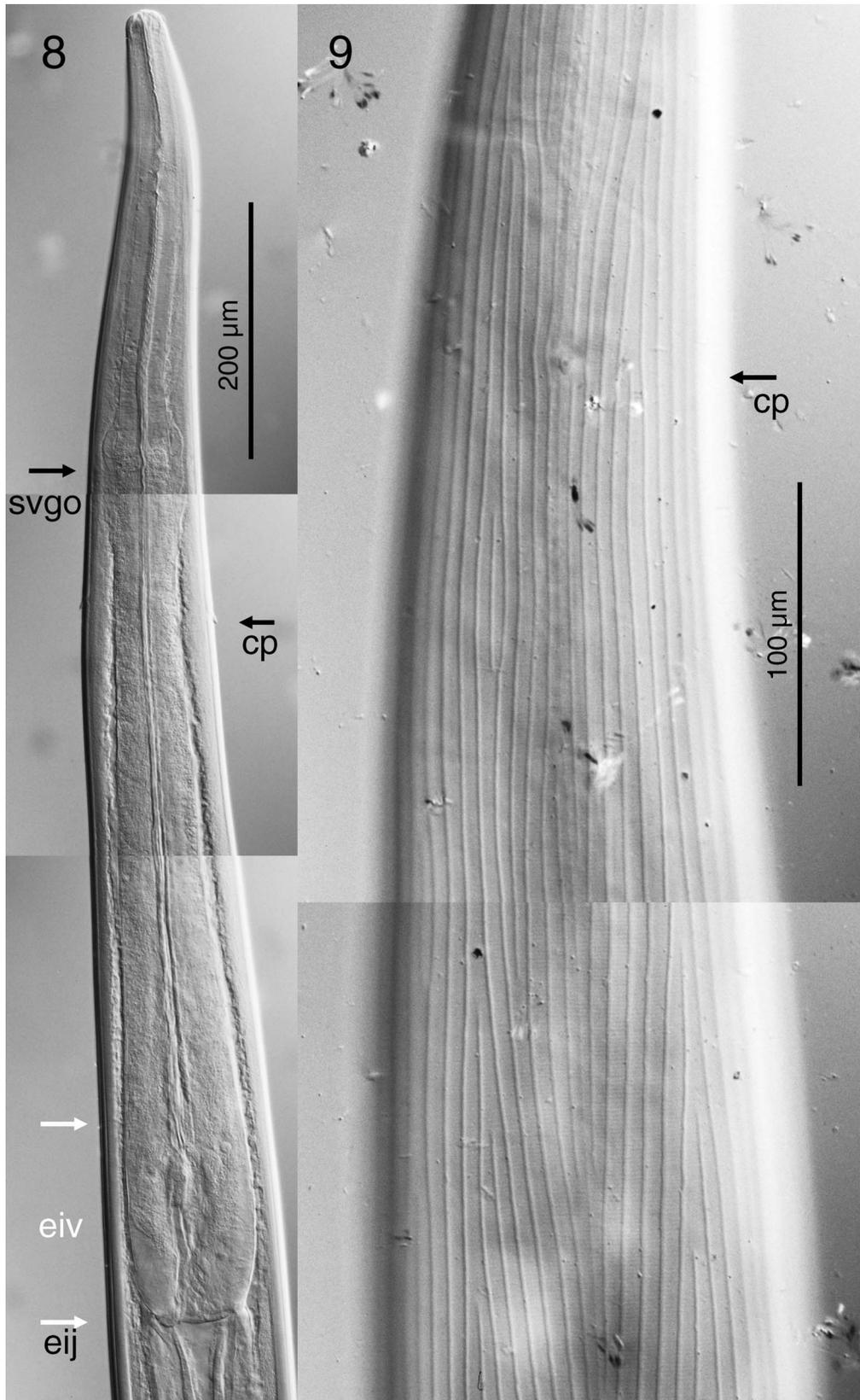
orifices (SVGO), and situated slightly posterior to level of excretory pore (EXP). Cuticular ornamentation at level of EXP lacking. Esophagus with prominent valve at esophageal–intestinal junction (EIJ). Males and females monomorphic.

Bilaterally symmetrical synlophe similar in males and females. Cervical zone (n = 3) with 29–30 ridges extending to level of cephalic expansion increasing to (n = 5) 50–58 ridges at the EIJ. Laterally, synlophe tapering, consistent with Type I pattern; 1–4 pairs of ridges terminate on lateralmost ridge anterior to EIJ; cervical papillae adjacent to lateralmost ridges in right and left fields. Ventral/dorsal ridge systems parallel, consistent with Type B pattern. Sublateral/ventral fields in cervical zone with 2–4 continuous ridges (n = 5) that may assume lateral or ventral orientation; continuous ridges may diverge or remain parallel; 4 of 5 specimens with 2 continuous ridges in sublateral/ventral fields. Lateral ridges and ventral/dorsalmost ridge (n = 3) extend anterior to level of cephalic expansion. Tapering pattern extends (n = 13) 38–61% (52% ± 5.6%) of total length from anterior. In transverse section (1 male and 1 female, respectively) ridges number from the anterior 56 and 51 at EIJ (51–58 based on counts of fields in cervical reconstructions in 3 whole nematodes); 60 and 53 at 1/4; 56 and 46 at midbody; 58 and 49 at 3/4, with initial loss in dorsal/ventral fields; and 44 ridges in the male at a level anterior to the spicules. Synlophe terminates anterior to bursa in males and anus in females. In females, ridges terminate laterally 62–212 and dorsoventrally 102–220 anterior to anus. In males ridges terminate laterally at 75–250 and dorsoventrally at 192–525 anterior to the prebursal papillae.

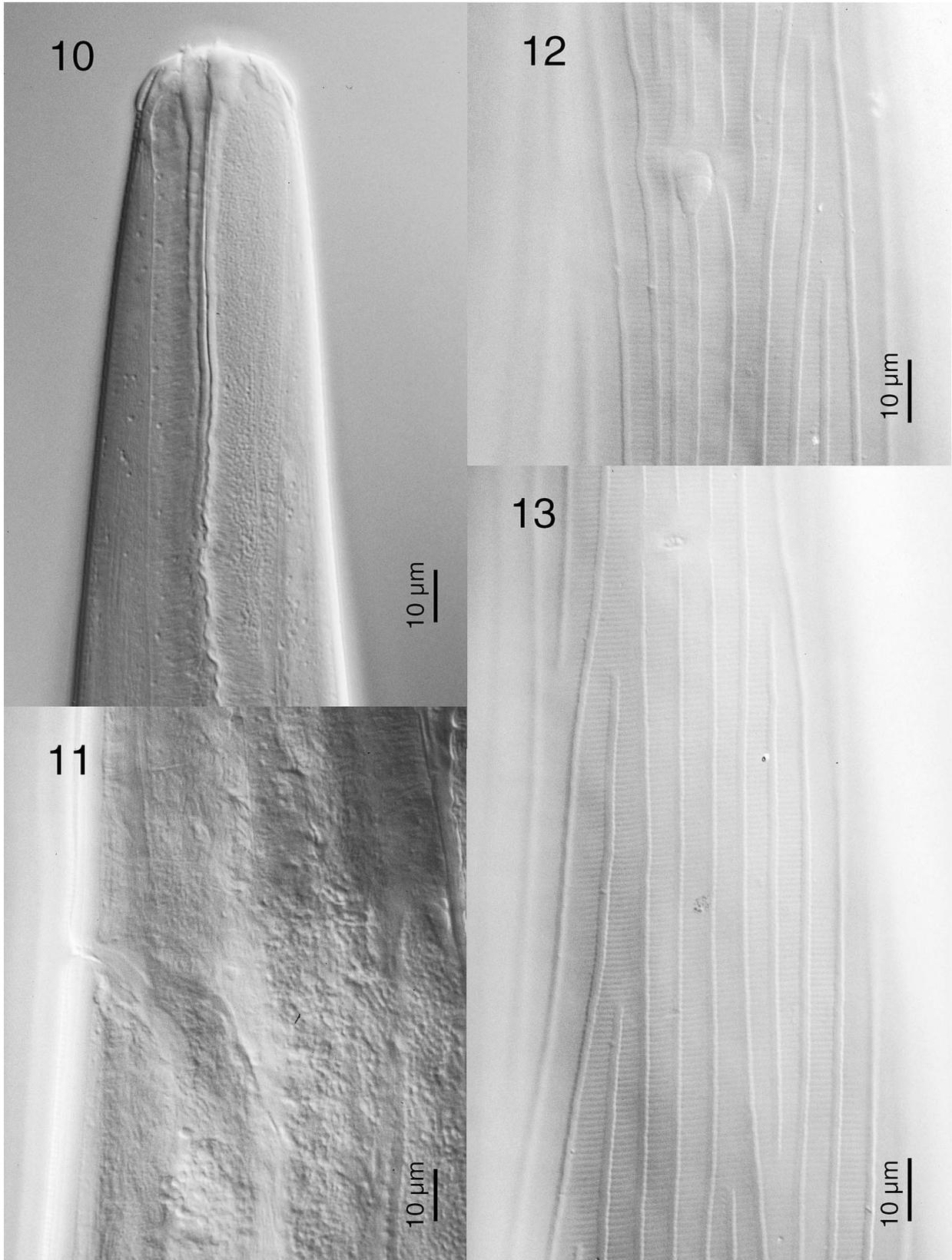
Male: Small nematodes with prominent copulatory bursa; discrete fields of bursal bosses lacking. Total length (n = 10) 6,350–8,555 (7,471 ± 642.7); maximum width 115 attained at level near prebursal papillae. Esophagus (n = 11) 688–825 (757 ± 49.6) long; 9.4–11.3% of total body length. Valve at EIJ cylindrical, longer than wide (n = 10) 80–98 (91 ± 5.5) in length by (n = 10) 48–75 (56 ± 7.93) in maximum width. SVGO (n = 10) 230–310 (276 ± 25.15), EXP (n = 10) 305–421 (370 ± 31.2), CP (n = 11) 330–445 (395 ± 32.04) from cephalic extremity. Copulatory bursa symmetrical, of type 2–2–1. Rays 2/3 curved, divergent through midlength, convergent distally, extending to margin of bursal membrane; Rays 3 with massive base. Rays 4/5 parallel through length, highly divergent distally, relatively narrow; length of Ray 4 ≤ Ray 5; Ray 4 not extending to margin of bursa. Rays 6 attaining margin of bursa, relatively straight, curved distally. Accessory bursal membrane, simple, deeply incised, strongly bilobed, containing narrow, filamentous, weakly curved papillae “7.” Rays 8, massive curved mediad, extending to margin of bursa. Dorsal lobe massive, reduced in length, laterally and dorsally inflated with prominent cuticular striations on dorsal aspect, weakly incised on ventral aspect, curving ventrally to externodorsal rays, containing massive Rays 9/10 with stout, expanded base proximally, positioned ventral relative to Rays 8 (n = 3) 33–41 in length with primary bifurcation at 18–28 from base, or in distal half at 54–68% from anterior; paired phasmids directed ventrolaterally, and papillae 9/10 on bifurcate distal tips of dorsal ray. Bursal membrane adjacent to dorsal lobe with region of curved thickened cuticle along medial margin. Genital cone with weakly developed

FIGURES 2–7. *Africanastrongylus buceros* gen. nov. et sp. nov., showing structure of synlophe based on photomicrographs of transverse sections in a male (2–4) and a female (5–7) paratype (series USNPC 66322); the general orientation is perpendicular and a gradient in size is not evident, although the lateralmost ridges are miniscule relative to those in adjacent fields. (2) Synlophe in male at esophageal–intestinal junction showing 56 ridges. (3) Synlophe in male at midbody showing 56 ridges. (4) Synlophe at beginning of third quarter in male showing 58 ridges. (5) Synlophe in female at esophageal–intestinal junction showing 51 ridges. (6) Synlophe in female at midbody showing 46 ridges. (7) Synlophe at beginning of third quarter in female showing 49 ridges.

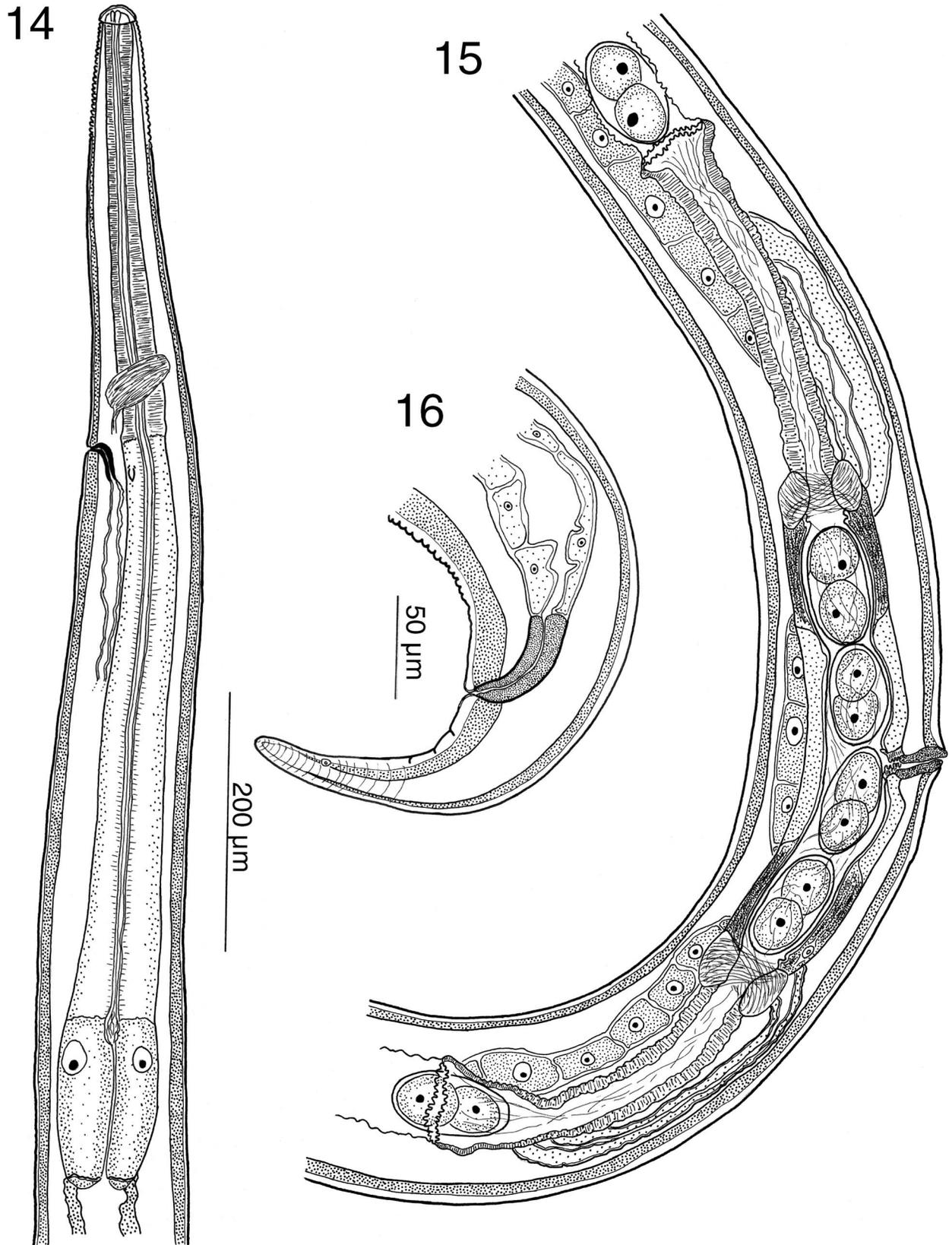




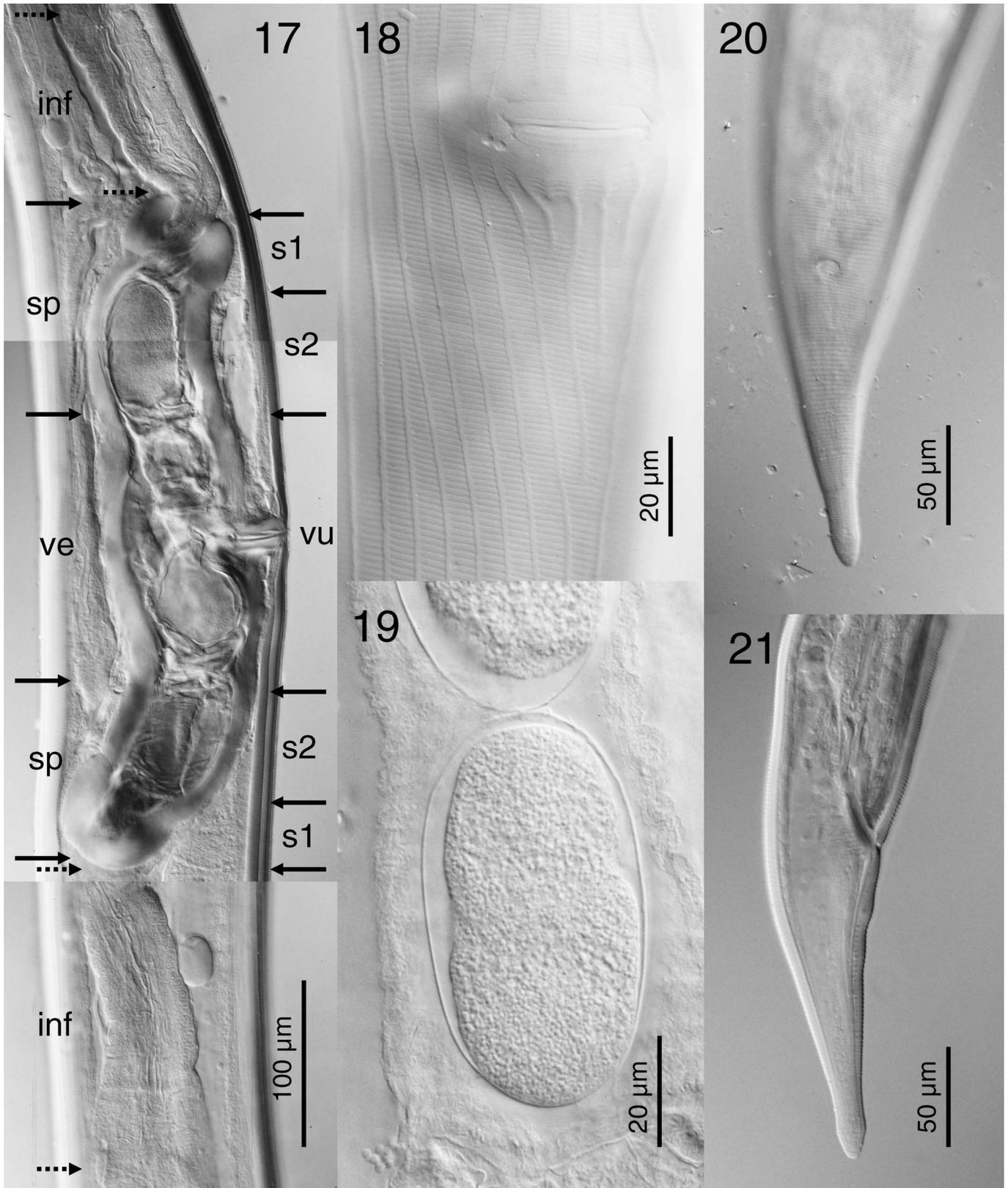
FIGURES 8–9. *Africanstrongylus buceros* gen. nov. et sp. nov., showing cervical and cephalic attributes based on photomicrographs. (8) Cervical zone in ventral view of a male paratype (USNPC 66322) denoting the position of the subventral gland orifices (svgo), cervical papillae (cp), esophageal–intestinal valve (eiv) and esophageal–intestinal junction (eij); note slight bulbous expansion of basal valve and esophagus. (9) Cervical synlophe in a female paratype (USNPC 99549) showing lateral view from near base of cephalic expansion in anterior to base of esophagus in posterior, showing Type-I tapering lateral pattern relative to miniscule lateralmost ridge and cervical papilla (cp).



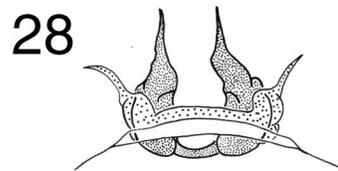
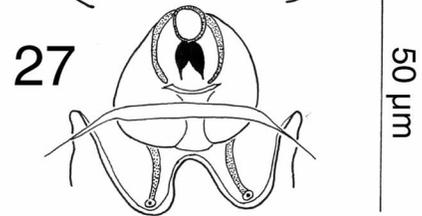
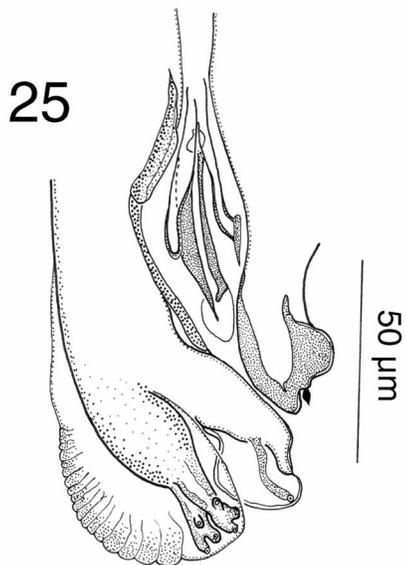
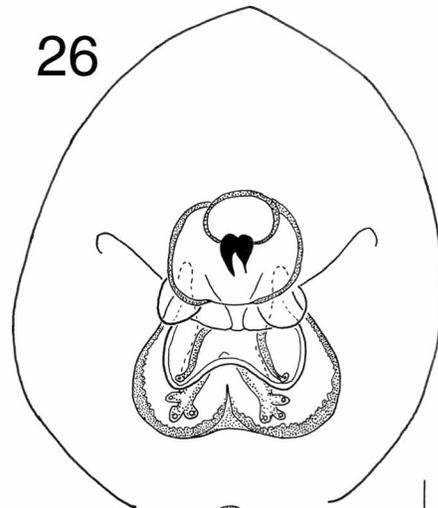
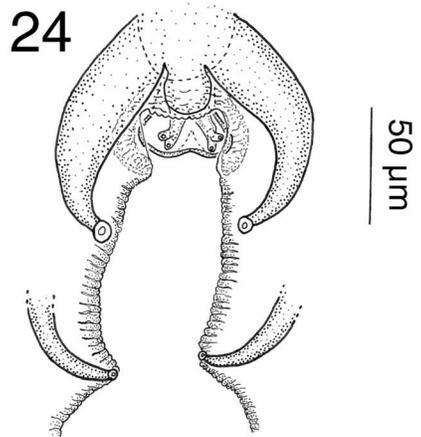
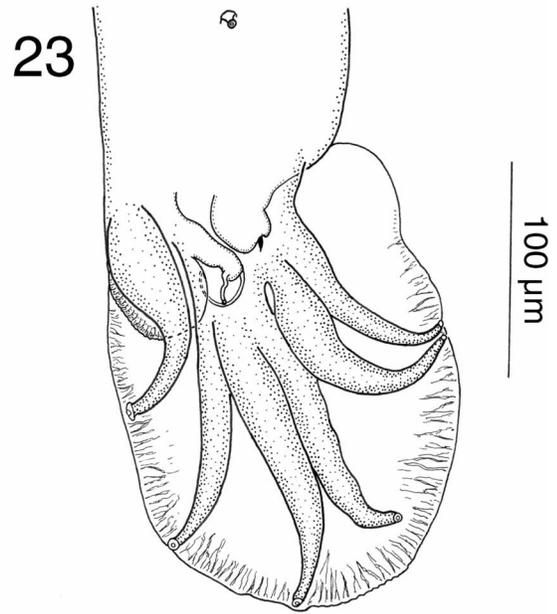
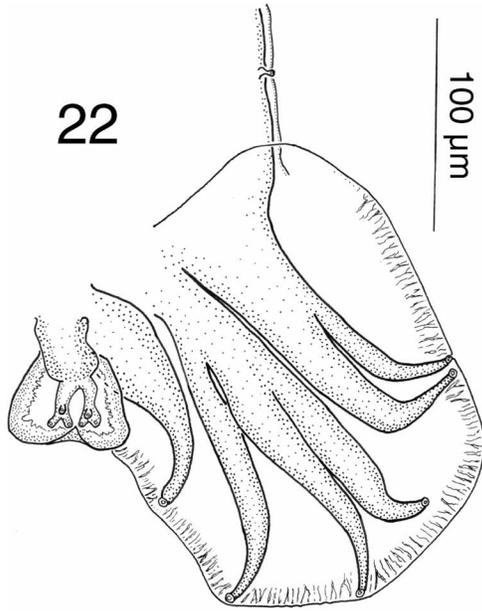
FIGURES 10–13. *Africanastrongylus buceros* gen. nov. et sp. nov., cervical and cephalic attributes based on photomicrographs in a female paratype (USNPC 99551). (10) Cephalic extremity in left lateral view. (11) Excretory pore in lateral view in a female specimen, showing absence of ornamentation. (12) Cervical papilla, showing thornlike structure and position relative to the lateralmost ridge and the cervical synlophes. (13) Excretory pore in ventral view in a female specimen, showing absence of ornamentation, and position on ventralmost ridge.



FIGURES 14–16. *Africanastrongylus buceros* gen. nov. et sp. nov., showing female attributes as depicted in line drawings from paratype specimens (USNPC 99551). (14) Cephalic and cervical zone in left lateral view. (15) Ovíjectors in right lateral view (same scale as Figure 14). (16) Tail and anus in left lateral view.



FIGURES 17–21. *Africanastrongylus buceros* gen. nov. et sp. nov., showing structural characters of females based on photomicrographs. (17) Ovijectors in right lateral view of a paratype (USNPC 66322), showing form and relative dimensions of the infundibula (inf, between dotted arrows), sphincters (sp) including the bulblike sphincter-1 (s1) and elongate sphincter-2 (s2), vestibule (ve), and transverse vulva (vu), lacking ornamentation. (18) Vulva, ventral view in a paratype (USNPC 99551), showing transverse structure and adjacent synlophe. (19) Eggs with thin shell *in utero* from a paratype (USNPC 99551). (20) Tail and anus in ventral view of a paratype (USNPC 99548). (21) Tail and anus in lateral view, showing slight bulbous expansion of apex.



proconus; paired “0” papillae with broadened bases proximally, miniscule, positioned posterior to proconus on ventral aspect of cloaca. Cloaca with telamon and cuticularized support structures surrounding orifice. Spicules subequal, left spicule longer in 12 of 13 specimens; left ($n = 14$) 195–246 (212 ± 14.1); right ($n = 13$) 190–240 (207 ± 15.2). Spicules, alate, narrow, weakly curved, filamentous in lateral view. Spicules trifurcate with acutely pointed main process, curved mediad, terminating distally in simple bulbous membrane; ventral and dorsal processes originating at level of “ostertagiine window” 76–83% of total length from anterior. Ventral process terminating in triangular barb; dorsal process terminating in narrow rounded point; length of dorsal < ventral process. Gubernaculum alate, shieldlike, concave ventrally, strongly cuticularized, with hornlike extensions on proximal margin, maximum width in dorsoventral view ($n = 10$) 35–42 (38 ± 1.8), tapering distally; in lateral view weakly S shaped, length ($n = 12$) 60–82 (67 ± 5.9).

Female: Small nematodes lacking prominent cuticular ornamentation other than synlophe. Total length ($n = 18$) 9,712–12,610 ($11,217 \pm 909.5$); maximum width 140 attained at level anterior to vulva. Esophagus ($n = 18$) 775–905 (834 ± 33.7) long; 6.4–8.7% (7.5 ± 0.7) total body length. Valve at EIJ (17) 92–112 (101 ± 5.8) long, (17) 45–74 (66 ± 8.2) in maximum width. SVGO (17) 285–342 (306 ± 13.9), EXP (18) 305–482 (394 ± 54.6), and CP (18) 320–545 (421 ± 63.5) from cephalic extremity. Ovaries didelphic. Vulva opens as ventral transverse slit ($n = 18$) 79–85% (82 ± 2.0) of body length from anterior; cuticular inflations and fans absent. Perivulvar pores bilateral, located 195–205 posterolateral to vulva in subventral fields. Anterior infundibulum ($n = 11$) 185–292 (240 ± 30.8), anterior sphincter, including s1 and s2 ($n = 13$) 110–192 (149 ± 24). Posterior infundibulum ($n = 11$) 170–267 (231 ± 26.1), posterior sphincter, including s1 and s2 ($n = 13$) 98–162 (140 ± 16.7). Vestibule length ($n = 13$) 70–205 (144 ± 42.3). Total ovijector length ($n = 10$) 795–1,016 (911 ± 77.1). Eggs ovoid, with thin shell ($n = 90$ in 9 specimens) 62–82 (72 ± 5.9) long by 30–50 (41 ± 4.2) wide, oriented in single rows in anterior and posterior uterine limbs. Tail digitate, weakly inflated distally, lacking prominent annulations adjacent to tip, lacking synlophe, 142–218 (167 ± 19.8) in length.

Taxonomic summary

Host: African buffalo, *S. caffer caffer* (Sparman), type and only known host.

Localities: Type locality: In type host at Anaka Village, West Acholi District, Uganda; ca. 02°45'N, 032°10'E. Additional localities: (1) Queen Elizabeth National Park, Toro District, Uganda; ca. 00°19'N, 032°058'E; (2) Mpala Ranch, Kenya, 00°17'N, 036°53'E; (3) Hluhluwe-iMfolozi Park, KwaZulu-Natal, South Africa, 28°00'S, 031°43'E.

Specimens: Holotype male, USNPC 99545, in host No. 11 from type locality. Allotype female, USNPC 99546 in host No. 33 from Queen Elizabeth National Park, Uganda. Paratypes include (1) USNPC 66322.02, 7 males and 7 females in host No. 11; (2) USNPC 99551, 5 males and 2 females in host No. 33; (3) USNPC 99547, 5 females in host BN1-200, from the Mpala Ranch, Kenya; (4) USNPC 99548, 2 males and 1 female from host B13 at Hluhluwe-iMfolozi Park, South Africa; (5) USNPC 99549, 2 females from host C72 at Hluhluwe-iMfolozi Park, South Africa. Vouchers, USNPC 86939, include 2 female nematodes in host No. 33.

Etymology: *Africanastrongylus* is derived from the Latin, *Afer* for African, and from the Greek *strongylos* for round, denoting a nematode

or roundworm from Africa. The species name, *buceros*, is derived from the New Latin and Greek *boukeros* for oxlike horns, denoting the hornlike extensions on the anterior margin of the gubernaculum of the male, and a host in the subfamily Bovinae.

Remarks

Hoberg and Lichtenfels (1994) provided the first phylogenetic hypothesis for the monophyly of the Ostertagiinae and its relationship to the Haemonchinae within what was named the Graphidiinae clade. Conclusions from this study were corroborated by Durette-Desset et al. (1999) in demonstrating monophyly for the subclade, but with inclusion of *Graphidium* Raillet and Henry, 1909 as the basal taxon in the Ostertagiinae. In this interpretation, the previously recognized Graphidiinae subclade is equivalent to the proposed Haemonchidae for the sister taxa Ostertagiinae + Haemonchinae (Hoberg and Lichtenfels, 1994; Durette-Desset et al., 1999). We would suggest that inclusion of *Graphidium* remains problematic and is not otherwise compatible with Ostertagiinae.

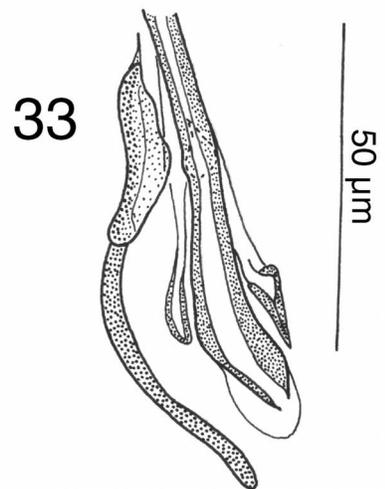
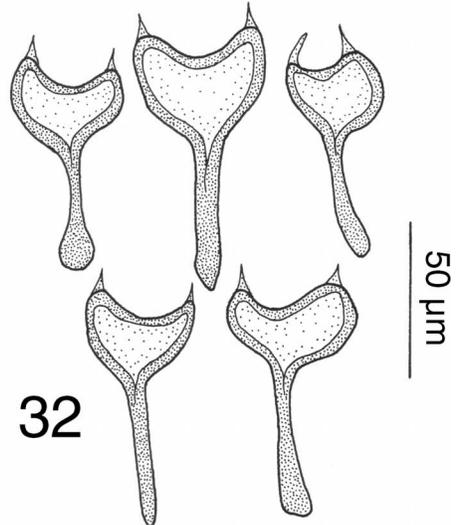
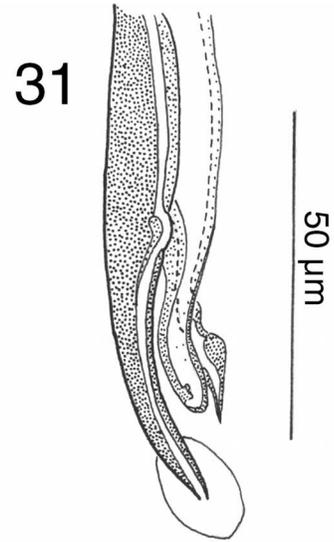
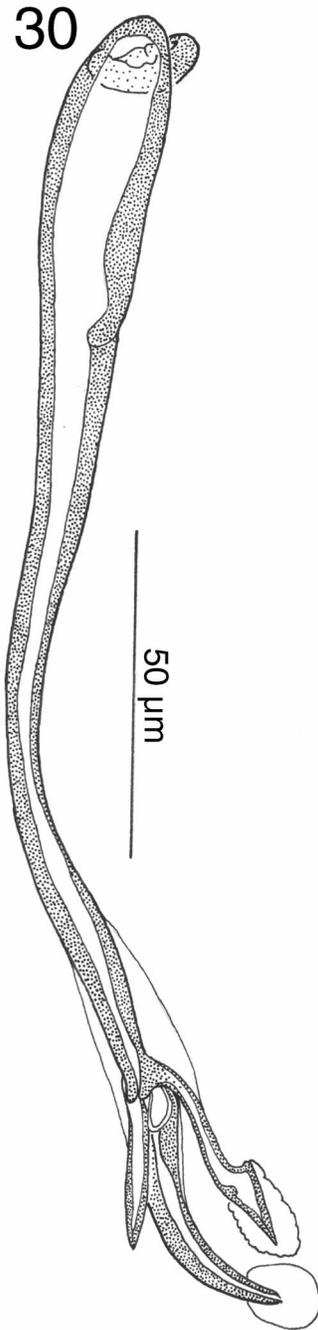
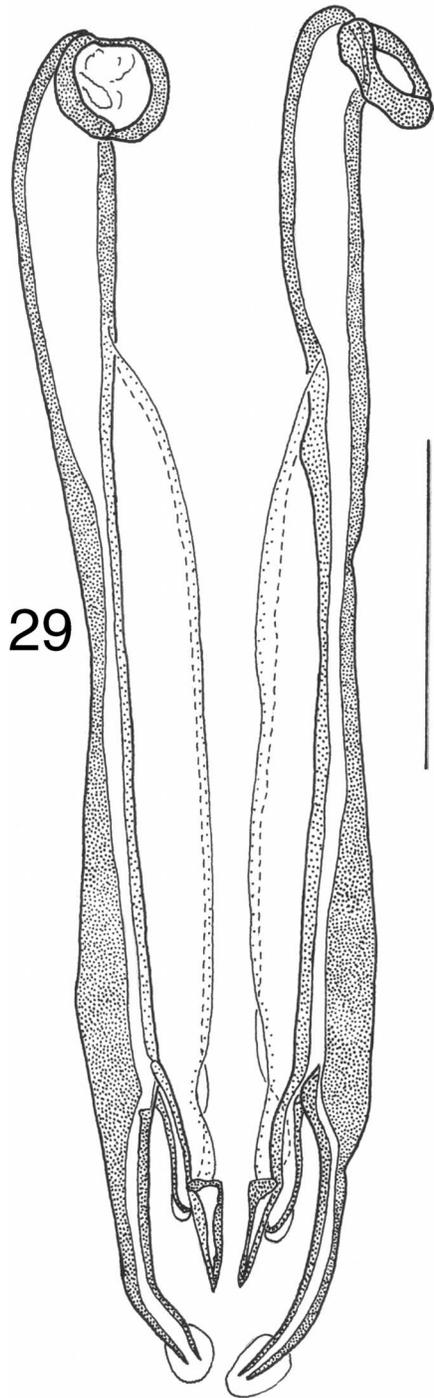
A morphological and phylogenetic diagnosis for the Ostertagiinae within Trichostrongyloidea and relative to their haemonchine sister group includes: (1) tripartite spicule tips; (2) spicules with an “ostertagiine window (a foramenlike structure that is visible at point of trifurcation for the primary, dorsal and ventral processes of the spicule tips);” (3) paired “0” papillae; (4) membranous and simple accessory bursal membrane containing filamentous “7” papillae (modified in minor morphotypes for males of polymorphic species, e.g., Drózdź, 1995); and (5) prominent esophageal valve separating the basal esophagus from the intestine. Additionally, other diagnostic characters exhibit some level of homoplasy, including (1) a vulva with cuticular ornamentation in the form of irregular inflations (Hoberg et al., 1993a); (2) genera characterized by species with polymorphic males (Drózdź, 1995); and (3) certain tapering patterns of the cervical synlophe appear limited to taxa within the subfamily, but overall are not indicative of monophyly (e.g., Lichtenfels et al., 1988; Lichtenfels and Hoberg, 1993; Lichtenfels et al., 1993; Hoberg, 1996). A suite of putative synapomorphies proposed for the Ostertagiinae is not represented in *Graphidium*, and placement of this taxon may require further consideration, but is beyond the scope of the current study.

Currently, a maximum of 12 genera, diagnosed by a suite of attributes outlined above, are represented among the Ostertagiinae. Clarification for generic-level taxonomy of the ostertagiines was recently proposed (Hoberg and Abrams, 2007) in the context of a revision involving *Sarwaria caballeroi* (Chabaud, 1977). The basis for the taxonomy in the current article in part adopts facets of different proposals for synonymies and the validity of certain taxa (e.g., Andreeva, 1956; Drózdź, 1965; Durette-Desset and Chabaud, 1981; Durette-Desset, 1982; Gibbons and Khalil, 1982a; Durette-Desset, 1983, 1985, 1989; Jansen, 1989; Durette-Desset et al., 1999). Fundamental differences in bursal structure and the patterns for Rays 2/3, Rays 4/5, and Rays 6 serve to distinguish larger inclusive groups within the subfamily (Durette-Desset, 1983; Durette-Desset et al., 1999).

Among the Ostertagiinae, 6 genera are characterized by a bursal pattern of 2–1–2 (*Camelostongylus* Orloff, 1933; *Longistongylus* LeRoux, 1931; *Marshallagia* (Orloff, 1933), *Orloffia* Drózdź, 1965; *Ostertagia* Ransom, 1907; and *Pseudommarshallagia* (Roetti, 1941)). Alternatively, a 2–2–1 pattern is typical among 6 genera (*Cervicaprastrongylus* Gibbons and Khalil, 1982; *Hyostongylus* Hall, 1921; *Mazamastrongylus* Cameron, 1935; *Sarwaria* Drózdź, 1965; *Spiculop-*

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FIGURES 22–28. *Africanastrongylus buceros* gen. nov. et sp. nov., showing bursa and genital cone in male as depicted in line drawings of the holotype and paratypes. (22) Bursa, left lobe in ventral view of a paratype (USNPC 66322) showing 2–2–1 pattern of lateral rays, massive base for Rays 8, ventral disposition for inflated dorsal lobe and reduced Rays 9/10. (23) Bursa in right lateral view of a paratype (USNPC 66322) showing 2–2–1 pattern, miniscule proconus, simple accessory bursal membrane containing “7” papillae and ventral disposition of the dorsal lobe. (24) Dorsal (Rays 9/10) and externodorsal rays (Rays 8) in dorsal view of a paratype (USNPC 66322); note massive bases for Rays 8, robust or stout base of dorsal ray, and lateral thickenings of bursal membrane adjacent to the dorsal lobe. (25) Genital cone in right lateral view of a paratype (USNPC 66322) showing inflated dorsal lobe with robust but reduced Rays 9/10, accessory bursal membrane with “7” papillae, “0” papillae, and proconus. (26) Genital cone in ventral view of holotype (USNPC 99545) showing paired “0” papillae, incised or bilobate accessory bursal membrane and laterally inflated, ventrally incised, dorsal lobe and reduced Rays 9/10. (27) Genital cone in ventral view of a paratype (USNPC 66322). (28) Telamon and cuticularized support structure at cloaca in ventral view of a paratype (USNPC 66322) (same scales for Figs. 25–27).



teragia (Orloff, 1933); and *Teladorsagia* Andreeva and Satubaldin, 1954); further criteria for, and validity of, *Cervicaprastrongylus*, *Mazamastrongylus*, and *Sarwaria*, are reviewed elsewhere (Gibbons and Khalil, 1982b; Lichtenfels et al., 1993; Hoberg, 1996; Lichtenfels et al., 1996; Hoberg and Abrams, 2007).

Africanastrongylus gen. nov. is immediately distinguished from all species of *Camelostongylus*, *Longistongylus*, *Marshallagia*, *Orloffia*, *Ostertagia*, and *Pseudommarshallagia* by the structure of the 2–2–1 bursa in males (Durette-Desset, 1983); note the concept for *Camelostongylus* as proposed by Durette-Desset (1989) that subsumes many species of *Ostertagia* within this genus is not accepted here. Among this group of genera, species of *Longistongylus* typically possess narrow filamentous spicules and a substantially reduced dorsal lobe and ray (Gibbons, 1972, 1973, 1977) that appear superficially similar to *A. buceros*. Among species of *Longistongylus*, based on descriptions and examination of some representatives (Table I), the reduced lobe is not strongly inflated laterally or dorsally and remains in a dorsal position relative to the external dorsals or Rays 8. The dorsal ray, although stout, is narrow at the base and the bursa contains numerous and discrete fields of bosses. The “0” papillae are filamentous, of constant diameter, highly divergent, disposed in an arcuate pattern, terminate in bulbous expansions, and are enclosed in a bilobed membrane; a proconus is consistently absent. Further, the accessory bursal membrane in species of *Longistongylus* is highly reduced or modified, and is not simple or membranous, as seen in *Africanastrongylus*. Females of all species of *Longistongylus* are characterized by irregular cuticular inflations at the level of the vulva (Hoberg et al., 1993a).

Gibbons (1977) reviewed *Longistongylus* and proposed synonymies for *Kobusinema* Ortlepp, 1963 and *Bigalkenema* Ortlepp, 1963. The bursal pattern in species once referred to *Bigalkenema*, namely, *Longistongylus sabie* (Mönnig, 1932), *Longistongylus curvispiculum* (Gibbons, 1973), and *Longistongylus namaquensis* (Ortlepp, 1963) approaches a 2–2–1; however, the distal tips of Rays 4, 5, and 6 are all highly divergent, the dorsal lobe is not strongly defined, and the bases of Rays 8 and the dorsal ray are not massive (Mönnig, 1933; Ortlepp, 1963; Gibbons, 1973, 1977).

Among ostertagiines with a 2–2–1 bursa, *Africanastrongylus buceros* can be distinguished in the following manner. In *Spiculoptera* and *Mazamastrongylus*, the absence of a proconus, Rays 4 < 5 in length, robust Rays 4, presence of a unique hood-ridge system in the ventral cervical synlophe, and a liplike and protruding excretory pore (Andreeva, 1958; Lichtenfels et al., 1993; Hoberg, 1996; Hoberg and Khrustalev, 1996) differentiate these genera from *Africanastrongylus*. Further, among species of *Spiculoptera*, males are polymorphic and spicules are adorned with prominent fanlike membranes. In *Cervicaprastrongylus* and *Hyostongylus*, the structure of the parallel cervical synlophe (Type 2 lateral), absence of a proconus, a bursa with Rays 4/5 parallel and not divergent distally, elongate Rays 8, and an elongate dorsal ray (Gibbons and Khalil, 1982a, 1982b; Durette-Desset et al., 1992; Hoberg et al., 1993b) contrast with this suite of attributes in *Africanastrongylus*. Compared to *Teladorsagia*, polymorphism among males, a robust Rays 4, an elongate dorsal ray and lobe, elongate and relatively straight Rays 8, and absence of a proconus (Andreeva, 1956, 1958; Drózd, 1965, 1995; Hoberg et al., 1999) represent consistent differences relative to *Africanastrongylus*.

Africanastrongylus buceros is morphologically similar but distinct from species of *Sarwaria*. Species of both genera are characterized by a tapering, Type 1, lateral synlophe, miniscule but thornlike cervical papillae, and a reduced but laterally inflated dorsal lobe disposed ventrally to Rays 8 (Lichtenfels et al., 1996; Hoberg and Abrams, 2007). In *Africanastrongylus*, Rays 2/3 are initially divergent and distally convergent, whereas Rays 4/5 are subequal in length, parallel through their

length, and divergent distally; Rays 8 are massive and medially curved, and both a proconus and gubernaculum are present. *Sarwaria*, including *Sarwaria bubalis* (Sarwar, 1956) and *S. caballeri* (Chabaud, 1977), however, contrasts in having Rays 2/3 weakly divergent along their entire length, Rays 4 < 5 in length, a robust Rays 4, a relatively elongate, narrow and straight Rays 8, and both a proconus and gubernaculum are absent (Drózd, 1965; Chabaud, 1977; Hoberg and Abrams, 2007). We propose *Africanastrongylus* as a previously unrecognized genus that is morphologically consistent with placement among the Ostertagiinae.

Among a diverse global assemblage, including 24 species and 7 genera of ostertagiines known from the African fauna (Table II), *A. buceros* gen. nov. et sp. nov. must also be differentiated from 2 problematic species, namely, *Ostertagia kenyensis* Gibbons and Khalil, 1980 in Damarara Dik Dik (*Madaqua kirkii* Günther) and Grant's gazelle (*Gazella granti* Brooke) and *Teladorsagia hamata* (Mönnig, 1932) in Springbok (*Antidorcas marsupialis* (Zimmerman)) and Bontebok (*Damaliscus pygargus* (Pallas)). The latter species, originally described in *Ostertagia* Ransom, 1907, was later transferred to *Spiculoptera* Orloff, 1933 by Travassos (1937), to *Apteria* Jansen, 1958 by Jansen (1958), and most recently to *Teladorsagia* Andreeva and Satubaldin, 1954 by Durette-Desset (1989). Gibbons and Khalil (1980) recognized the similarity of these nematodes, both with a 2–2–1 bursal formula, and distinguished *O. kenyensis* based on the configuration of the dorsal process of the spicules (lacking a prominent hooklike structure), and weakly curved and parallel Rays 4/5.

Paratype specimens of *O. kenyensis*, and a syntype male specimen of *T. hamata*, were in general agreement with original descriptions (Mönnig, 1932; Gibbons and Khalil, 1980). Observations of the structure of the synlophe and other attributes in *T. hamata* are limited to the single specimen available to us and the original description (Mönnig, 1932). Other type and voucher specimens of *T. hamata* were unfortunately lost in transit to the USNPC from the Onderstepoort Helminthological Collection.

New data on structural attributes of the synlophe, bursa, and spicules are partially described based on these specimens of *O. kenyensis* and *T. hamata*. The lateral synlophe in the cervical region is parallel and Type 2 and the cervical papillae are massive and thornlike; a greater number of ridges characterize *T. hamata* (Mönnig, 1932; Gibbons and Khalil, 1980). Overall, the structure and configuration of the bursa and bursal rays and dorsal lobe is similar; “7” papillae are contained in an accessory bursal membrane that is reduced and inconspicuous. The spicules are robust and massive, resembling those characteristic of minor morphotypes among the ostertagiines (Drózd, 1995) and have a simple ventral process and modified dorsal process. Additionally, spicules in paratypes of *O. kenyensis* were characterized by a weakly developed barb on the curved dorsal process, which is not visible in all orientations. Although these species exhibit extensive overlap in some meristic characters (Mönnig, 1932; Gibbons and Khalil, 1980; Tables III, IV), they can be unequivocally distinguished. We conclude the *O. kenyensis* and *T. hamata* are morphologically similar congeners representing an undetermined genus among the ostertagiines; a taxonomic decision regarding these species is deferred, and is considered beyond the scope of the current study.

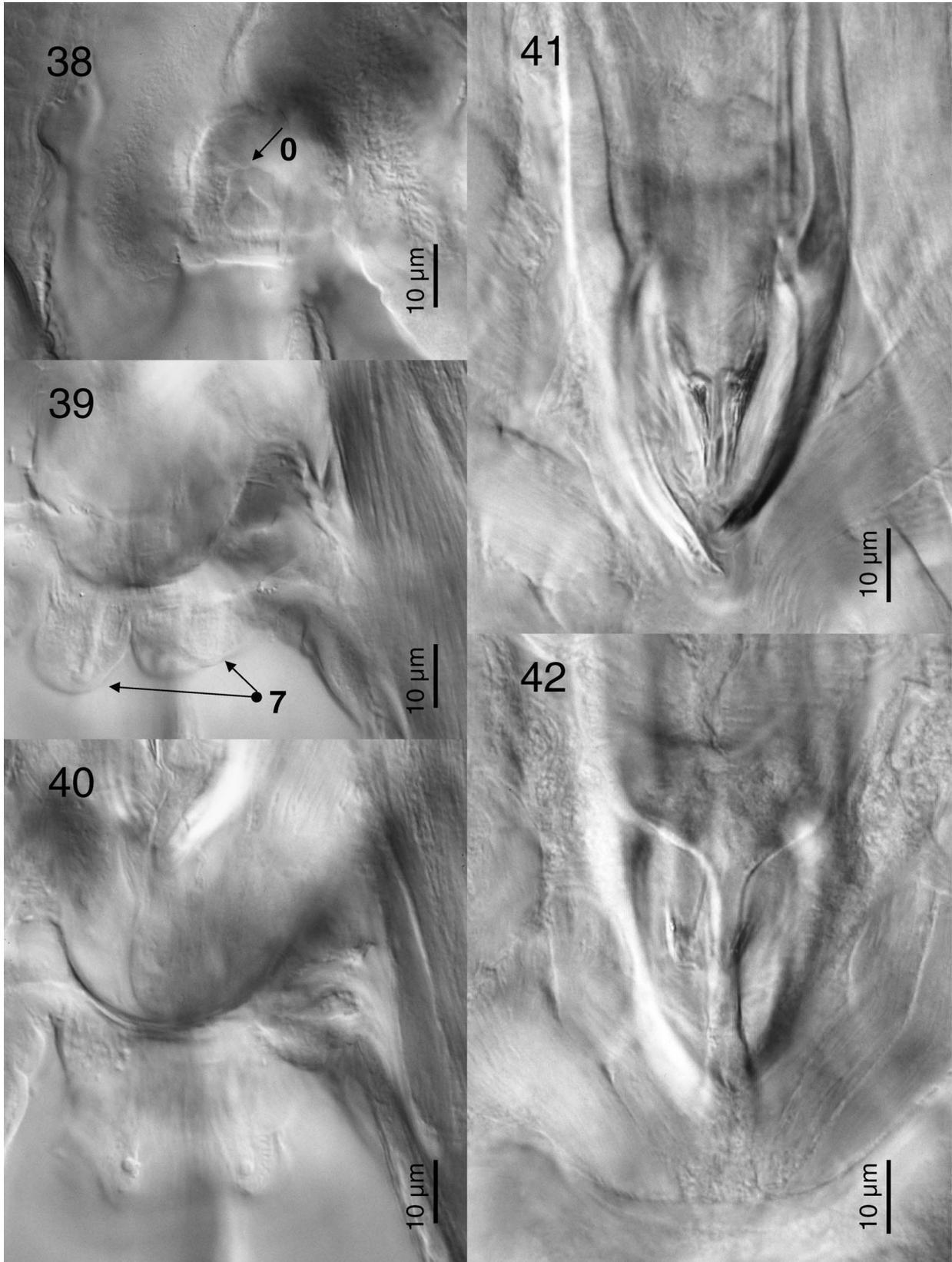
Together with *A. buceros*, specimens of *O. kenyensis* and *T. hamata* share a suite of characters, including a bursal formula of 2–2–1, where Rays 4/5 are subequal to equal in length, parallel, relatively straight and narrow, and which diverge distally at the tips adjacent to the bursal margin; Rays 2/3 are divergent throughout and become convergent distally. The dorsal lobe is strongly reduced, and curves ventrally relative to Rays 8 and the dorsal ray, or Rays 9/10, bifurcate in the distal half. In *O. kenyensis* the bursal margin adjacent to the dorsal lobe is thick-

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FIGURES 29–33. *Africanastrongylus buceros* gen. nov. et sp. nov., showing spicules and gubernaculum depicted in line drawings in the male holotype and paratypes. (29) Spicules in ventral view of holotype (USNPC 99545) showing alate structure with medially curved main processes, triangular ventral processes and simple, weakly pointed to rounded dorsal processes. (30) Spicule, left, in mediolateral view of paratype (USNPC 66322) showing bent or kinked main shaft, trifurcation of dorsal and ventral processes and the ostertagiine window. (31) Spicule, left, in dorsal view of a paratype (USNPC 66322) showing rounded, weakly pointed dorsal process. (32) Gubernaculum in ventral view of paratypes (USNPC 66322, 99548, 99551) showing shieldlike structure in anterior and hornlike processes consistent among all male specimens. (33) Gubernaculum and spicule in right lateral view of paratype (USNPC 66322) showing weakly S-shaped structure and relative positions.



FIGURES 34–37. *Africanastrongylus buceros* gen. nov. et sp. nov., showing male bursal attributes based on photomicrographs of paratypes. (34) Bursa in left lateral view (USNPC 66322) showing position of proconus (pc), “0” papillae (0), accessory bursal membrane and “7” papillae (7), and ventrally disposed dorsal lobe (dl). (35) Bursa in lateral view (USNPC 99548) showing bend in spicules and S-shaped gubernaculum. (36) Bursa in dorsal view (USNPC 66322) showing disposition of narrow, filamentous spicules, shieldlike anterior of gubernaculum, dorsal lobe, and lateral thickening of bursal membrane (arrows). (37) Dorsal lobe in ventral view (USNPC 66322) showing laterally inflated form and incision.



FIGURES 38–42. *Africanastrongylus buceros* gen. nov. et sp. nov., showing genital cone in male based on photomicrographs of holotype (USNPC 99545). (38) 0 papillae paired, ventral view (Figs. 38–40 are sequential from ventral to dorsal through single specimen). (39) Accessory bursal membrane in ventral view showing straight, filamentous “7” papillae (7) and bilobate or incised structure. (40) Dorsal lobe and Rays 9/10 in ventral view showing ventrally directed papillae near terminus of short, stout ray. (41) Spicule tips in ventral view showing triangular structure at termination of ventral processes and medially curved main shafts capped with hyaline tips. (42) Gubernaculum and dorsal processes of spicules in dorsal view; note plate or shieldlike structure of anterior gubernaculum and simple termination of dorsal processes.

TABLE II. Diversity for genera and species of Ostertagiinae in African ungulates and other mammalian hosts, with a listing of geographic localities and host records for the sub-Saharan region.

Species	Host species	Geographic localities	Authors*
<i>Cervicaprastrongylus</i> Gibbons and Khalil, 1982†			
<i>C. gabonensis</i> (Durette-Desset and Chabaud, 1974)‡	<i>Hyemoschus aquaticus</i>	Gabon	(14)
<i>C. moreli</i> (Durette-Desset and Denke, 1978)‡	<i>Lepus timidus</i>	Mali	(15)
<i>Hyostrongylus</i> Hall, 1921			
<i>H. kigeziensis</i> Durette-Desset et al., 1992‡	<i>Gorilla gorilla beringei</i>	Uganda	(16)
<i>H. okapiæ</i> (Berghe, 1937)‡§	<i>Okapia johnstoni</i>	Congo	(1)
<i>H. rubidus</i> (Hassall and Stiles, 1892)	<i>Cephalophus natalensis</i>	South Africa	(7)
<i>Longistrongylus</i> Le Roux, 1931‡			
<i>L. albifrontis</i> (Mönnig, 1931)‡	<i>Alcelaphus buselaphus</i> , <i>Antidorcas marsupialis</i> , <i>Damaliscus pygargus</i> , <i>Kobus ellipsiprymnus</i>	Chad, South Africa	(24, 31, 40, 41, 42, 43)
<i>L. banagiense</i> (Gibbons, 1972)‡	<i>Aepyceros melampus</i> , <i>Alcelaphus buselaphus</i> , <i>Damaliscus lunatum</i> , <i>Gazella granti</i> , <i>Gazella thomsonii</i> , <i>Oryx gazelle</i> , <i>Redunca</i> sp.	Kenya, Tanzania, Uganda	(18, 19)
<i>L. curvispiculum</i> (Gibbons, 1973)‡	<i>Aepyceros melampus</i> , <i>Antidorcas marsupialis</i> , <i>Connochaetes taurinus</i> , <i>Damaliscus lunatus</i> , <i>Damaliscus pygargus</i> , <i>Gazella granti</i> , <i>Gazella thomsonii</i> , <i>Neotragus moschatus</i> , <i>Pelea capreolus</i> , <i>Capra hircus</i> , <i>Ovis aries</i>	Kenya, Tanzania, South Africa	(6, 19, 22, 28, 29, 31, 32, 40, 41, 42, 43)
<i>L. meyeri</i> Le Roux, 1931‡	<i>Aepyceros melampus</i> , <i>Alcelaphus buselaphus</i> , <i>Connochaetes taurinus</i> , <i>Gazella granti</i> , <i>Gazella thomsonii</i>	Chad, Kenya, South Africa, Tanzania, Uganda	(2, 13, 20, 22, 24, 36, 43, 45, 52)
<i>L. namaquensis</i> (Ortlepp, 1963)‡	<i>Hippotragus equinus</i> , <i>Kobus ellipsiprymnus</i> , <i>Madoqua kirkii</i> , <i>Syncerus caffer</i> , <i>Capra hircus</i>	South Africa	(6, 28, 29, 31, 44)
<i>L. sabie</i> (Mönnig, 1932)‡	<i>Antidorcas marsupialis</i> , <i>Damaliscus pygargus</i> , <i>Pelea capreolus</i> , <i>Ovis aries</i>	Kenya, South Africa, Tanzania	(10, 20, 27, 39, 41, 42, 43, 46)
<i>L. schrenki</i> (Ortlepp, 1939)‡	<i>Aepyceros melampus</i> , <i>Gazella granti</i> , <i>Gazella thomsonii</i> , <i>Raphicerus melanotis</i> , <i>Redunca arundinum</i> , <i>Sylvicapra grimmia</i> , <i>Bos taurus</i>	Kenya, Mozambique, South Africa, Tanzania, Uganda	(6, 7, 10, 11, 13, 20, 24, 43, 52)
<i>L. thalæ</i> (Troncy and Graber, 1932)‡	<i>Cephalophus natalensis</i> , <i>Hippotragus equinus</i> , <i>Kobus ellipsiprymnus</i> , <i>Kobus kob</i> , <i>Kobus</i> sp., <i>Madoqua kirkii</i> , <i>Ourebia ourebi</i> , <i>Pelea capreolus</i> , <i>Redunca arundinum</i> , <i>Redunca</i> sp., <i>Alcelaphus buselaphus</i> , <i>Hippotragus equinus</i> , <i>Ourebia ourebi</i>	Central Africa, Kenya	(21, 48)
<i>Ostertagia</i> Ransom, 1907			
<i>O. angusdunnii</i> (Gibbons and Khalil, 1980)‡	<i>Taurotragus oryx</i>	Kenya	(23)
<i>O. harrisi</i> (Le Roux, 1930)‡	<i>Cephalophus natalensis</i> , <i>Tragelaphus angasii</i> , <i>Tragelaphus scriptus</i> , <i>Capra hircus</i> (Angora Goat, Boer Goat)	South Africa	(4, 7, 8, 10, 35, 43, 50)
<i>O. neveuilemairi</i> Gutterres, 1947‡	<i>Alcelaphus</i> sp., <i>Hippotragus equinus</i> , <i>Ourebia ourebi</i> , <i>Bos taurus</i> , <i>Ovis aries</i>	Congo	(26)

TABLE II. Continued.

Species	Host species	Geographic localities	Authors*
<i>O. ostertagi</i> Ransom, 1972‡#	<i>Redunca arundinum</i> , <i>Tragelaphus strepsiceros</i> , <i>Bos taurus</i> , <i>Capra hircus</i> (Angora Goat, Boer Goat)	South Africa	(9, 10, 27, 30)
<i>O. siassokoi</i> Diaouré, 1964‡	<i>Sylvicapra grimmia</i>	Congo	(12)
<i>O. triquetra</i> Boomker and Durette-Des- set, 2003‡	<i>Pelea capreolus</i>	South Africa	(3, 5, 6, 29)
<i>Ostertagia</i> sp.	<i>Aepyceros melampus</i> , <i>Syncerus caffer</i> , <i>Tragelaphus angassi</i>	South Africa, Uganda	(2, 4, 13, 42)
<i>Pseudomarschallagia</i> (Roetti, 1941)‡¶	<i>Ovis aries</i> , <i>Capra hircus</i>	Ethiopia	(25, 47, 53)
<i>Marshallagia</i> (Orloff, 1933)	<i>Ovis aries</i>	South Africa	(27)
<i>M. marshalli</i> (Ransom, 1907)¶	<i>Bos taurus</i>	Uganda	(2)
<i>Marshallagia</i> sp.¶			
<i>Teladorsagia</i> Andreeva and Saubaldin, 1954**	<i>Cephalophus maxwellii</i> , <i>Cephalophus natalensis</i> , <i>Damaliscus albifrons</i> , <i>Gazella thomsonii</i> , <i>Pelea capreolus</i> , <i>Raphicerus melanotis</i> , <i>Sylvicapra grimmia</i> , <i>Taurotragus oryx</i> , <i>Tragelaphus angasii</i> , <i>Tragelaphus strepsiceros</i> , <i>Bos taurus</i> , <i>Ovis aries</i>	Kenya, South Africa, Zambia	(2, 7, 10, 17, 27, 30, 33, 34, 35, 37, 38, 40, 42)
<i>T. circumcincta</i> (Stadelman, 1894)¶	<i>Capra hircus</i> (Angora Goat, Boer Goat)		
Ostertagiines of undetermined affinities			
<i>Ostertagia kenyensis</i> Gibbons and Khalil, 1980‡††	<i>Gazella grantii</i> , <i>Madoqua kirkii</i>	Kenya	(23)
<i>Teladorsagia hamata</i> (Mönnig, 1932)‡††	<i>Anitidorcas marsupialis</i> , <i>Damaliscus pygargus</i>	South Africa	(31, 41, 43, 49)
<i>Africanastrongylus</i> gen. nov.‡	<i>Syncerus caffer</i>	Kenya, Uganda, South Africa	Current study
<i>A. buceros</i> n. sp.‡			

* Authors: (1) Berghe (1937); (2) Bwangamoi (1968); (3) Boomker (1990); (4) Boomker et al. (1996); (5) Boomker and Durette-Desset (2003); (6) Boomker and Horak (1992); (7) Boomker et al. (1991a); (8) Boomker et al. (1991b); (9) Boomker et al. (1991); (10) Boomker, Horak, and Maelvor (1989); (11) Cruz e Silva (1971); (12) Diaouré (1964); (13) Dinnik et al. (1963); (14) Durette-Desset and Chabaud (1974); (15) Durette-Desset and Denke (1978); (16) Durette-Desset et al. (1992); (17) Gebauer (1932); (18) Gibbons (1972); (19) Gibbons (1973); (20) Gibbons (1974); (21) Gibbons (1981); (22) Gibbons and Khalil (1976); (23) Gibbons and Khalil (1980); (24) Graber (1969); (25) Graber and Delavenay (1978); (26) Gutierrez (1947); (27) Horak (1981); (28) Horak, Brown, et al. (1982); (29) Horak, de Vos, and De Klerk (1982); (30) Horak et al. (1991); (31) Horak, Meltzer, and de Vos (1982); (32) Khalil and Gibbons (1976); (33) Keep (1971); (34) Le Roux (1929); (35) Le Roux (1930); (36) Le Roux (1931); (37) Le Roux (1932); (38) Le Roux (1950); (39) Meeser (1952); (40) Mönnig (1931); (41) Mönnig (1932); (42) Mönnig (1933); (43) Ortlepp (1961); (44) Ortlepp (1963); (45) Pester and Laurence (1974); (46) Pletcher et al. (1984); (47) Roetti (1941); (48) Tronev and Graber (1973); (49) Verster et al. (1975); (50) Vincent et al. (1968); (51) Yeh (1956); (52) Unpublished records established by M. Kinsella and V. Ezenwa include *Madoqua kirkii* from Kenya as a host for *L. schrenki* and *L. meyeri*; (53) Tembley et al. (1997).

† Considered a synonym of *Hyostromylus* by Durette-Desset (1983), and as an independent genus by Gibbons and Khalil (1982a, 1982b) and Hoberg et al. (1993b).
‡ Considered to be endemic to Africa.

§ Originally described in *Ostertagia*, later transferred to *Hyostromylus* by Jansen (1958), and then to *Bergheia* Drózdík (1965); see history for this species outlined by Jansen (1958), Drózdík (1965) and Gibbons and Khalil (1982a).
¶ Considered to have been introduced to Africa from Eurasia.

Records for *O. ostertagi* in domestic ungulates are not exhaustive.
¶ Considered a synonym of *Longistromylus* by Durette-Desset (1983), and independent by Gibbons (1981); records listed here for *P. elongata* are not exhaustive.

** *Teladorsagia circumcincta* here includes *T. trifurcata* and *T. davitiani*, which in many reports may have been considered as separate, rather than as morphotypes within a single polymorphic species (e.g., Drózdík, 1995). Records reported are not exhaustive for geographic and host distribution in domestic ungulates.
‡† *Teladorsagia hamata* and *Ostertagia kenyensis* are morphologically similar and likely to be congeneric, but are not consistent with any of the known genera of the Ostertagiinae.

TABLE III. Morphometric comparisons for male specimens of *Africanastrongylus buceros* gen. nov. et sp. nov., *Teladorsagia hamata* and *Ostertagia kenyensis*.

Characters	<i>Africanastrongylus buceros</i>	<i>Teladorsagia hamata</i> *	<i>Ostertagia kenyensis</i> †
Number examined‡	12	—	2
Body length	(10) 6,350–8,555 (7,471 ± 642.70)	6,600–7,850	9,740–12,110
Esophagus length§	(11) 688–825 (757 ± 49.65)	710–800	776–943
Esophagus % of body length	(10) 9.4–11.3 (10.1 ± 0.69)	10.2–10.7	7.8–8.0
Esophageal-intestinal valve length	(10) 80–90 (91 ± 5.48)	71	129
Esophageal-intestinal valve width	(10) 48–75 (56 ± 7.93)	39	64
Nerve ring§	(8) 250–335 (303 ± 25.61)	240–290	—
Subventral esophageal gland orifices§	(10) 230–310 (276 ± 25.15)	—	—
Excretory pore§	(10) 305–421 (370 ± 31.16)	Near cervical papillae	315–378
Cervical papillae§	(11) 330–445 (395 ± 32.04)	330–420	329–414
Spicule length, left	(14) 195–246 (212 ± 14.08)	161–191	186–210
Spicule, left, % trifurcation	(13) 76–83 (79 ± 2.2)	60	60
Spicule, length, right	(13) 190–240 (207 ± 15.19)	161–191	186–210
Spicule, right, % trifurcation	(12) 76–83 (79 ± 2.6)	60–61	60–62
Gubernaculum length	(12) 60–82 (67 ± 5.9)	112	95–129
Gubernaculum width	(10) 35–42 (38 ± 1.8)	—	—

* Based on original description by Monnig (1932), and observations from a single male syntype.

† Based in part on original description by Gibbons and Khalil (1980), and examination of 2 male paratype specimens.

‡ Numbers of individual specimens examined.

§ Measured from anterior, cephalic extremity.

|| Percentage from anterior to trifurcation of spicules.

ened. Additionally it appears that males of these species are monomorphic, although this requires confirmation through assessment of larger numbers of specimens in individual hosts.

Africanastrongylus buceros is distinguished, however, from *O. kenyensis* and *T. hamata* in the following manner: (1) tapering Type 1 synlophe (parallel Type 2 in *O. kenyensis* and *T. hamata*); (2) miniscule

and thornlike cervical papillae; (3) midbody ridges numbering >56 in males and >45 in females (about 25–29 in *O. kenyensis*; about 35 in *T. hamata*); (4) presence of a proconus (absent in *O. kenyensis* and *T. hamata*); (5) membranous accessory bursal membrane containing divergent “7” papillae; (6) massive Rays 8 and Rays 9/10 (in *O. kenyensis* and *T. hamata* these rays have bases that are not inflated); (7)

TABLE IV. Morphometric comparisons for female specimens of *Africanastrongylus buceros* gen. nov. et sp. nov., *Teladorsagia hamata* and *Ostertagia kenyensis*.

Characters	<i>Africanastrongylus buceros</i>	<i>Teladorsagia hamata</i> *	<i>Ostertagia kenyensis</i> †
Number examined‡	18	—	2
Body length	(18) 9,712–12,610 (11,217 ± 909.5)	8,090–11,020	13,230–15,120
Esophagus length§	(18) 775–905 (834 ± 33.7)	710–860	893–1,057
Esophagus % of body length	(18) 6.4–8.7 (7.5 ± 0.7)	7.8–8.8	6.7–7.0
Esophageal-intestinal valve length	(17) 92–112 (101 ± 5.8)	—	112
Esophageal-intestinal valve width	(17) 45–78 (66 ± 8.2)	—	57
Nerve ring§	(10) 270–362 (317 ± 31.6)	240–290	—
Subventral esophageal gland orifices§	(17) 285–342 (306 ± 13.9)	—	—
Excretory pore§	(18) 305–482 (394 ± 54.6)	Near cervical papillae	306–381
Cervical papillae§	(18) 320–545 (421 ± 63.5)	320–420	320–410
Vulva position§	(18) 8,075–10,275 (9,239 ± 648)	6,750–9,260	11,050–12,600
Vulva % body length	(18) 79–85 (82 ± 2.0)	83–84	83–84
Ovejector total length	(10) 795–1,016 (911 ± 77.1)	—	381–827
Anterior infundibulum length	(11) 185–292 (240 ± 30.8)	—	129–229
Anterior sphincter length#	(13) 110–192 (149 ± 23.9)	—	—
Vestibule length	(13) 70–205 (144 ± 42.3)	—	—
Posterior infundibulum length	(11) 170–267 (231 ± 26.1)	—	133–219
Posterior sphincter length#	(13) 98–162 (140 ± 16.7)	—	—
Egg length	(90) 62–82 (72 ± 5.9)	71	70–84
Egg width	(90) 30–50 (41 ± 4.2)	39	41–54
Tail length	(15) 142–218 (167 ± 19.8)	176–190	143–219

* Based on original description by Monnig (1932). Type or voucher specimens of females of this species were not available for examination.

† Based in part on original description by Gibbons and Khalil (1980), and examination of 2 paratype specimens.

‡ Numbers of individual specimens examined.

§ Measured from anterior, cephalic extremity.

|| Complete ovijector, combining infundibula, sphincters, and vestibule.

Combining Sphincter s1 and s2, consistent with Lichtenfels et al. (2003).

absence of numerous fields of bursal bosses (numerous in *O. kenyensis*; absent in *T. hamata*); (8) the structure and dimensions of the alate gubernaculum with anteriorly directed horns (in *T. hamata* and *O. kenyensis* the gubernaculum is irregularly narrow); (9) structural differences in the spicule tips including the barbed and triangular ventral process and simple dorsal process of near equal length; (10) narrow, filamentous spicules; (11) substantially longer spicules; and (11) trifurcation of the spicule tips at 76–83% from the anterior (60% in *O. kenyensis* and *T. hamata*) (Tables III, IV). Differences in the synlophe, genital cone, and bursal structure relative to *A. buceros* are those that separate genera. The generic placement of *T. hamata* and *O. kenyensis* remains undetermined, as neither species conforms to known ostertagiines with a 2–2–1 bursal pattern.

Africanstrongylus buceros is somewhat unusual among the ostertagiines in that males appear to have consistently greater numbers of ridges than females at all levels of the body. The only other report of this phenomenon of which we are aware is in *Longistrongylus thalae* (Troncy and Graber, 1973). In multiple specimens of *L. thalae* examined by Boomker and Durette-Desset (1997), there were 44–51 ridges in males and 42–45 in females at the level of the midbody. Males of *L. thalae* have a bursal formula of 2–1–2 and differ in other structural attributes relative to *A. buceros* (Troncy and Graber, 1973; Gibbons, 1981; Boomker and Durette-Desset, 1997).

DISCUSSION

Dilemma of ostertagiine generic taxonomy

Recognition of *A. buceros* gen. nov. et sp. nov. represents a dilemma for generic taxonomy among the ostertagiines, and highlights the continuing difficulty in establishing taxonomic limits and in defining unequivocal phylogenetic criteria for species groups within the subfamily. Although we have a reasonable understanding of phylogenetic criteria for the subfamily and hypotheses for a suite of synapomorphies that diagnose this larger taxon (Durette-Desset, 1983; Hoberg and Lichtenfels, 1994; Durette-Desset et al., 1999), the problematic nature of generic taxonomy remains. It appears accepted that differences in the 2–2–1 and 2–1–2 bursa, the configuration of lateral rays, dorsal lobe, and the structure of the synlophe, represent fundamental criteria in diagnosing genera and assemblages of genera within Ostertagiinae (e.g., Andreeva, 1956, 1958; Drózdź, 1965; Durette-Desset and Chabaud, 1981; Gibbons and Khalil, 1982a; Durette-Desset, 1982, 1983, 1985, 1989; Jansen, 1989; Lichtenfels and Hoberg, 1993; Lichtenfels et al., 1993; Hoberg, 1996; Durette-Desset et al., 1999). It remains uncertain, however, when generic diagnoses should be emended to recognize the discovery of previously unknown diversity.

In establishing *Africanstrongylus*, we had 2 options: (1) extensively emend one or another of the existing genera to accommodate this species, or (2) recognize the apparent distinct nature of these nematodes relative to what we currently know about ostertagiine diversity. In the absence of a generic-level phylogeny, these alternatives each represent introduction of potential errors in a system where the goal should be to delineate monophyletic taxa or lineages as a basis for taxonomy. Thus, an incorrect inclusion of *A. buceros* among *Longistrongylus* or *Sarwaria* would confuse our potential interpretations of character evolution, biogeography, and host association if this species is actually not associated with either of these lineages. As a consequence, we consider our decision to recognize the distinct nature of *A. buceros* by establishing the new genus as conservative. As genetic, molecular, and morphological criteria increasingly become established with more extensive taxon sampling within this group, it will become possible to fully

evaluate the hypothesis that *Africanstrongylus* represents. Concurrently, the problematic nature and incompatibility for the current taxonomy of *O. kenyensis* in *Ostertagia* and *T. hamata* in *Teladorsagia* remains apparent.

Ostertagiines in African buffalo

Wild African buffalo, or Cape buffalo, from the West Acholi District and the Queen Elizabeth National Park, Toro District, Uganda in the late 1960s, from Laikipia, Kenya in 2000, and from Hluhluwe-iMfolozi Park, South Africa in 2006, were infected with a previously undescribed species of ostertagiine nematode. We have established *A. buceros* for this unique abomasal nematode. There are relatively few reports of ostertagiine or trichostrongyloid nematodes as abomasal parasites in African buffalo (Table II), and these have been limited to *L. meyeri* and *Ostertagia* sp. from Uganda (Dinnik et al., 1963; Bwangamoi, 1968); *A. lerouxi* Diaouré, 1964 from Congo (Diaouré, 1964); *H. bedfordi* Le Roux, 1929 from Uganda (Dinnik et al., 1963) and South Africa (Le Roux, 1929; Ortalepp, 1961; V. O. Ezenwa, data not shown); *H. contortus* (Rudolphi, 1803) from Kenya and South Africa (Curson, 1928; Ezenwa, 2003); and *H. placei* Place, 1893 from Kenya (Ezenwa, 2003).

Ostertagiine diversity in Africa

Ostertagiines in the African fauna now include 25 species, representing 8 genera (Table II); among these, 21 species in 7 genera are apparently endemic to Africa, whereas 4 species in 4 genera have been introduced. Species diversity for *Longistrongylus* (8 species), *Africanstrongylus* (1), and *Pseudomarsshallagia* (1) is restricted to Africa, with primary distributions among Antelopinae, Bovinae, Cephalophinae, and Hippotraginae. Although the latter genus has thus far only been reported in domestic caprines, species of *Longistrongylus* are also known as incidental parasites in sheep (Gibbons and Khalil, 1976). Endemic species from Africa are represented among *Hyostrongylus* (2) in gorillas and okapi (Berghe, 1937; Durette-Desset et al., 1992) and among *Cervicaprastrongylus* (2) in leporids and chevrotains (Durette-Desset and Chabaud, 1974; Durette-Desset and Denke, 1978), but additional diversity in these genera is distributed in Eurasia (Gibbons and Khalil, 1982b; Hoberg et al., 1993b). Durette-Desset (1983, 1989) reduces *Bergheia* Drózdź, 1965 and *Cervicaprastrongylus* as synonyms of *Hyostrongylus*. The status of *Hyostrongylus okapiae* (Berghe, 1937), although retained here in *Hyostrongylus*, remains to be determined and will require additional and new specimens from okapi (Gibbons and Khalil, 1982b).

In Africa, *Ostertagia* constitutes a mosaic of endemic species (5, with exclusion of *O. kenyensis*) among Antelopinae, Bovinae, Cephalophinae, and Hippotraginae, and a single introduced species (*Ostertagia ostertagi*) found in domestic and wild ungulates. Additionally, *Hyostrongylus rubidus*, *Marshallagia marshalli*, and *Teladorsagia circumcincta*, including minor morphotypes for the latter, have been introduced and distributed in Africa coincidental with independent translocations and establishment of domestic swine, cattle, sheep, or goats (e.g., Daubney, 1933).

Placement for either *O. kenyensis* or *T. hamata* remains unresolved. Neither appears morphologically consistent with any known genus attributed to the Ostertagiinae. Among the group

of 7 genera having a 2–2–1 bursa and either a tapering or a parallel lateral synlophe, a suite of structural characters would negate an unequivocal diagnosis for either species. Interestingly, specimens of both *T. hamata* and *O. kenyensis* are most similar to those attributed to minor morphotypes among the ostertagiines (e.g., Drózdź, 1995) with robust spicules which trifurcate near 60% from the anterior, and a cuticularized and reduced accessory bursal membrane. Specimens of *T. hamata* have not been found in association with a putative major morphotype (Mönnig, 1932; Ortlepp, 1961; Verster et al., 1975; Horak et al., 1982), whereas *O. kenyensis* has not been reported since the original description (Gibbons and Khalil, 1980). A proposal to establish and diagnose another genus among the ostertagiines for *O. kenyensis* and *T. hamata* is deferred until such time as sufficient specimens become available for comparative studies.

Round (1968) includes a record for *Camelostrongylus mentulatus* (Railliet et Henry, 1909) in *Gazella dama* (Pallas), but this represents specimens collected from captive animals in a zoo; other records from Africa are lacking. Additionally, specimens referred to as *Camelostrongylus harrisi* (Le Roux, 1930) and *Camelostrongylus* sp. by Boomker et al. (1996) are correctly placed in *Ostertagia*. *Camelostrongylus* should be retained only for *C. mentulatus*, and confusion over the taxonomy of *Ostertagia* and *Camelostrongylus* emanates from nomenclatural decisions proposed by Durette-Desset (1989).

Structure of the African ostertagiine fauna

The African ostertagiine fauna is a complex mosaic reflecting historical processes across relatively deep to shallow temporal scales. Endemic faunas have origins associated with dispersal and biotic expansion from Eurasia into Africa and subsequent radiation for ungulates and their parasites extending from the late Tertiary. In Africa, structure of the fauna was likely to have been influenced by the differential timing of expansion events from Eurasia and periods of occupation for respective pecoran groups, including Antelopinae, Bovinae, Hippotraginae, Reduncinae, and others since the Miocene, in parallel to radiation among species of *Haemonchus* (Vrba 1985, 1995; Vrba and Schaller, 2000; Hoberg et al., 2004). Subsequently, domestication and later translocations during the Holocene for cattle and sheep (Ryder, 1984; Loftus et al., 1994) influenced distribution and diversity for trichostrongylid faunas (e.g., Daubney, 1933). Mosaic faunas among ungulate nematodes have now been demonstrated for all biogeographic regions (e.g., Hoberg et al., 1999, 2001, 2004; Hoberg, 2005).

Among 13 genera of the Ostertagiinae in the global fauna, 3 are entirely limited in distribution to Africa, including *Africanaststrongylus*, *Longistrongylus*, and *Pseudommarshallagia* (Table II); the number would increase to 4 of 14 genera if a new taxon were established for *T. hamata* and *O. kenyensis*. *Spiculostrongylus* among Cervidae and *Camelostrongylus* among antelopes and Caprinae, are the sole genera limited in distribution to Eurasia and the Palearctic; *Sarwaria* among Tragulidae and Bovinae appears limited to southern Asia. All other recognized genera are distributed in 2 or more biogeographic regions (discounting the influence of recent translocation). Among these, *Cervicaprastrongylus* among Tragulidae, Antelopinae, and Leporidae and *Hyostrongylus* among Suidae, Giraffidae, and Pon-

gidae, are found in Asia and Africa, whereas *Marshallagia*, *Mazamastrongylus*, *Orloffia*, *Ostertagia*, and *Teladorsagia* among artiodactyls occur across the Holarctic. Among approximately 130–140 nominal species of ostertagiines, based in part on lists compiled by Durette-Desset (1989) (discounting synonymies due to polymorphism among species of certain genera), 21 are limited to the African fauna. Thus, Africa is characterized by relatively few endemic species, but an apparently disproportionate number of endemic genera.

The diverse nature of the ostertagiine fauna may reflect the number and timing of episodic expansion events for artiodactyls into Africa from Eurasia during the Tertiary and Quaternary, their subsequent occupation times, and interactions with environmental variation over the past 3 million years (Hoberg and Brooks, 2008). Groups such as *Orloffia*, *Ostertagia*, *Marshallagia*, and *Teladorsagia*, or more generally trichostrongyloids among Cervidae and Caprinae (including the Nematodirinae), appear underrepresented or absent in the African fauna. Environmental tolerances established for such temperate and boreal adapted groups may have further limited expansion into African ecosystems (Hoberg et al., 2004; Hoberg, 2005).

Ostertagiines, other than species of *Longistrongylus*, contrast with Cooperiinae and Haemonchinae (*Haemonchus* and *Ashworthius*), as these latter taxa appear to have their greatest diversity centered in Africa, consistent with a history of radiation among artiodactyls (Gibbons, 1977, 1981; Durette-Desset, 1985; Hoberg et al., 2002, 2004). Cosmopolitan distributions for some species of *Haemonchus* and *Cooperia* were acquired subsequent to European exploration and a history of introductions from Africa after 1500 (Hoberg, 2005). Consequently, an understanding of the history and structure of parasite faunas in artiodactyls becomes increasingly important in defining the potential for translocation and establishment, geographic, and host colonization, and patterns of emergence for disease (Hoberg, 1997; Hoberg and Brooks, 2008). Baseline data are essential in formulating predictions about responses of complex host–parasite systems to ecological perturbation and climate change over time (Brooks and Hoberg, 2000; Hoberg et al., 2001; Hoberg, 2005; Brooks and Hoberg, 2006).

Biodiversity baselines are important in establishing a framework to document introductions and dissemination. Species of ostertagiines and haemonchines that could emanate from Africa as a source region have been recognized (Table II) (Hoberg et al., 2001). This concept was further validated by discovery of *L. sabie* in free ranging *Hippotragus niger* (Harris), *Addax nasomaculatus* (Blainville), and *Oryx gazelle* (Linnaeus), reported as *Oryx biesa*, from west Texas in a surrogate African ecosystem (Craig, 1993); *Longistrongylus curvispiculum* was also found in *Oryx dammah* (Cretzschmar), reported as *Oryx tao*, from England (Gibbons and Khalil, 1977). *Africanaststrongylus buceros* may represent yet another species with the potential for successful translocation with infected ungulate hosts (Hoberg et al., 2001). Introduction and establishment of helminths with otherwise tropical histories and adaptations may have eventual consequences linked to the cascading effects of habitat change driven by global warming (Hoberg et al., 2004). Equally significant is the recognition that ecological disruption is a primary driver for geographic and host colonization, the emergence of novel associations of hosts, parasites, and pathogens, and for

disease (Hoberg, 1997; Brooks and Hoberg, 2006; Hoberg and Brooks, 2008).

ACKNOWLEDGMENTS

We thank E. A. Harris of the Parasitic Worms Group, Department of Zoology, Natural History Museum, London, United Kingdom, for loan of specimens of *O. kenyensis*. We thank J. Boomker from the Department of Veterinary Tropical Diseases, University of Pretoria, South Africa, for access to African ostertagiines, including *T. hamata*. We thank M. Kinsella for referral of specimens that initiated the current study and for providing the image represented in Figure 35. We also thank P. Pilitt of the USNPC for reviews and comments on various drafts of this manuscript. Field collections for hosts and parasites by VOE in South Africa were funded by the National Science Foundation (DEB-0541762) and by the Division of Biological Sciences, University of Montana.

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