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DISCOVERY AND DESCRIPTION OF A NEW TRICHOSTRONGYLOID SPECIES (NEMATODA: OSTERTAGIINAE), ABOMASAL PARASITES IN MOUNTAIN GOAT, *OREAMNOS AMERICANUS*, FROM THE WESTERN CORDILLERA OF NORTH AMERICA

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ABSTRACT: *Marshallagia lichtenfelsi* sp. n. is a dimorphic ostertagiine nematode occurring in the abomasum of mountain goats, *Oreamnos americanus*, from the Western Cordillera of North America. Major and minor morphotype males and females are characterized and distinguished relative to the morphologically similar *Marshallagia marshalli*/*Marshallagia occidentalis* from North America and *Marshallagia dentispicularis*, along with other congeners, from the Palearctic region. The configuration of the convoluted and irregular synlophes in the cervical region of males and females of *M. lichtenfelsi* is apparently unique, contrasting with a continuous and parallel system of ridges among those species of *Marshallagia*, including *M. marshalli*/*M. occidentalis*, which have been evaluated. Specimens of *M. lichtenfelsi* are further defined by the rectangular form of the accessory bursal membrane (width > length) in the major morphotype and by the trapezoidal Sjöberg's organ in the minor morphotype, in addition to specific attributes of the spicules and spicule tips. We regard 12 species, including the proposed new taxon, to be valid. Primary diagnostic characters are reviewed for *Marshallagia* and a framework is presented for standardization of future descriptions incorporating the synlophes in males and females and the structure of the spicules and genital cone in major and minor morphotype males. The center of diversity for species of *Marshallagia* is the mountain–steppe region of central Eurasia where 11 species (including the Holarctic *M. marshalli*) are recognized in association with Caprini, Rupicaprini, and Antelopinae; only 2 species occur in the Nearctic. In this assemblage, *M. lichtenfelsi* is endemic to North America and limited in host distribution to mountain goats. An intricate history for refugial isolation and population fragmentation demonstrated for mountain goats and wild sheep indicates the potential for considerable cryptic diversity for *Marshallagia* and other nematodes. Shifting patterns of contact and sympatry among assemblages of ungulates during the Pleistocene are consistent with geographic and host colonization as a process involved in diversification of these parasites.

Species of *Marshallagia* Orloff, 1933 are typical abomasal parasites in free-ranging and domesticated ungulates, most often associated with the Caprinae from the Holarctic region (Boev et al., 1963; Govorka et al., 1988; Ivashkin et al., 1989; Hoberg et al., 2001). Diversity for these ostertagiines is centered in Eurasia, where numerous species have been described among an assemblage of Caprini and Rupicaprini (sporadic reports among Cervidae) across the region of mountain–steppe habitats circumscribed by western China, Tibet, Mongolia, Kazakhstan, and Azerbaijan (Appendix 1). Although a rich fauna characterizes the east-central Palearctic, only *Marshallagia marshalli* (Ransom, 1907)/*M. occidentalis* (Ransom, 1907), in the notation used to denote dimorphic males representing single species among the Ostertagiinae, has been recognized in North America, and this appears to have a broader Holarctic distribution (Wu and Shen, 1960; Boev et al., 1963).

Male conspecifics among *Marshallagia* spp. are characterized by polymorphism (Daskalov, 1974; Drózdź, 1974, 1995; Lancaster and Hong, 1981; Dallas et al., 2001), a phenomenon documented among 5 of the 15 genera of the Ostertagiinae (Hoberg and Abrams, 2008; Hoberg et al., 2009a). Discrete structural characters of the genital cone and spicules are associated with major morphotypes (referred to *Marshallagia*) and minor morphotypes (often referred to *Grosspiculagia* Orloff, 1933) which historically have been relegated to different nominal species, often in separate genera (e.g., Orloff, 1933; Gibbons and Khalil, 1982; Drózdź, 1995). Respective major morphotypes are recognized by their numerical dominance (relative to minor morphotypes) within infrapopulations involving single hosts and appear to represent a

balanced polymorphism (Daskalov, 1974; Drózdź, 1974, 1995; Hoberg and Abrams, 2008), although seasonal variation in relative abundance has been noted (e.g., Hoberg et al., 1999). Consistent with other Ostertagiinae, the recognition, application, and misapplication of polymorphism among males has considerably confused the taxonomy and recognition of species referred to *Marshallagia* over the past century (Drózdź, 1995; Hoberg et al., 1999).

At a minimum, based on current taxonomy and recognized nominal taxa, there are 11 dimorphic species in *Marshallagia*. Four species have both the major and minor morphotype characterized or identified; 7 are known only from the major morphotype (Appendix 1; Drózdź, 1995). Species limits remain poorly defined in this assemblage where subtle or cryptic morphological differences, incomplete descriptions, and circumscribed differential diagnoses hinder identification (e.g., Boev et al., 1963; Hu and Jiang, 1984; Luo et al., 1993). It is probable that some number of named taxa in Eurasia, particularly China, will be found as synonyms of previously established major or minor morphotypes. In these cases, access to unabridged descriptions (beyond often attenuated summaries in English), accurate detailed figures, and representative specimens is especially problematic and complicates the possibility of complete and direct comparisons among otherwise similar species and respective morphotypes (Appendix 1). Accordingly, comprehensive revision of *Marshallagia* appears warranted but is currently intractable.

These complications have also been confounded by inconsistent taxonomy applied in a diverse number of studies since the recognition of polymorphism as a typical phenomenon among the ostertagiines (Luo et al., 1991; Drózdź, 1995). Taxonomy proposed by Durette-Desset (1989) for *Marshallagia* and related ostertagiines is disregarded, as the phenomenon of polymorphism among male conspecifics was not recognized in her conclusions. Further, some taxonomies proposed in web-based and authoritative species lists are rejected as these often have not been validated, are incomplete,

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and do not recognize the problems or complications associated with polymorphism in these nematodes (Appendix 1).

In the current study, we explore the diversity of *Marshallagia* in North America and examine the implications of recognizing a previously undescribed species from the Nearctic. *Marshallagia marshalli* *M. occidentalis* was originally described based on major and minor morphotype males and a single female form found in domesticated sheep (*Ovis aries* Linnaeus) from Montana (Ransom, 1907, 1911). Subsequently, *M. marshalli* was found to be predominately a parasite of wild sheep (*Ovis canadensis* Shaw and *Ovis dalli* Nelson), mountain goats (*Oreamnos americanus* [de Blainville]), and pronghorn (*Antilocapra americana* [Ord]) from temperate to sub-Arctic latitudes of western North America (Luckner and Dikmans, 1945; Bergstrom, 1975a, 1975b; Hoberg et al., 2001) and also commonly occurs in muskoxen (*Ovibos moschatus* [Zimmermann]) and occasionally barren-ground caribou (*Rangifer tarandus groenlandicus* [Borowski]), Grant's caribou (*Rangifer tarandus granti* Allen), and Peary caribou (*Rangifer tarandus pearyi* Allen) at high latitudes of the Arctic (Kutz et al., 2012). A Holarctic distribution for *M. marshalli* *M. occidentalis* appears probable given the similarity in redescrptions for major and minor morphotypes attributable to this species from Eurasia, many of which have emanated from the Russian literature (Skrjabin et al., 1954; Andreeva, 1958; Boev et al., 1963; Ivashkin and Mukhamadiev, 1981). Conspicuity of *Marshallagia* across this spectrum of free-ranging hosts and a broad latitudinal gradient from the Arctic to temperate zones requires confirmation (Drózd, 1995; Hoberg et al., 1999; Dallas et al., 2001; Hoberg et al., 2001). It is possible that *Marshallagia*, in relation to host biogeography and historical patterns of expansion, fragmentation, and isolation (Hoberg, 2005; Shafer, Cullingham et al., 2010), represents an extensive and largely cryptic complex of ostertagiines similar to that which is being demonstrated among species of *Teladorsagia* (Hoberg et al., 1999; Leignel et al., 2002).

In this regard, Lichtenfels and Pilitt (1989) distinguished, but declined to name, an apparently undescribed species of *Marshallagia* associated with mountain goats from the Western Cordillera of North America, originally considered conspecific with *M. marshalli*. These nematodes were initially differentiated by characters of the cervical synlophe from specimens of *M. marshalli* *M. occidentalis* in wild and domesticated sheep and other ungulate hosts (Lichtenfels and Pilitt, 1989). Subsequently, new collections and discovery of nematodes in a mountain goat from central British Columbia have provided the basis for a more complete assessment of this putative species, which is likely to be endemic to North America.

In the current study, we propose establishment of a new species of *Marshallagia* and describe the major and minor forms and females of this polymorphic species. Materials were derived from the current collection and geographically disjunct localities spanning north-central British Columbia, the region near Banff and Jasper, Alberta in the central Canadian Rocky Mountains, and into Idaho, Montana, and Wyoming. Concurrently, we examined the type series and numerous representative specimens for *M. marshalli* *M. occidentalis* in multiple caprine hosts at disparate localities (some in relative sympatry with mountain goats) extending from Nunavut, Canada, through Alaska to Wyoming and Montana. Further, we examined a limited number of Eurasian species of *Marshallagia* that were available. These comparative studies provide the context for understanding the host and geographic distribution of this previously unrecognized species.

MATERIALS AND METHODS

Specimens examined

Nematodes in *Oreamnos americanus* were derived from materials held in the U.S. National Parasite Collection (USNPC) and through necropsy of a male mountain goat, collected following natural mortality, near the Ospika River, British Columbia by Pamela Hegenveld in March 2004 (Table I). Additional nematodes for comparative purposes from the USNPC were represented by the morphospecies *Marshallagia marshalli* (including the minor morphotypes designated as *Ostertagia occidentalis* or *M. occidentalis*) in free-ranging sheep (*Ovis canadensis*, *O. dalli*), muskoxen (*O. moschatus*), pronghorn (*Antilocapra americana*), and domesticated sheep (*Ovis aries* L.) from North America (Table I). Other specimens from Eurasian ungulates were made available by the K. I. Skrjabin Institute of Helminthology, Moscow (*Marshallagia dentispicularis* Asadov, 1954, *Marshallagia mongolica* Schumakovitsch, 1938, *Marshallagia schumakovitschi* Kadyrov, 1959, and *Ostertagia belockani* Asadov, 1954) or were held in the USNPC (*Marshallagia* sp. and *Ostertagia trifida* Guille, Marotel and Panisset, 1911) (Table II).

Microscopy

Nematodes were prepared as temporary whole mounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) and examined with interference contrast microscopy. The synlophe was examined in whole mounts, with particular attention given to the pattern of ridge systems in the cervical zone and their extent posteriorly, consistent with prior studies among the ostertagiines (Lichtenfels et al., 1988; Hoberg et al., 1999, 2009b). Patterns for the synlophe in the cervical region are defined according to Lichtenfels et al. (1988) and Lichtenfels and Pilitt (1989). Transverse sections were hand-cut with a cataract knife and mounted in glycerin jelly for 7 specimens representing 2 major morphotype and 3 minor morphotype males (USNPC 104774, 104776, USNPC 104917) and 2 females (USNPC 104917) in *O. americanus*. Sections were used to count the number of ridges at the mid-body and other regions of the body. This facilitated a comparison with data for the major and minor morphotypes of *M. marshalli* *M. occidentalis* from North American populations derived from Lichtenfels and Pilitt (1989) with the results of the current study.

Male and female nematodes were evaluated. Among males, the formula for bursal ray patterns and numbering of the bursal papillae are consistent with Chabaud et al. (1970) and Durette-Desset (1983). Structure and description of the ovejectors are consistent with Lichtenfels et al. (2003), except that demarcation between sphincter-1 and sphincter-2 was not visible in all specimens and, consequently, the anterior and posterior sphincters + vestibule 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 \pm 1 SD in parentheses. Meristic data in the description are derived from specimens collected at Ospika River (Table III); additional measurements from Lichtenfels and Pilitt (1989), representing a summary of original raw data in USNPC archives, are presented separately (Table IV). Data for *M. marshalli* *M. occidentalis* are based on a series of measurements of specimens, from various domesticated and free-ranging caprine hosts and a limited number of nematodes from pronghorn, conducted during the current study (Tables V–VII) and do not include prior data from Lichtenfels and Pilitt (1989).

Taxonomy for hosts follows Grubb (2005) in all text and tables. Hosts reported in the literature have been modified where necessary to conform to current taxonomy and usage.

RESULTS

DESCRIPTION

Marshallagia lichtenfelsi sp. n.

(Figs. 1–32)

General description: Trichostrongyloidea, Ostertagiinae, uncoiled, nematodes of small to medium dimensions, reddish-brown in color prior to fixation. Polymorphic, with 2 male morphotypes, single female morphotype. Cuticle with well-developed synlophe.

TABLE I. Specimens of *Marshallagia* spp. examined in the current study including *Marshallagia lichtenfelsi* sp. n. (type series from type and additional localities) and *Marshallagia marshalli*/*M. occidentalis* in free-ranging and domesticated ungulate hosts from North America.

USNPC*	Species	Host	Locality	Specimens†
45154	<i>Marshallagia lichtenfelsi</i> sp. n.	<i>Oreamnos americanus</i>	Alberta, Canada	1/ 1/ 0
45161	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	3/ 0/ 5
46225	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Idaho, U.S.A.	12/ 1/ 0
46298	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Wyoming, U.S.A.	26/ 3/ 4
46566	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Idaho, U.S.A.?‡	2/ 0/ 2
46575	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Idaho, U.S.A.?‡	3/ 4/ 0
46918	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	0/ 1/ 0
56702	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Wyoming, U.S.A.	15/ 0/ 10
58743	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	-----§
104773	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	1/ 1/ 2
104774#	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	22/ 7/ 10
104776#	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	5/ 9/ 9
104913	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	Alberta, Canada	0/ 1/ 0
104914¶	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	British Columbia	1/ 0/ 0
104915¶	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	British Columbia	0/ 0/ 1
104916¶	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	British Columbia	0/ 1/ 0
104917**	<i>M. lichtenfelsi</i> sp. n.	<i>Or. americanus</i>	British Columbia	33/ 8/ 35
45507	<i>Marshallagia marshalli</i>	<i>Antilocapra americana</i>	South Dakota	0/ 0/ 1
45555	<i>M. marshalli</i>	<i>A. americana</i>	Montana, U.S.A.	0/ 0/ 1
87957	<i>M. marshalli</i>	<i>A. americana</i>	Wyoming, U.S.A.	1/ 0/ 0
104770#	<i>M. marshalli</i>	<i>Or. americanus</i>	Alberta, Canada	1/ 0/ 0
104775#	<i>M. marshalli</i> / <i>Marshallagia occidentalis</i>	<i>Or. americanus</i>	Alberta, Canada	1/ 2/ 0
56742	<i>M. marshalli</i> / <i>M. occidentalis</i>	<i>Ovis canadensis</i>	Montana, U.S.A.	0/ 1/ 11
56743	<i>M. marshalli</i>	<i>O. canadensis</i>	Montana, U.S.A.	3/ 0/ 0
59207	<i>M. marshalli</i>	<i>O. canadensis</i>	Montana, U.S.A.	8/ 0/ 9
59745	<i>M. marshalli</i>	<i>O. canadensis</i>	British Columbia	5/ 0/ 0
59746	<i>M. occidentalis</i>	<i>O. canadensis</i>	British Columbia	0/ 4/ 0
66603	<i>M. occidentalis</i>	<i>O. canadensis</i>	Alberta, Canada	0/ 6/ 0
103047	<i>M. occidentalis</i>	<i>Ovis dalli</i>	Alaska, U.S.A.	0/ 4/ 0
103053	<i>M. marshalli</i>	<i>O. dalli</i>	Alaska, U.S.A.	4/ 0/ 0
103069	<i>M. marshalli</i>	<i>O. dalli</i>	Alaska, U.S.A.	1/ 0/ 8
103070	<i>M. occidentalis</i>	<i>O. dalli</i>	Alaska, U.S.A.	0/ 8/ 0
103090	<i>M. marshalli</i>	<i>O. dalli</i>	Alaska, U.S.A.	13/ 0/ 3
103091	<i>M. occidentalis</i>	<i>O. dalli</i>	Alaska, U.S.A.	0/ 5/ 0
104897	<i>M. marshalli</i>	<i>O. dalli</i>	Alaska, U.S.A.	0/ 0/ 8
91538	<i>M. occidentalis</i>	<i>Ovibos moschatus</i>	Nunavut, Canada	0/ 1/ 0
91559	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Nunavut, Canada	9/ 0/ 0
91570	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 1/ 0
92073	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 2/ 0
95953	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 0/ 10
96129	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 2/ 0
96254	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 3/ 0
96342	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 2/ 0
99164	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Nunavut, Canada	6/ 0/ 9
99165	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Nunavut, Canada	0/ 1/ 0
103053	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Nunavut, Canada	1/ 0/ 0
4689 (type)	<i>M. marshalli</i>	<i>Ovis aries</i>	Montana, U.S.A.	7/ 0/ 0
4691 (type)	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	0/ 2/ 0
14467	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	8/ 0/ 2
14488	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	1/ 0/ 0
14878	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	0/ 0/ 9
15587	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	0/ 1/ 0
15864	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Montana, U.S.A.	1/ 0/ 1
16219	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Colorado, U.S.A.	0/ 0/ 1
16315	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Colorado, U.S.A.	1/ 0/ 0
16320	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Colorado, U.S.A.	0/ 0/ 3

(Table I continued)

TABLE I. Continued.

USNPC*	Species	Host	Locality	Specimens†
16322	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Colorado, U.S.A.	0/ 0/ 1
16324	<i>M. occidentalis</i>	<i>Ov. moschatus</i>	Colorado, U.S.A.	0/ 1/ 0
29493	<i>M. marshalli</i>	<i>Ov. moschatus</i>	Idaho, U.S.A.	2/ 0/ 0

* Catalogue numbers from the U.S. National Parasite Collection.

† Specimens designated as forma major ♂/ forma minor ♂/ and ♀.

‡ Collection sites designated as "Idaho?" were originally listed as Pullman, Washington, a locality that is not within the geographic range for *Oreamnos americanus*. The field collector, O. J. Hummon, had however collected specimens from sites in Idaho and these appear to have been transported to the veterinary college at Washington State University located in Pullman, WA.

§ USNPC 58743, representing a mountain goat from Pinto Creek, Alberta was reported to have been *Marshallagia occidentalis* based on the original collection record, and these are likely to have been *M. lichtenfelsi*. These specimens could not be examined as they had been loaned to researchers at the University of Alberta and were not returned to the USNPC.

|| USNPC 58736 and 58738 represented mixed infections of *M. lichtenfelsi* and *Teladorsagia* cf. *boreoarcticus*; specimens of the latter are retained under the original numbers and those of *M. lichtenfelsi* are reallocated, respectively, to USNPC 104773 and 104913.

USNPC 58746 and 58748 represented mixed infections of *M. lichtenfelsi*, *M. marshalli*, and *T. cf. boreoarcticus*; specimens of *Teladorsagia* were retained in the original numbers. Specimens of *M. lichtenfelsi* and *M. marshalli* from 58746 were reallocated under USNPC 104774 and 104770, respectively. Specimens of *M. lichtenfelsi* and *M. marshalli* from 58748 were reallocated under USNPC 104776 and 104775, respectively.

¶ Holotype male (major morphotype), allotype female, and paratype male (minor morphotype) from type locality at Ospika River, British Columbia, Canada.

** Additional specimens in the type series including both male morphotypes and females from type locality at Ospika River.

Cervical papillae (CP) prominent, triangular, thorn-like, situated posterior to sub-ventral gland orifices (SVGO) and excretory pore (EXP) near mid-length of esophagus. Cuticular ornamentation at EXP lacking. Esophagus with prominent valve at esophageal-intestinal junction (EIJ).

Synlophe: Synlophe bilaterally symmetrical, with ridges extending from base of cephalic expansion to near caudal extremity; to level of prebursal papillae (PBP) in male morphotypes, posterior to anus in females. Ridges acutely pointed, with perpendicular orientation and absence of gradient as viewed in transverse section. Anterior to esophageal-intestinal junction (EIJ), lateral cervical pattern complex and irregular. Ventral-most ridge generally continuous through cervical zone to near EIJ, later becoming intermittent; definable sub-ventral and sub-dorsal ridges absent. Lateral-most ridge miniscule, in right and left fields, generally continuous throughout body length; laterally, incomplete or interrupted 3-ridge parallel system evident in some specimens. Synlophe otherwise characterized by irregular pattern

of sinuous, discontinuous ridges in all fields. Convoluted pattern of intermittent ridges extends posterior to EIJ into third quarter of body in males and females, becoming largely parallel in dorso-ventral and lateral fields; posterior to EIJ with 5–8+ narrowly spaced ridges in each field laterally; interval between ridges consistently greater dorso-ventrally than laterally at all levels of body. Maximum number of ridges attained from end of first quarter into mid-body and through third quarter in males, near mid-body in females; in cervical zone about 20 ridges extend to base of cephalic expansion. In major and minor morphotype, males with 37–44 ridges near level of EIJ, 37–57 in first quarter, 52–58 at mid-body, 55–58+ in third quarter, 22–26 anterior to bursa, and PBP retained only in lateral fields. In females, 37–42 ridges near level of EIJ, 46–52 in first quarter, 52–56 at mid-body, 42–44 in third quarter, 41+ at level of vulva, 48–50 anterior to anus adjacent to tail.

Male (*Marshallagia lichtenfelsi forma major*): Nematodes of small to medium dimensions with prominent, elongate, copulatory

TABLE II. Specimens of *Marshallagia* spp. examined from hosts and localities across Eurasia.

Museum	Species	Host	Locality	Specimens*
9094†	<i>Marshallagia dentispicularis</i>	<i>Ovis aries</i>	Mongolia	5 ♂
14781†	<i>M. dentispicularis</i>	<i>Saiga tatarica</i>	Volgograd District, Russia	4 ♂
19478†	<i>M. dentispicularis</i>	<i>S. tatarica</i>	Volgograd District, Russia	5 ♂
6195†	<i>Marshallagia mongolica</i>	<i>O. aries</i>	Mongolia	3 ♂
9096†	<i>M. mongolica</i>	<i>O. aries</i>	Mongolia	5 ♂
14777†§	<i>Marshallagia schumakovitschi</i>	<i>S. tatarica</i>	Volgograd District, Russia	8 ♂
14977†§	<i>M. schumakovitschi</i>	<i>S. tatarica</i>	Volgograd District, Russia	5 ♂
15000†	<i>M. schumakovitschi</i>	<i>O. aries</i>	Kirgizstan	5 ♂
22287†	<i>M. schumakovitschi</i>	<i>O. aries</i>	Kirgizstan	2 ♂
22288†	<i>M. schumakovitschi</i>	<i>O. aries</i>	Kirgizstan	5 ♂
70162‡	<i>Marshallagia</i> sp.	<i>O. aries/Capra hircus</i>	Pakistan	11 ♂
17314†	<i>Marshallagia belockani</i>	<i>Capra aegagrus</i>	Azerbaijan	2 ♂
70163‡	<i>Marshallagia trifida</i>	<i>O. aries</i>	Pakistan	1 ♂

* Based on examination of major morphotype males except for the minor morphotypes represented by *M. belockani* and *M. trifida*. The latter species were originally named in *Ostertagia* (Appendix 1).

† Catalogue numbers from the K. I. Skrjabin Institute of Helminthology (KIS), Central Helminthological Museum, Moscow, Russia.

§ Numbers designated as KIS 14777 and 14977, originally identified as *M. dentispicularis*, were redetermined as *M. schumakovitschi* in the current study based on structure of the spicule tips.

‡ Catalogue numbers from the U.S. National Parasite Collection.

|| Specimens most closely resemble *M. schumakovitschi*. The minor morphotype may be represented by USNPC 70163 based on the cervical synlophe.

TABLE III. *Marshallagia lichtenfelsi* sp. n. with morphometric data for the type series including major and minor morphotype males and female specimens in *Oreamnos americanus* from the type locality, Ospika River, British Columbia.

Characters	<i>Marshallagia lichtenfelsi</i> forma major ♂	<i>M. lichtenfelsi</i> forma minor ♂	<i>M. lichtenfelsi</i> ♀
Number examined*	20	9	15
Body length	(19) 11,115–14,600 (12,336 ± 736)	(8) 13,560–14,700 (14,354 ± 349)	(15) 14,965–20,320 (17,149 ± 1,278)
Cephalic capsule	(18) 85–112 (97 ± 8)	(8) 92–118 (106 ± 8)	(15) 85–112 (99 ± 9)
Esophagus length	(18) 600–745 (694 ± 36)	(8) 700–795 (752 ± 36)	(15) 675–800 (740 ± 38)
Esophagus % of body length	(18) 5.0–6.2 (5.6 ± 0.4)	(8) 4.9–5.5 (5.2 ± 0.2)	(15) 3.9–5.0 (4.3 ± 0.3)
Esophageal–intestinal valve length	(20) 110–142 (121 ± 8)	(8) 112–140 (124 ± 10)	(15) 118–145 (128 ± 8)
Esophageal–intestinal valve width	(20) 38–62 (51 ± 6)	(8) 38–62 (54 ± 8)	(15) 45–68 (57 ± 6)
Subventral esophageal gland orifices	(19) 230–296 (279 ± 16)	(8) 275–312 (297 ± 15)	(15) 262–316 (290 ± 16)
Nerve ring†	(8) 234–292 (271 ± 17)	(6) 265–315 (294 ± 16)	(12) 240–294 (267 ± 14)
Excretory pore†	(19) 260–365 (321 ± 22)	(8) 288–358 (337 ± 24)	(15) 295–366 (326 ± 21)
Cervical papillae†	(19) 318–408 (358 ± 23)	(8) 322–405 (378 ± 26)	(15) 310–410 (358 ± 25)
Spicule length, left	(20) 250–290 (269 ± 12)	(9) 292–327 (311 ± 11)	—
Spicule, left, % trifurcation	(20) 73–78 (76 ± 2)	(9) 56–61 (58 ± 2)	—
Spicule length, right	(20) 240–282 (262 ± 12)	(9) 282–327 (302 ± 14)	—
Spicule, right, % trifurcation	(20) 73–78 (76 ± 1)	(9) 58–61 (59 ± 1)	—
Dorsal ray length	(18) 295–385 (352 ± 26)	(7) 230–295 (259 ± 24)	—
Dorsal ray, % bifurcation	(18) 66–79 (73 ± 4)	(7) 67–78 (71 ± 4)	—
Bursa length	(20) 450–600 (526 ± 43)	(9) 450–518 (482 ± 24)	—
Vulva position†	—	—	(15) 11,300–15,715 (13,250 ± 1,070)
Vulva, % body length	—	—	(15) 76–80 (77 ± 1.2)
Anterior infundibulum length	—	—	(10) 235–348 (285 ± 41)
Anterior sphincter and vestibule‡	—	—	(15) 290–455 (388 ± 41)
Posterior infundibulum length	—	—	(13) 262–360 (303 ± 30)
Posterior sphincter and vestibule‡	—	—	(12) 300–400 (366 ± 30)
Ovejector length	—	—	(12) 740–1,422 (1,270 ± 189)
Eggs length × width	—	—	(25) 155–190 (174 ± 9.3) × 55–95 (76 ± 9.6)
Tail length	—	—	(15) 280–375 (323 ± 28)

* Data presented as (n =) range (mean ± 1 SD).

† Determined from cephalic extremity.

‡ Sphincter includes combined sphincter-1, sphincter-2, and vestibule.

bursa. Total body length (n = 20) 11,115–14,600 (12,336 ± 736); maximum width attained at pre-bursal papillae. Cephalic vesicle (n = 18) 85–112 (97 ± 8) long. Esophagus (n = 18) 600–745 (694 ± 36) long; 5.0–6.2% (5.6 ± 0.4) of total body length. Esophageal valve (n = 20) 110–142 (121 ± 8) long, 38–62 (51 ± 6) in maximum width. Nerve ring (NR) (n = 8) 234–292 (271 ± 17), SVGO (n = 19) 230–296 (279 ± 16), EXP (n = 19) 260–365 (321 ± 22), CP (n = 19) 318–408 (358 ± 23) from cephalic extremity.

Copulatory bursa symmetrical, elongate, strongly bilobed, lacking prominent dorsal lobe; lateral bursal rays disposed in 2-1-2 pattern; length of bursa from PBP (n = 20) 450–600 (526 ± 43). Ventral or “0” papillae paired, narrow, strongly divergent, elongate, on ventral aspect of genital cone; PBP prominent. Bursal rays generally narrow, elongate, nearly all reaching margin of copulatory bursa. Rays 2/3 curved ventrally, convergent at tips. Rays 4/5 of near-equal length, strongly divergent distally. Rays 6, parallel to rays 5. Rays 7 strongly divergent, straight, contained in rectangular, wider than long, delicate accessory bursal membrane (ABM) situated on dorsal aspect of genital cone; ABM with median chitinized bar extending from anterior margin to near posterior border of membrane. Externo-dorsal, rays 8, narrow, highly elongate, supporting dorsal aspect of bursal membrane. Dorsal ray arising symmetrically or asymmetrically from common origin with rays 8; length of dorsal ray < externo-dorsal rays. Dorsal ray (n = 18) 295–385 (352 ± 26) in length, with primary

bifurcation (n = 18) at 66–79% (73) of length from anterior; laterally directed papillae near tip, terminating in rays 9/10. Genital cone prominent, complex, with well-developed, cuticularized telamon surrounding cloaca; proconus lacking.

Spicules alate, narrow, trifurcate, bent or curved in lateral view, symmetrical, near equal, with tendency for right spicule < left spicule in length; right spicule (n = 20) 240–282 (262 ± 12) with trifurcation 73–78% (76 ± 1.0) from anterior; left spicule (n = 20) 250–290 (269 ± 12) with trifurcation at 73–78% (76 ± 2.0); trifurcation at level of weakly developed eyelet. Main shaft of each spicule terminates in narrow, medially curved, sharply pointed foot enveloped by small, balloon-like membrane; ventral and dorsal processes of dissimilar structure and length. Ventral process straight, narrow, parallel throughout (n = 10), 52–62 in length, extending to near distal end of main shaft, terminating in small, bulbous, asymmetrical, strongly chitinized knob-like tip, with 2–3 miniscule rounded denticulate projections. Dorsal process weakly chitinized, relatively broad, recurved, cupped distally near triangular tip, (n = 10) overall 31–44 in length, extending 57–77% of ventral process from trifurcation; chitinized transverse bar across dorsal ala of spicule in dorso-ventral view about 58–60% of distance from capitulum. Gubernaculum present, poorly chitinized, cryptic in dorso-ventral view, body appears as granular, rounded cone extending anteriorly from chitinized transverse basal plate; overall (n = 5) 41–51 in length, 16–25 in maximum width

TABLE IV. Morphometric data for *Marshallagia lichtenfelsi* sp. n. based on paratype specimens in *Oreamnos americanus* from Alberta, Idaho, and Montana as originally presented in Lichtenfels and Pilitt (1989)*.

Characters	<i>Marshallagia lichtenfelsi</i> forma major ♂	<i>M. lichtenfelsi</i> forma minor ♂	<i>M. lichtenfelsi</i> ♀
Number examined	13	15	7
Body length	(13) 9,240–12,800 (10,872 ± 1,153) †	(15) 11,200–14,800 (12,797 ± 1,035)	(7) 11,400–18,900 (14,900 ± 2,835)
Esophagus length	(13) 628–908 (716 ± 69)	(15) 680–836 (773 ± 42)	(7) 760–796 (774 ± 14)
Esophagus % of body length	(13) 5.5–8.0 (6.6 ± 0.7)	(15) 5.3–7.1 (6.1 ± 0.5)	(7) 4.1–6.8 (5.4 ± 1)
Esophageal–intestinal valve length	(13) 100–188 (127 ± 25)	(15) 100–158 (126 ± 16)	(7) 112–144 (134 ± 11)
Subventral esophageal gland orifices ‡	(13) 252–364 (283 ± 31)	(15) 232–324 (288 ± 29)	(7) 220–332 (286 ± 37)
Nerve ring ‡	(13) 220–280 (263 ± 21)	(15) 200–300 (274 ± 24)	(7) 220–300 (263 ± 27)
Excretory pore ‡	(13) 248–340 (301 ± 33)	(14) 280–376 (343 ± 25)	(7) 232–364 (294 ± 52)
Cervical papillae ‡	(13) 248–380 (328 ± 40)	(15) 312–420 (369 ± 26)	(7) 232–396 (316 ± 58)
Spicule length (left and right)	(13) 240–292 (268 ± 16)	(15) 292–348 (327 ± 17)	—
Vulva position	—	—	(7) 8,641–14,591 (11,474 ± 2,306)
Vulva, % body length	—	—	(7) 74–80 (77 ± 2)
Anterior ovejector §	—	—	(5) 480–804 (657 ± 116)
Posterior ovejector §	—	—	(5) 400–760 (608 ± 133)
Ovejector length	—	—	(5) 880–1,564 (1,265 ± 249)
Eggs length × width	—	—	(18) 172–193 (182 ± 8) × 82–93 (88 ± 5)
Tail	—	—	(7) 216–324 (276 ± 44)

* Calculated from original raw data for male and female specimens as documented in Lichtenfels and Pilitt (1989); *Marshallagia lichtenfelsi* forma major reported as *Marshallagia* sp. and *M. lichtenfelsi* f. minor reported as *Ostertagia* sp. Actual lot numbers from the USNPC were not reported in the original study. These series of measurements generally correspond to those completed in the current study, although all characters now considered important for these ostertagiines were not completely assessed by Lichtenfels and Pilitt (1989).

† Data presented as (n =) range (mean ± 1 SD).

‡ Determined from cephalic extremity.

§ Ovejectors include infundibulum, sphincter, and vestibule.

near base; sinuous in lateral view, about 65 long including a posteriorly directed tail not visible in dorso-ventral view.

Male (*Marshallagia lichtenfelsi* forma minor): Nematodes of small to medium dimensions with prominent, elongate copulatory bursa. Total body length (n = 8) 13,560–14,700 (14,354 ± 349); maximum width attained at PBP. Cephalic vesicle (n = 8) 92–118 (106 ± 8) long. Esophagus (n = 8) 700–795 (752 ± 36) long; 4.9–5.5% (5.2 ± 0.2) of total body length. Esophageal valve (n = 8) 112–140 (124 ± 10) long, 38–62 (54 ± 8) in maximum width. NR (n = 6) 265–315 (294 ± 16), SVG0 (n = 8) 275–312 (297 ± 15), EXP (n = 8) 288–358 (337 ± 24), CP (n = 8) 322–405 (378 ± 26) from cephalic extremity.

Copulatory bursa symmetrical, elongate, strongly bilobed, lacking prominent dorsal lobe, structure as in major morphotype; lateral bursal rays disposed in 2-1-2 pattern; length of bursa from PBP (n = 9) 450–518 (482 ± 24). Ventral or “0” papillae paired, narrow, strongly divergent, markedly elongate on ventral aspect of genital cone; pre-bursal papillae prominent. Bursal rays generally narrow, elongate, nearly all attaining margin of copulatory bursa; disposition similar to that in *M. lichtenfelsi* forma major. Rays 7, sinuous, weakly divergent distally, contained in tapering, trapezoidal, distally bilobed, delicate Sjöberg’s organ situated on dorsal aspect of genital cone. Dorsal ray (n = 7) 230–295 (259 ± 24) in length, with primary bifurcation (n = 7) at 67–78% (71 ± 4.0) of length from anterior; laterally directed papillae near tip, terminating in rays 9/10. Genital cone prominent, complex, with well developed, chitinized telamon surrounding cloaca; proconus lacking. Bilobed membrane on antero-ventral aspect of genital cone prominent at level of paired “0” papillae.

Spicules alate, robust, trifurcate, straight in lateral view, symmetrical, near equal, with prominent eyelet at level of

trifurcation; right spicule (n = 9) 282–327 (302 ± 14) with trifurcation 58–61% (59 ± 1.0) from anterior; left spicule (n = 9) 292–327 (311 ± 11) with trifurcation at 56–61% (58 ± 2.0). Main shaft of each spicule terminates in robust, curved hyaline foot. Dorsal, ventral processes near equal in length, extending approximately 77–83% of length of spicule tip from trifurcation. Ventral process narrow, straight, acutely pointed. Dorsal process broad, with transverse chitinized bar dorsally demarcating triangular tip; in lateral view with dorsally directed barb. Gubernaculum ovoid in anterior with narrow posterior extension or tail in dorsal-ventral view, poorly chitinized, (n = 4) 78–111 long, 13–23 in maximum width; sinuous, narrow in lateral view.

Female: Small to medium nematodes, generally straight. Total length (n = 15) 14,965–20,320 (17,149 ± 1,278); maximum width attained near level of vulva. Cephalic vesicle (n = 15) 85–112 (99 ± 9.0) long. Esophagus (n = 15) 675–800 (740 ± 38) long; 3.9–5.0% (4.3 ± 0.3) of total body length. Esophageal valve (n = 15) 118–145 (128 ± 8.0) long, 45–68 (57 ± 6.0) in maximum width. SVG0 (n = 15) 262–316 (290 ± 16), NR (n = 12) 240–294 (267 ± 14), EXP (n = 15) 295–366 (326 ± 21), CP (n = 15) 310–410 (358 ± 25) from cephalic extremity.

Ovaries didelphic. Vulva transverse, ventral, situated at (n = 15) 11,300–15,715 (13,250 ± 1,070), or 76–80% (77 ± 1.2) of body length, from anterior. Vulval flap present in (based on n = 42 females) 43% of specimens; flap absent in 57% of specimens; cuticular inflations or fans only present in absence of flap, disposed antero-ventrally, postero-ventrally, or laterally to vulva in 30% of specimens; vulval flap rectangular, with straight posterior margin. Ovejectors (n = 12) 740–1,422 (1,270 ± 189) in total length, including anterior–posterior infundibulum, sphincters, vestibule; distinction between bulb-like sphincter-1

TABLE V. Morphometric data for male specimens (major morphotype) of the morphospecies *Marshallagia marshalli* in free-ranging and domestic ungulates from North America, based on new observations during the current study.

Characters	<i>Ovibos moschatus</i>			<i>Ovis dalli</i>			<i>Ovis canadensis</i>			<i>Ovis aries</i>		
	15			17			16			18		
Number examined	(15)	12,310–14,500	(13,573 ± 738)*	(17)	7,340–11,400	(9,764 ± 911)	(16)	8,800–12,650	(10,635 ± 934)	(18)	9,050–12,500	(10,146 ± 829)
Body length	(7)	104–118	(111 ± 5)	(10)	88–105	(97 ± 6)	(8)	80–118	(103 ± 12)	(7)	88–105	(95 ± 6)
Cephalic capsule	(15)	872–1,010	(944 ± 40)	(16)	725–910	(808 ± 53)	(16)	650–910	(786 ± 67)	(15)	650–860	(725 ± 61)
Esophagus length	(15)	6.3–7.4	(7.0 ± 0.3)	(16)	7.2–10.2	(8.3 ± 0.7)	(16)	6–8.6	(7.4 ± 0.6)	(14)	6.2–8.2	(7.2 ± 0.7)
Esophageal–intestinal valve length	(14)	140–190	(167 ± 14)	(16)	115–148	(131 ± 11)	(15)	108–150	(126 ± 13)	(16)	102–162	(125 ± 17)
Esophageal–intestinal valve width	(14)	52–68	(57 ± 6)	(17)	45–56	(49 ± 3)	(15)	40–58	(51 ± 4)	(16)	40–58	(48 ± 5)
Subventral esophageal gland orifices	(14)	355–398	(368 ± 12)	(16)	275–350	(309 ± 22)	(16)	262–340	(300 ± 21)	(15)	235–322	(272 ± 28)
Nerve ring†	(7)	295–354	(324 ± 23)	(10)	250–300	(271 ± 19)	(13)	258–300	(277 ± 13)	(12)	225–295	(252 ± 22)
Excretory pore†	(15)	342–468	(394 ± 38)	(16)	290–384	(340 ± 30)	(16)	315–405	(350 ± 23)	(17)	278–356	(312 ± 22)
Cervical papillae†	(15)	362–492	(422 ± 42)	(16)	306–416	(364 ± 30)	(16)	346–444	(379 ± 26)	(17)	295–388	(337 ± 27)
Spicule length, left	(14)	260–305	(284 ± 14)	(16)	200–250	(235 ± 14)	(16)	238–288	(256 ± 13)	(16)	235–285	(263 ± 18)
Spicule, left, % trifurcation	(12)	73–77	(75 ± 1.4)	(16)	71–77	(74 ± 2)	(16)	71–75	(73 ± 1)	(16)	70–78	(74 ± 2)
Spicule length, right	(13)	245–298	(274 ± 17)	(16)	202–250	(231 ± 15)	(16)	228–275	(253 ± 13)	(17)	238–292	(260 ± 17)
Spicule, right, % trifurcation	(11)	73–78	(76 ± 1.4)	(16)	72–77	(73 ± 1)	(16)	71–74	(73 ± 1)	(17)	70–77	(74 ± 2)
Dorsal ray length	(15)	315–442	(382 ± 35)	(14)	212–305	(263 ± 22)	(11)	212–308	(261 ± 31)	(15)	232–375	(279 ± 35)
Dorsal ray, % bifurcation	(15)	67–86	(77 ± 5)	(14)	57–79	(69 ± 6)	(11)	59–70	(64 ± 4)	(16)	69–77	(73 ± 2)
Bursa length	(13)	475–625	(584 ± 45)	(17)	350–500	(437 ± 46)	(14)	410–525	(465 ± 31)	(14)	415–600	(473 ± 44)

* Data presented as (n =) range (mean ± 1 SD).
 † Determined from cephalic extremity.

(S1) and muscular sphincter-2 (S2) indistinct. Anterior infundibulum (n = 10) 235–348 (285 ± 41) long; sphincter, with S1, S2 + vestibule (n = 15), 290–455 (388 ± 41) in length. Posterior infundibulum (n = 13) 262–360 (303 ± 30) long; sphincter (n = 12) 300–400 (366 ± 30) in length. Eggs, large, (n = 25, from 4 specimens) 155–190 (174 ± 9.3) long, 55–95 (76 ± 9.6) wide; arranged in single lines in anterior and posterior uterine limbs. Tail conical, strongly tapering to narrow terminal end with slightly bulbous tip, (n = 15) 280–375 (323 ± 28) in length.

Taxonomic summary

Host: Type, and currently only known, host, *Oreamnos americanus* (de Blainville).

Specimens: Holotype male representing *M. lichtenfelsi* forma major USNPC 104914, allotype female USNPC 104915, and paratype male representing *M. lichtenfelsi* forma minor USNPC 104916 from type host and locality. Additional male and female paratypes (USNPC 104917) from type locality.

Locality: Type locality: South of Mt. Lady Laurier and near Ospika River, central British Columbia, ca. 56°47'57"N, 123°47'03"W, during January 2004 by P. Hengeveld. Other localities and specimens in the type series: (1) USNPC 104773 and 104913 on 1 September 1961; 104774 on 18 May 1963, and 104776 on 6 June 1963 from the central Canadian Rocky Mountains, Mt. Hammell, Alberta, ca. 54°05'N, 119°05'W, by G. R. Kerr; (2) USNPC 46298 and 56702, Yellowstone National Park, Buffalo Ranch, Wyoming, by L. Seghetti, 13 May 1948; (3) USNPC 58743, Pinto Creek, Alberta, ca. 53°48'N, 118°50'W, by G. R. Kerr, 2 September 1961; (4) USNPC 46918, Berland River Alberta, by W. E. Swales, 15 November 1950. Also documented by specimens, but without complete geographic data for collection, as *M. marshalli* and *O. occidentalis* from: (1) Idaho, 1941 by O. J. Hummon (USNPC 46225 and 46575); and (2) Banff, Alberta, Canada, by I. McTaggart Cowan (USNPC 45154 and 45161). Specimens attributed to hosts in Washington State (reported as Pullman, WA) by O. J. Hummon during March 1942 and on 9 April 1943 (USNPC 46566, 46575) remain without known provenance, given that this region does not represent habitat for *Oreamnos americana*, but they are likely to have been collected in Idaho. Lichtenfels and Pilitt (1989) listed Alaska incorrectly as a locality and this record represents a host from Berland River, Alberta (as indicated above).

Etymology: *Marshallagia lichtenfelsi* sp. n. is named in honor of J. Ralph Lichtenfels, former Curator of the USNPC, recognizing his substantial contributions to the systematics of the Ostertagiinae.

Remarks

Marshallagia, with the characterization of *M. lichtenfelsi* sp. n., is considered to contain 12 polymorphic species, with 5 based on both major and minor morphotype males and 7 in which the putative minor morphotype remains to be discovered or described (Appendix 1); females are known for 6 species, including *M. lichtenfelsi*. Overall, species of *Marshallagia* are diagnosed by the structure of the copulatory bursa and dorsal ray (exceptionally long and narrow rays), long divergent “0” papillae, and configuration of the spicules among males and by a generally long, sinuous tail and very large eggs among females

TABLE VI. Morphometric data for male specimens (minor morphotype) of the morphospecies *Marshallagia marshalli* *M. occidentalis* in free-ranging and domestic ungulates from North America, based on new observations during the current study.*

Characters	<i>Ovibos moschatus</i>	<i>Ovis dalli</i>	<i>Ovis canadensis</i>
Number examined	12	17	11
Body length	(12) 9,830–15,175 (13,550 ± 1,952)†	(17) 7,900–12,600 (9,917 ± 1,496)	(11) 8,900–14,700 (12,335 ± 1,643)
Cephalic capsule	(7) 95–125 (108 ± 12)	(12) 85–115 (101 ± 8)	(7) 82–115 (99 ± 12)
Esophagus length	(12) 745–1,020 (938 ± 80)	(17) 725–930 (820 ± 56)	(10) 790–1,005 (858 ± 71)
Esophagus % of body length	(12) 5.9–8.5 (7 ± 0.7)	(17) 6.9–10.3 (8.4 ± 1)	(10) 5.7–8.9 (7.1 ± 1)
Esophageal–intestinal valve length	(12) 130–188 (161 ± 17)	(17) 102–150 (126 ± 13)	(10) 120–160 (141 ± 17)
Esophageal–intestinal valve width	(12) 42–55 (49 ± 4)	(17) 35–55 (46 ± 6)	(10) 44–70 (58 ± 8)
Subventral esophageal gland orifices	(12) 332–402 (369 ± 18)	(17) 272–372 (326 ± 22)	(10) 305–366 (331 ± 17)
Nerve ring‡	(7) 312–346 (329 ± 14)	(12) 190–326 (279 ± 35)	(10) 280–325 (301 ± 16)
Excretory pore‡	(12) 332–445 (395 ± 37)	(17) 240–435 (358 ± 45)	(11) 325–420 (376 ± 27)
Cervical papillae‡	(12) 352–475 (427 ± 40)	(17) 250–460 (382 ± 45)	(11) 368–450 (409 ± 28)
Spicule length, left	(12) 305–342 (325 ± 14)	(17) 242–285 (262 ± 11)	(10) 278–315 (293 ± 12)
Spicule, left, % trifurcation	(12) 56–60 (58 ± 1)	(17) 55–60 (57 ± 1)	(10) 56–60 (58 ± 1)
Spicule length, right	(12) 298–338 (318 ± 14)	(17) 240–278 (259 ± 10)	(10) 275–312 (289 ± 12)
Spicule, right, % trifurcation	(12) 56–61 (58 ± 1.5)	(17) 55–59 (58 ± 1)	(10) 56–59 (58 ± 1)
Dorsal ray length	(8) 188–300 (252 ± 35)	(13) 160–220 (196 ± 22)	(3) 188–270 (229 ± 41)
Dorsal ray, % bifurcation	(8) 66–82 (74 ± 5)	(13) 61–78 (69 ± 5)	(3) 72–78 (74 ± 3)
Bursa length	(11) 350–575 (500 ± 62)	(16) 350–435 (387 ± 26)	(8) 290–530 (460 ± 78)

* Few specimens attributable to *M. occidentalis* in domesticated sheep were available for study. As a consequence, data from these lots are not included herein. Material of this morphotype reported in Lichtenfels and Pilitt (1989) predominately included lots from *Ovis aries*/*Ovis dalli* hybrids.

† Data presented as (n =) range (mean ± 1 SD).

‡ Determined from cephalic extremity.

(Orloff, 1933; Andreeva, 1956; Boev, 1963; Durette-Desset, 1983).

Although *M. lichtenfelsi* is distinct, relative to comparisons outlined below, there remains considerable disagreement over species diversity within the genus. Complications for taxonomy arise, in part, from a nearly impenetrable literature from central Asia; differing opinions about what species should, or should not, be included in the genus; and how different authorities treat the phenomenon of polymorphism (e.g., Durette-Desset, 1989; Drózdź, 1995). For example, among the many species referred to *Grosspiculagia* (the putative minor morphotype forms for *Marshallagia* according to Drózdź [1995]), some are compatible with *Marshallagia* whereas others are clearly referable to other genera within the Ostertagiinae (Appendix 1). Confusion has been confounded by the release of some authoritative, web-based taxonomies which simply list species names irrespective of synonymy or polymorphism; this may be a general problem for the Ostertagiinae in such data resources. Further, names are often represented without specific reference to the authorities on which these broader taxonomic decisions are based. Thus, in the case of one such resource, there are 24 taxa listed in *Marshallagia* and, among these, only 10 are valid species considering synonymies (including 4 with major and minor morphotypes) and 6 should be relegated to other genera; an additional valid species from China (*Marshallagia singkiangensis* Wu and Shen, 1960) was completely missed in the compilation, as was the minor morphotype for *Marshallagia schmakovitschi* Kadyrov, 1959 (Appendix 1). Consequently, as a basis for taxonomic comparisons and recognition of *M. lichtenfelsi*, we have reviewed the status of all species that have been linked to *Marshallagia*, with annotations about validity and structural characters (Appendix 1).

Among 12 species in the genus, most have been incompletely described and only 5 (including *M. lichtenfelsi*) have had the synlophe characterized. Lichtenfels et al. (1988) provided the initial descriptions of the cervical synlophe among some genera

and species of Ostertagiinae and later explored this character in *M. marshalli*/*M. occidentalis* based on North American specimens (Lichtenfels and Pilitt, 1989; Lichtenfels and Hoberg, 1993). These investigations and subsequent studies of the synlophe among various genera and species among the Ostertagiinae have established the utility of this character, in most cases, for unequivocal identification of conspecific male morphotypes and females (Lichtenfels and Hoberg, 1993; Hoberg et al., 2009b).

Specimens of *M. lichtenfelsi*, including male morphotypes and females, have a unique synlophe relative to populations of *M. marshalli* that have been examined in North America (Figs. 1–5; Table I, current study; Lichtenfels and Pilitt, 1989). Populations of *M. marshalli* in domesticated sheep and an array of free-ranging ungulates including muskoxen, Dall's sheep, bighorn sheep, and pronghorn all are characterized by a largely parallel synlophe defined by a continuous, 3-ridge lateral system that grades to 5+ ridges posterior to the EIJ. In this system, a series of ridges originate in the sub-lateral fields and terminate along the lateral field (Lichtenfels and Pilitt, 1989; Lichtenfels and Hoberg, 1993). Ventrally through the excretory pore, and dorsally, the synlophe is largely parallel and continuous.

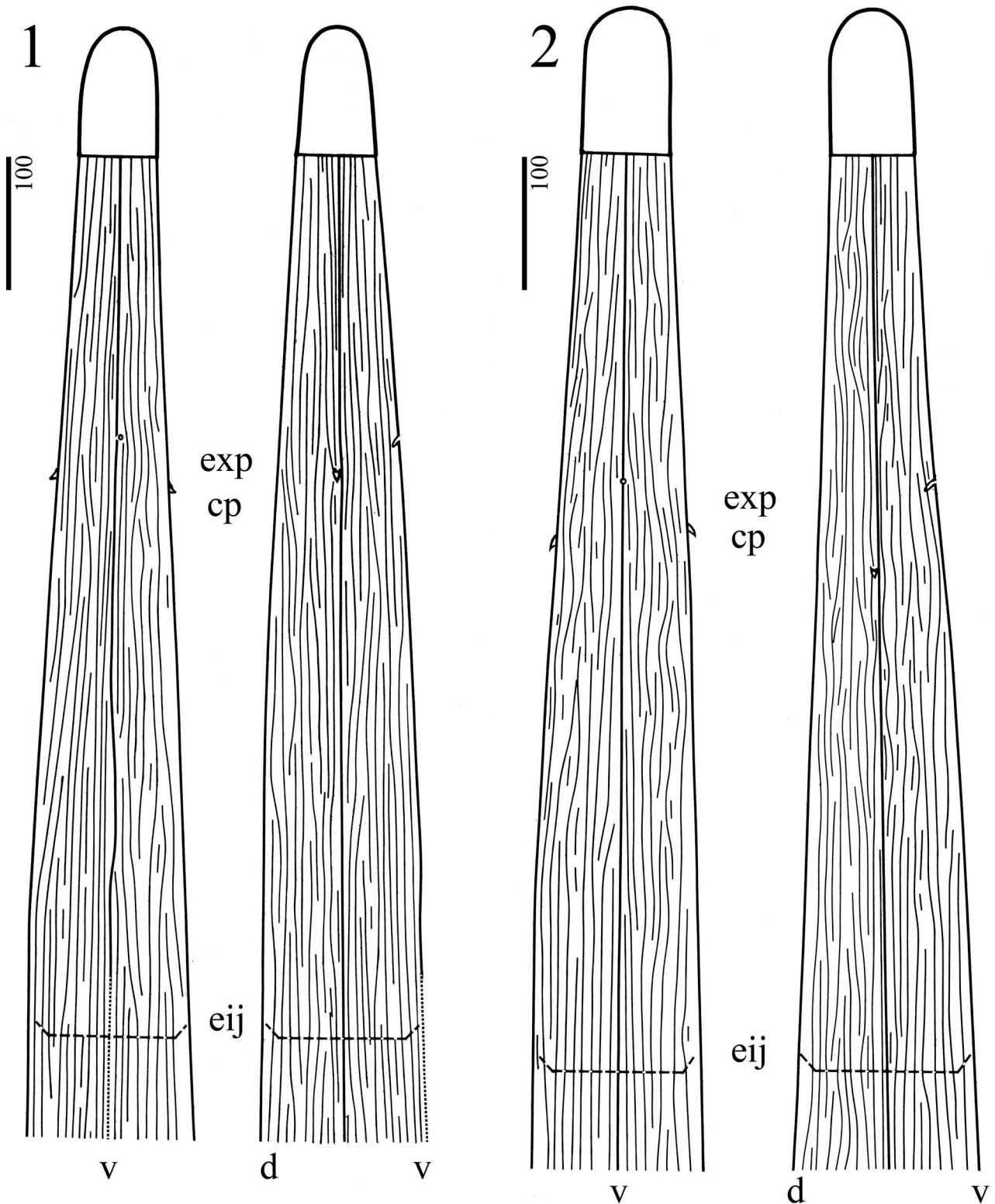
The synlophe has not been universally evaluated across all species in the genus, particularly from those considered endemic to Eurasian localities (Lichtenfels and Pilitt, 1989). Based on a limited number of specimens across 3–4 species, however, it is apparent that, laterally, a 1- or 3-ridge system in the cervical zone with 3–5+ continuous parallel ridges in lateral fields posterior to the EIJ is characteristic in *M. mongolica* Schumakovitsch, 1938, *M. dentispicularis* Asadov, 1954, and *M. schumakovitschi* and probably in *Marshallagia skrjabini* Asadov, 1954 (Appendix 1). The cervical synlophe is parallel in specimens of *Marshallagia grosspiculum* Li, Yin, Kong and Jang, 1987 (the putative minor morphotype of *M. mongolica*) as depicted in the original description (Li et al., 1987). The synlophe is parallel in

TABLE VII. Morphometric data for female specimens of the morphospecies *Marshallagia marshalli* in free-ranging and domestic ungulates from North America, based on new observations during the current study.

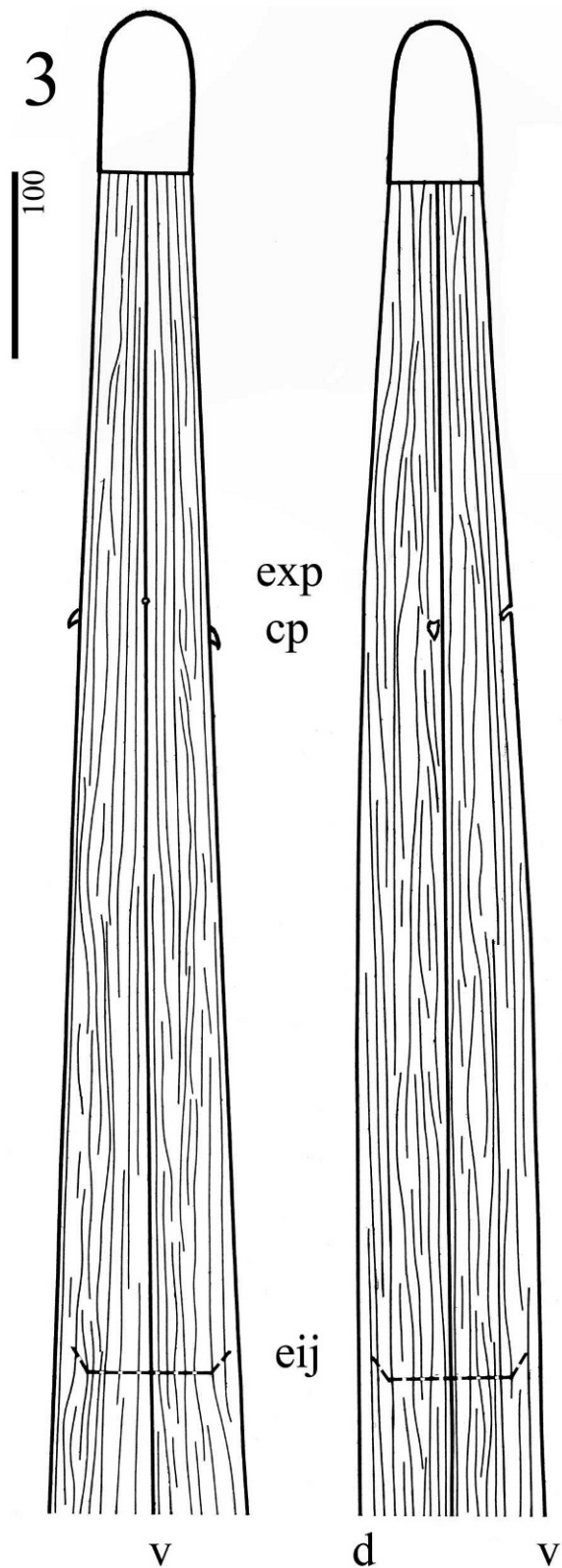
Characters	<i>Ovibos moschatus</i>	<i>Ovis dalli</i>	<i>Ovis canadensis</i>	<i>Ovis aries</i>
	19	19	20	17
Number examined	(19)	(19)	(20)	(17)
Body length	16,050–19,175 (17,194 ± 939)*	10,625–15,090 (13,300 ± 1,399)	12,200–17,400 (14,553 ± 1,202)	12,000–19,450 (14,656 ± 1,767)
Cephalic capsule	105–138 (113 ± 9)	—	98–112 (106 ± 5)	84–115 (97 ± 7)
Esophagus length	875–1,080 (980 ± 56)	765–920 (847 ± 46)	740–885 (811 ± 42)	730–930 (801 ± 56)
Esophagus % of body length	5.1–6.3 (5.7 ± 0.4)	5.4–7.9 (6.4 ± 0.7)	4.9–6.2 (5.6 ± 0.4)	4.8–7.4 (5.5 ± 0.7)
Esophageal–intestinal valve length	142–190 (166 ± 13)	125–162 (140 ± 10)	118–175 (139 ± 16)	120–160 (132 ± 11)
Esophageal–intestinal valve width	45–60 (52 ± 5)	42–70 (52 ± 8)	50–70 (58 ± 5)	45–75 (55 ± 7)
Subventral esophageal gland orifices	328–415 (379 ± 24)	302–372 (333 ± 19)	262–342 (310 ± 19)	265–340 (310 ± 21)
Nerve ring†	305–342 (320 ± 11)	262–304 (280 ± 11)	262–312 (280 ± 15)	236–368 (264 ± 34)
Excretory pore†	348–440 (383 ± 22)	322–382 (350 ± 18)	325–384 (351 ± 17)	262–384 (310 ± 28)
Cervical papillae†	370–485 (411 ± 28)	348–425 (378 ± 22)	340–408 (380 ± 20)	295–415 (339 ± 29)
Vulva position	12,325–14,575 (13,243 ± 757)	8,270–11,765 (10,269 ± 1,048)	8,700–13,150 (11,072 ± 1,028)	9,100–14,850 (11,140 ± 1,382)
Vulva, % body length	75–78 (77 ± 1)	74–79 (77 ± 1)	71–77 (76 ± 2)	74–78 (76 ± 1)
Anterior infundibulum length	150–325 (245 ± 47)	172–260 (228 ± 25)	152–265 (201 ± 28)	135–262 (181 ± 32)
Anterior sphincter and vestibule	290–400 (339 ± 34)	242–345 (289 ± 25)	258–390 (295 ± 37)	245–320 (289 ± 23)
Posterior infundibulum length	200–275 (239 ± 29)	171–258 (209 ± 24)	150–250 (195 ± 25)	140–262 (180 ± 32)
Posterior sphincter and vestibule	275–390 (322 ± 30)	232–335 (276 ± 28)	225–360 (278 ± 32)	232–310 (278 ± 21)
Ovejector length	1,050–1,265 (1,147 ± 70)	886–1,164 (1,000 ± 76)	856–1,265 (975 ± 107)	864–1,050 (934 ± 55)
Eggs length × width	175–192 (183 ± 6) × 75–98 (84 ± 7)	132–182 (162 ± 17) × 58–82 (73 ± 7)	150–170 (164 ± 5) × 70–80 (74 ± 3)	158–185 (167 ± 7) × 62–82 (70 ± 6)
Tail	248–325 (285 ± 22)	170–280 (222 ± 25)	205–310 (251 ± 30)	170–275 (248 ± 28)

* Data presented as (n =) range (mean ± 1 SD).

† Determined from cephalic extremity.



FIGURES 1–3. Synlophes structure in the cervical zone of *Marshallagia lichtenfelsi* sp. n. showing uniformity of general pattern for ridge systems in the lateral and dorso-ventral fields based on male and female paratypes (USNPC 104917). Scale bars in micrometers. Note the structure of the irregular, convoluted, and interrupted pattern, apparently unique among those species known in *Marshallagia*. (1) *Marshallagia lichtenfelsi* f. major male in ventral and right lateral view. (2) *Marshallagia lichtenfelsi* f. minor male in ventral and right lateral view. (3) *Marshallagia lichtenfelsi* female in ventral and right lateral view. Labels indicate positions of the lateral (l), dorsal (d), and ventral (v) fields, excretory pore (exp), cervical papillae (cp), and esophageal-intestinal junction (eij).

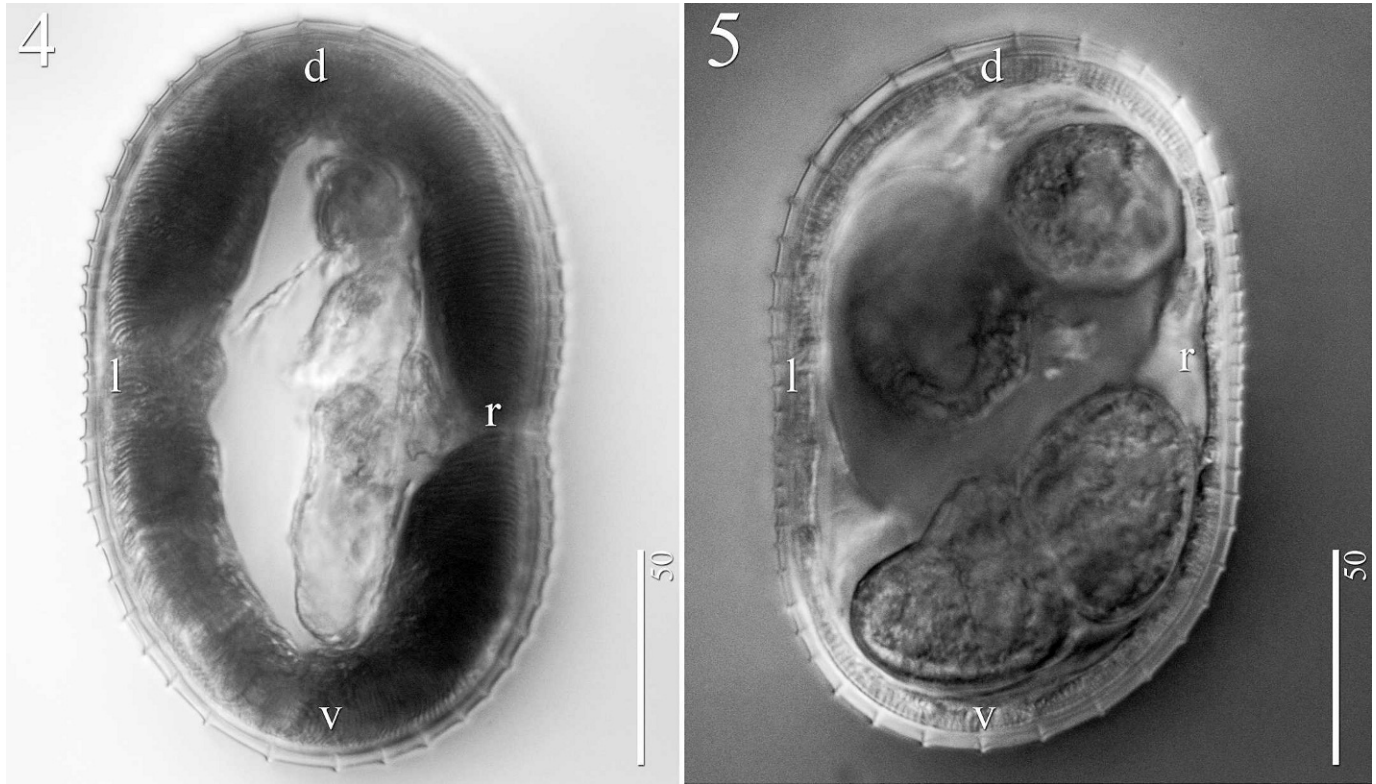


FIGURES 1-3. Continued.

Marshallagia belockani (Asadov, 1954) (putative minor morphotype of *M. skrjabini*), based on KIS 17314, but details of the pattern could not be clearly defined. In specimens of *Marshallagia trifida* (Guille, Marotel and Panisset, 1911) (putative minor morphotype of *M. schumakovitschi*), there is a single-ridge lateral system in the cervical zone, which becomes 3-5+ continuous and parallel posterior to the EIJ (USNPC Archives, J. R. Lichtenfels, unpubl. obs.). Specimens available at the current time preclude accurate and complete descriptions of the synlophe for all species of *Marshallagia*, although a general pattern for parallel and continuous ridges can be recognized. Such does not negate the possibility of convoluted and irregular patterns among Eurasian species yet to be examined, but does serve to highlight the unique nature of the synlophe in *M. lichtenfelsi*, which appears endemic to North America. Specimens of *M. lichtenfelsi* are, consequently, immediately distinguished from this assemblage of 5 North American and Eurasian species by a pattern of irregular and discontinuous ridges extending from the cervical zone into the posterior quarter of the body in males and females (Figs. 1-3).

Aside from uniformity in cervical patterns, synlophe ridge counts for specimens of *M. lichtenfelsi* were in general agreement except for those associated with the major morphotype (Lichtenfels and Pilitt, 1989). We describe 52-58 ridges at the mid-body, with the maximum attained from the mid-body into the third quarter among 5 male specimens (including both major and minor morphotypes) (Fig. 4). Lichtenfels and Pilitt (1989) reported 40-50 ridges attained in the first quarter, with no substantial increase through the mid-body (the mid-body section of the major morphotype in their study shows 44 ridges). This may reflect variation across geographically separated and isolated populations of nematodes (British Columbia, Alberta, and Idaho). The 5 male and 2 female specimens examined by us were derived from ostensibly separate populations at Ospika River, British Columbia and adjacent to Mt. Hammell, Alberta (Figs. 1-5). Overall counts from specimens of *M. lichtenfelsi* do not differ substantially from those established for *M. marshalli* from various localities and hosts, and the maximum observed for the latter species was 61 in females and 56 in males (Lichtenfels and Pilitt, 1989). Mönning (1940) reported 28 ridges at the mid-body (single field in whole mount?) of specimens attributed to *M. marshalli* from southern Africa.

Marshallagia lichtenfelsi can be distinguished from *M. schumakovitschi* based on a greater number of ridges at the mid-body, among other characters (see below). Our current observations from 3 male specimens (KIS-14777) indicate that there are 36-40 ridges in the latter species in contrast to 52-58 (and 40-50) documented for *M. lichtenfelsi* (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.; Appendix 1). Ridge counts reported among major morphotypes of 5 other species, i.e., *Marshallagia brevicauda* Hu and Jiang, 1984 (51 ridges), *Marshallagia qilianensis* Luo, Chen, Zhang, Wu and Bai, 1993 (38), *Marshallagia quinghaiensis* Luo, Chen, Zhang, Wu and Bai, 1993 (32), *Marshallagia schikobalovi* Altaev, 1953 (16 on a side?), and *Marshallagia sinkiangensis* (36) are considered unreliable as it cannot be determined at what level of the body these were derived. Additionally, it is not certain that these were based on counts from whole worms or on cross-sections (Altaev, 1953; Wu and Shen, 1960; Hu and Jiang, 1984; Luo et al., 1993). If these do represent counts from the mid-body region, then only *M. brevicauda* approaches the numbers reported for either *M. lichtenfelsi* or *M. marshalli*.



FIGURES 4–5. Synlophe as shown in transverse sections at the mid-body of male and female of *Marshallagia lichtenfelsi* sp. n. Scale bars in micrometers. (4) Minor morphotype male (Paratype, USNPC 104774) showing 57 ridges, oriented with dorsal to top, and left (l) and right (r) sides indicated. Note narrow interval between ridges in the lateral fields. (5) Female (Paratype, USNPC 104917) showing 56 ridges. Variation in ridge counts in the description relates in part to ridges initiating or terminating within a particular section.

Distinguishing *M. lichtenfelsi* from congeners

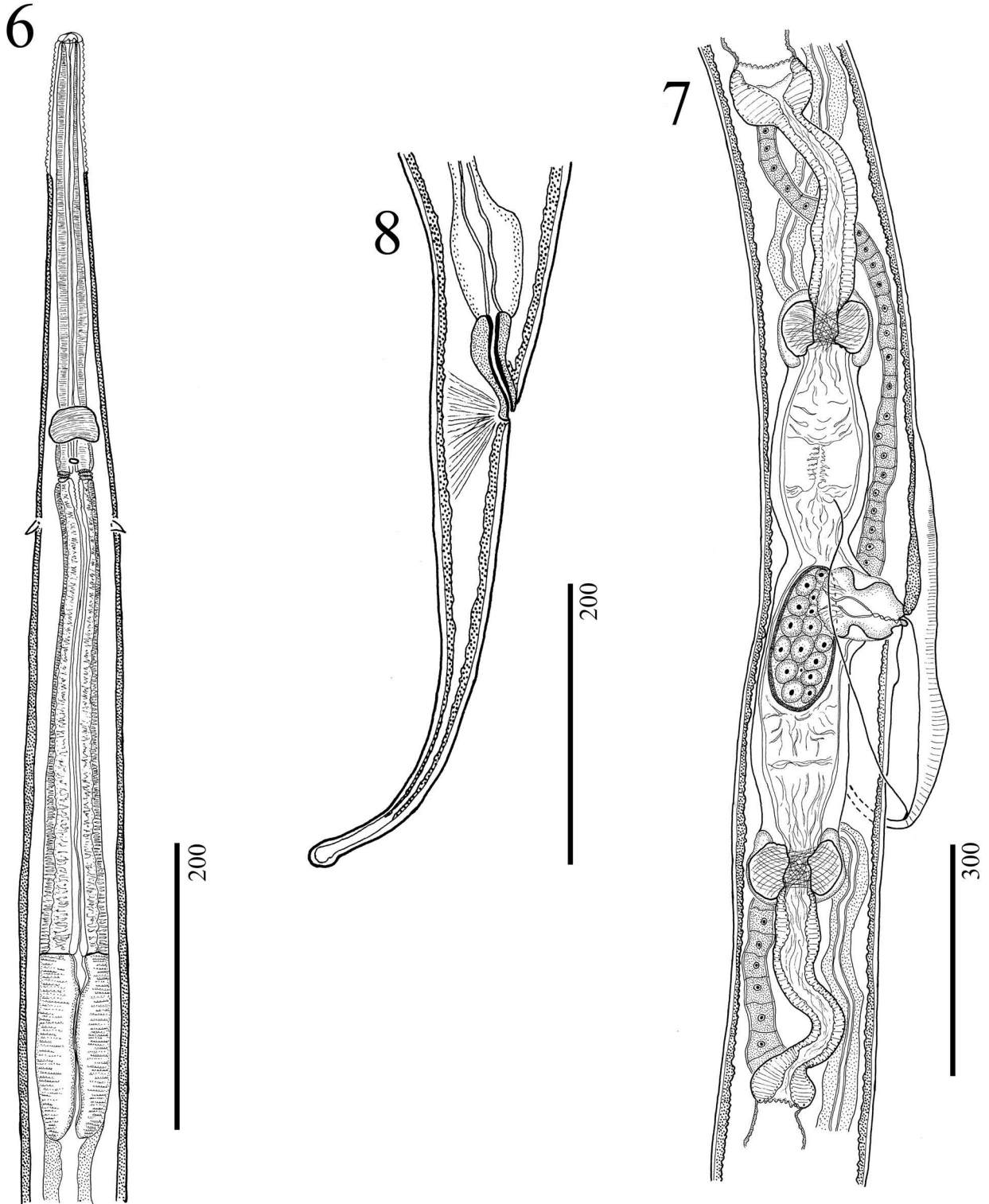
The most reliable characters for differentiation among species of *Marshallagia*, and specifically the major morphotypes of respective species, include the placement of the trifurcation of the spicule tips, the form of the dorsal and ventral processes (relative length, curved or straight), the chitinized structure of the tip of respective processes, and the form of the ABM (Figs. 15–23, 31). Although other characters of males and females may also contribute in specific situations (Figs. 6–32) to separation among an assemblage of morphologically similar species, prior studies, particularly by Russian helminthologists, established the importance for attributes of the spicules (e.g., Andreeva, 1958; Kadyrov, 1959; Boev et al., 1963). As a basis for the following comparisons, we relied on examination of available specimens representing 4 of the recognized species (Tables I, II) and references to the original descriptions and some re-descriptions in the literature.

Among the 11 other species of *Marshallagia*, *M. lichtenfelsi* is most similar to *M. marshalli* and *M. dentispicularis* based on a comparison of major morphotypes (Tables III–VII; Figs. 15–23, 31). We examined representative specimens of the latter 2 species (Tables I, II), thus allowing for a detailed comparison. Specimens of *M. marshalli* included those from populations occurring in either domesticated or free-ranging hosts across the known range in North America (Tables I, V–VII). In a redescription of *M. marshalli*/*M. occidentalis*, Lichtenfels and Pilitt (1989) had grouped all meristic data for North American specimens across

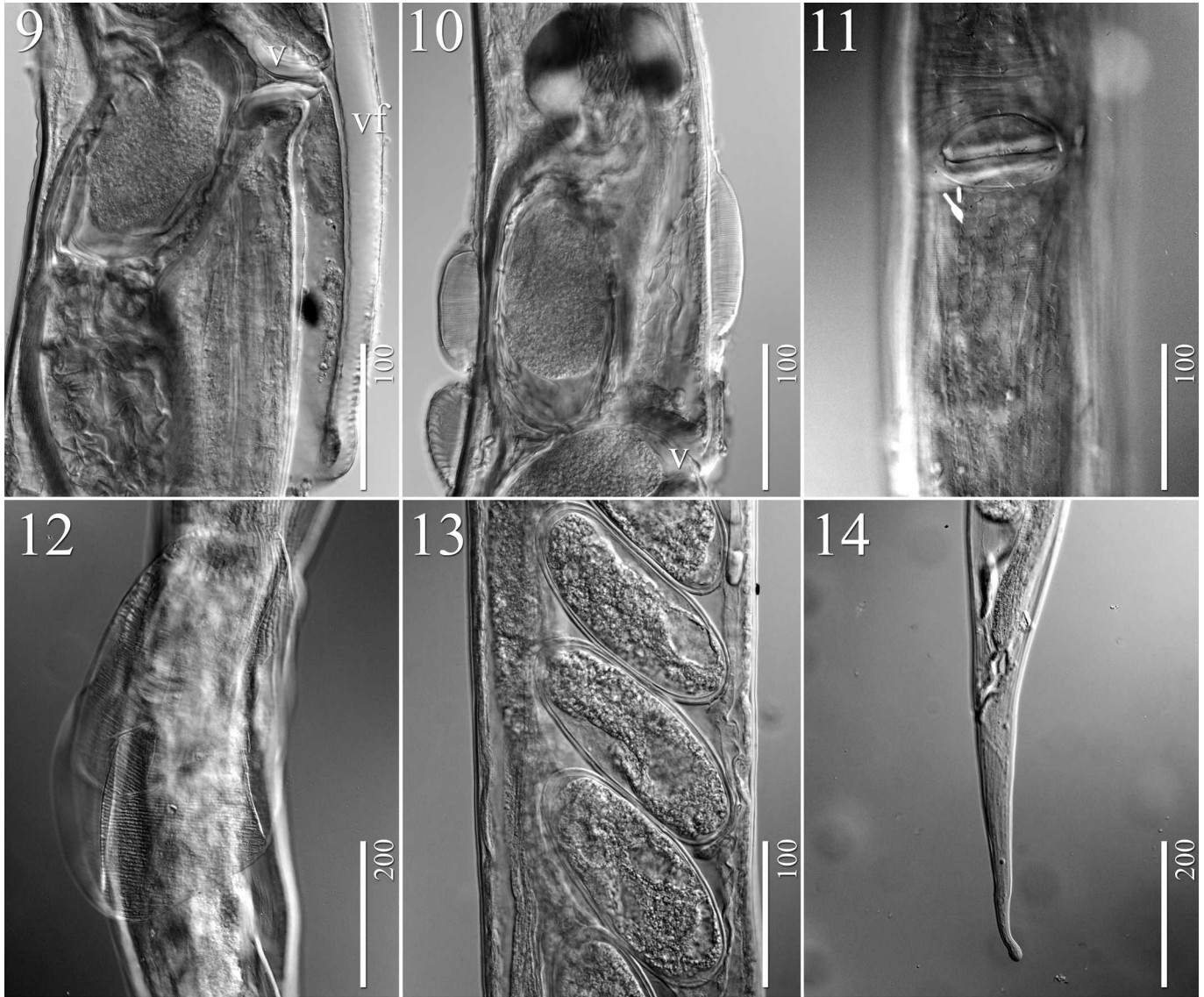
multiple host species. Segregation of those measurements, and new data, provide perspective about the range of variation associated with populations in respective ungulate hosts (Tables V–VII). We reconfirm morphologically the identity and uniformity of those specimens, including both male morphotypes and females previously designated as *M. marshalli*/*M. occidentalis* in North American hosts (*A. americana*, *O. moschatus*, *O. dalli*, *O. canadensis*, *O. aries*) according to Lichtenfels and Pilitt (1989); included was a re-examination of the type series in domesticated sheep from Montana (Ransom, 1907, 1911).

Specimens of *M. lichtenfelsi* f. major/*M. lichtenfelsi* f. minor resemble those of *M. marshalli*/*M. occidentalis* in most meristic and structural characters (Figs. 6–32; Tables III–VII; Ransom, 1907, 1911; Lichtenfels and Pilitt, 1989). Among males, these species are distinguished based on attributes of the genital cone and spicules in addition to characteristics of the synlophe previously outlined. Aside from the synlophe, females cannot be easily separated, although the ovejectors and tail are slightly larger in specimens of *M. lichtenfelsi* (Tables III, IV, VII).

Considering major morphotypes, in specimens of *M. marshalli* the spicules are 224–340 μm in length with a trifurcation near 70–75%; laterally the spicules are strongly bent near mid-length. The ventral process is straight, narrow, gradually broadening distally, and extends to near termination of the main shaft with a slightly asymmetric, small, bulbous expansion on the tip. The dorsal process is broad, from 67–89% of ventral in length to near equal, and recurved with a bluntly rounded membranous tip; a



FIGURES 6–8. *Marshallagia lichtenfelsi* sp. n. showing the cephalic, vulval, and caudal structures in females. Scale bars in micrometers. (6) Cephalic extremity in ventral view (Allotype, USNPC 104915) showing structure of the esophagus and esophageal–intestinal valve along with the relative positions of the nerve ring, excretory pore, sub-ventral gland orifices, and cervical papillae. (7) Ovejectors and vulva in lateral view (Allotype), showing the structure of the ventrally positioned flap. (8) Tail in lateral view (Allotype).



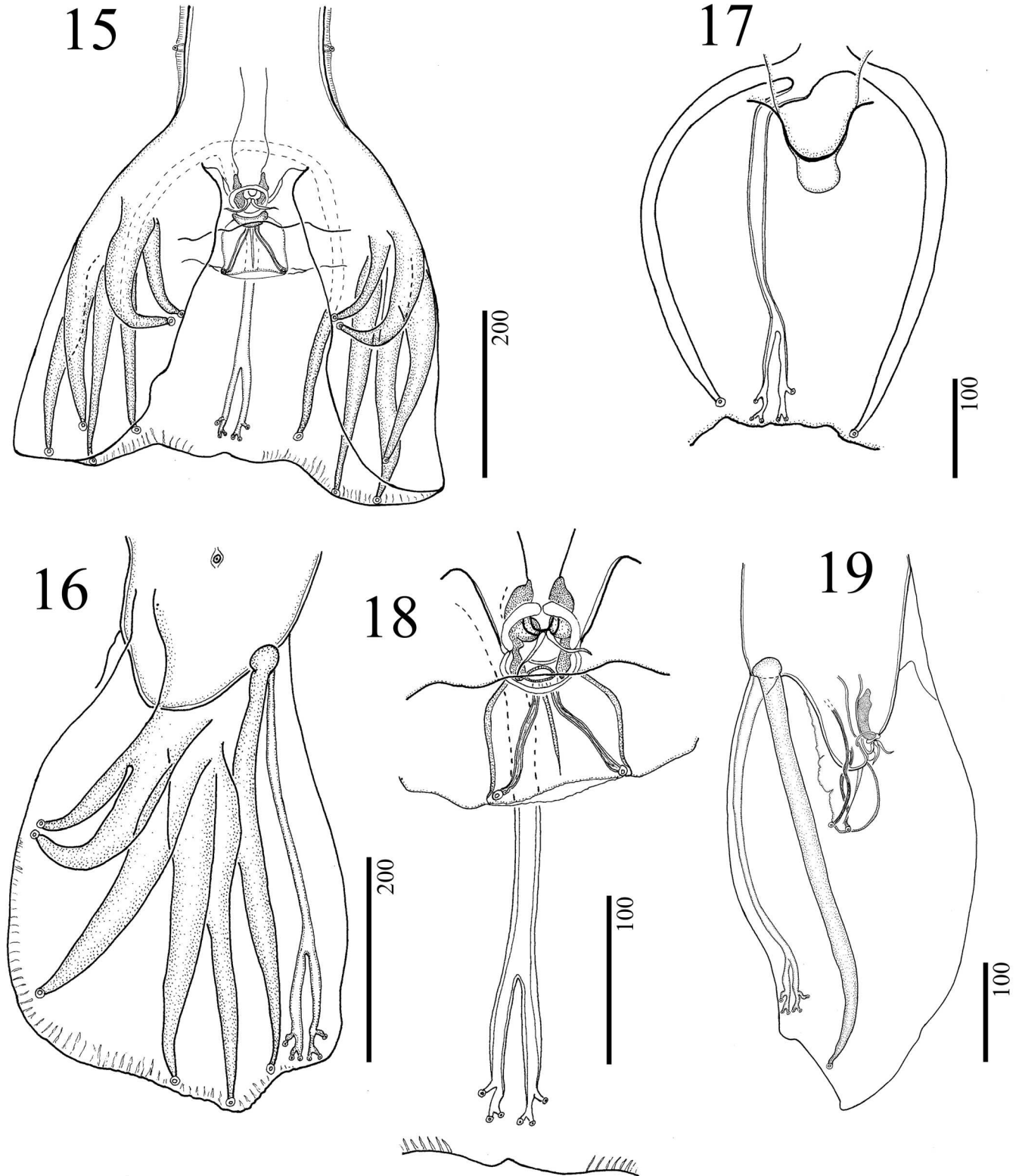
FIGURES 9–14. *Marshallagia lichtenfelsi* sp. n. showing characters associated with female specimens. Scale bars in micrometers. (9) Vulva (v) and vulval flap (vf) in lateral view (Paratype, USNPC 58746). (10) Region near level of vulva (v) in lateral view showing position and structure of dorsal and ventral cuticular inflations (Paratype, USNPC 104774). (11) Vulva, ventral view, in specimen lacking vulval flap (Paratype, USNPC 45161). (12) Vulval flap in ventral view (Paratype, USNPC 104774). (13) Eggs in uterus (Paratype, USNPC 104917). (14) Tail, lateral view (Paratype, USNPC 104774).

transverse chitinized bar is evident in the dorsal ala. A gubernaculum is present, poorly chitinized, conical, granular, and extends from a transverse basal plate; not previously demonstrated in specimens of *M. marshalli* (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs. from USNPC 56743). The ABM is longer than wide, distinctly rounded, and contains divergent and curved “7” papillae. In contrast, in *M. lichtenfelsi* f. major the ventral process of the spicules is parallel throughout and terminates in a strongly chitinized knob with miniscule, rounded projections (Figs. 20–22). The dorsal process, relative to the ventral, extends 57–77% of the distance from the trifurcation (Figs. 20–21). The ABM is rectangular, wider than long, and contains straight, divergent “7” papillae (Figs. 18, 31).

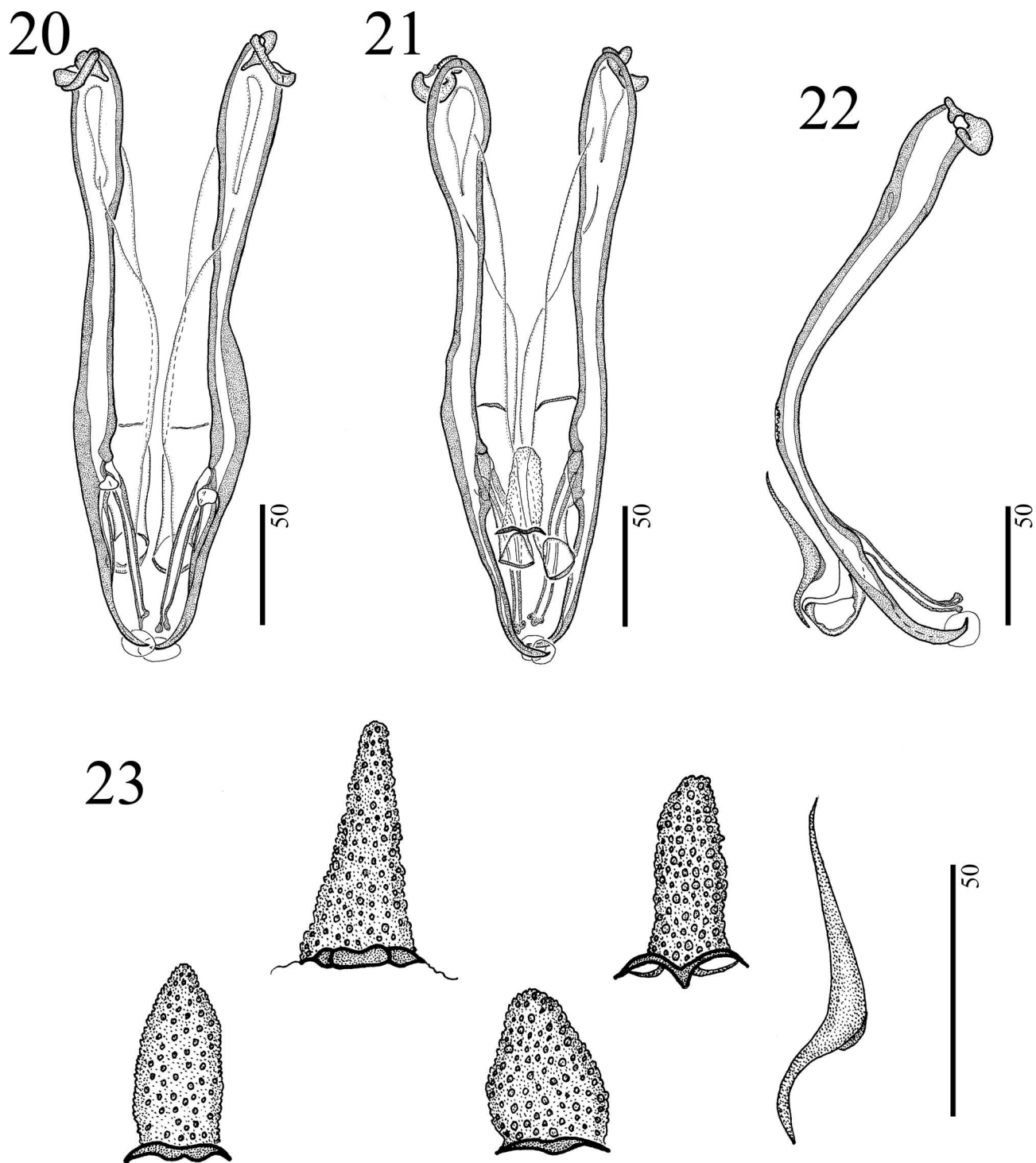
Considering minor morphotypes, few characters provide the basis for clearly distinguishing between the species (Figs 24–30, 32; Tables III, IV, VI; Shul'ts and Andreeva, 1953; Lichtenfels

and Pilitt, 1989). In specimens of *M. occidentalis*, the Sjöberg's organ is ovoid, equal in length and width, and contains sinuous and divergent “7” papillae. The gubernaculum is narrow and somewhat cylindrical. In contrast, there is a tapering, trapezoidal structure for the Sjöberg's organ and sinuous, weakly divergent “7” papillae in specimens of *M. lichtenfelsi* f. minor (Figs. 26, 32). Further, the gubernaculum is ovoid with an elongate tail (Fig. 27).

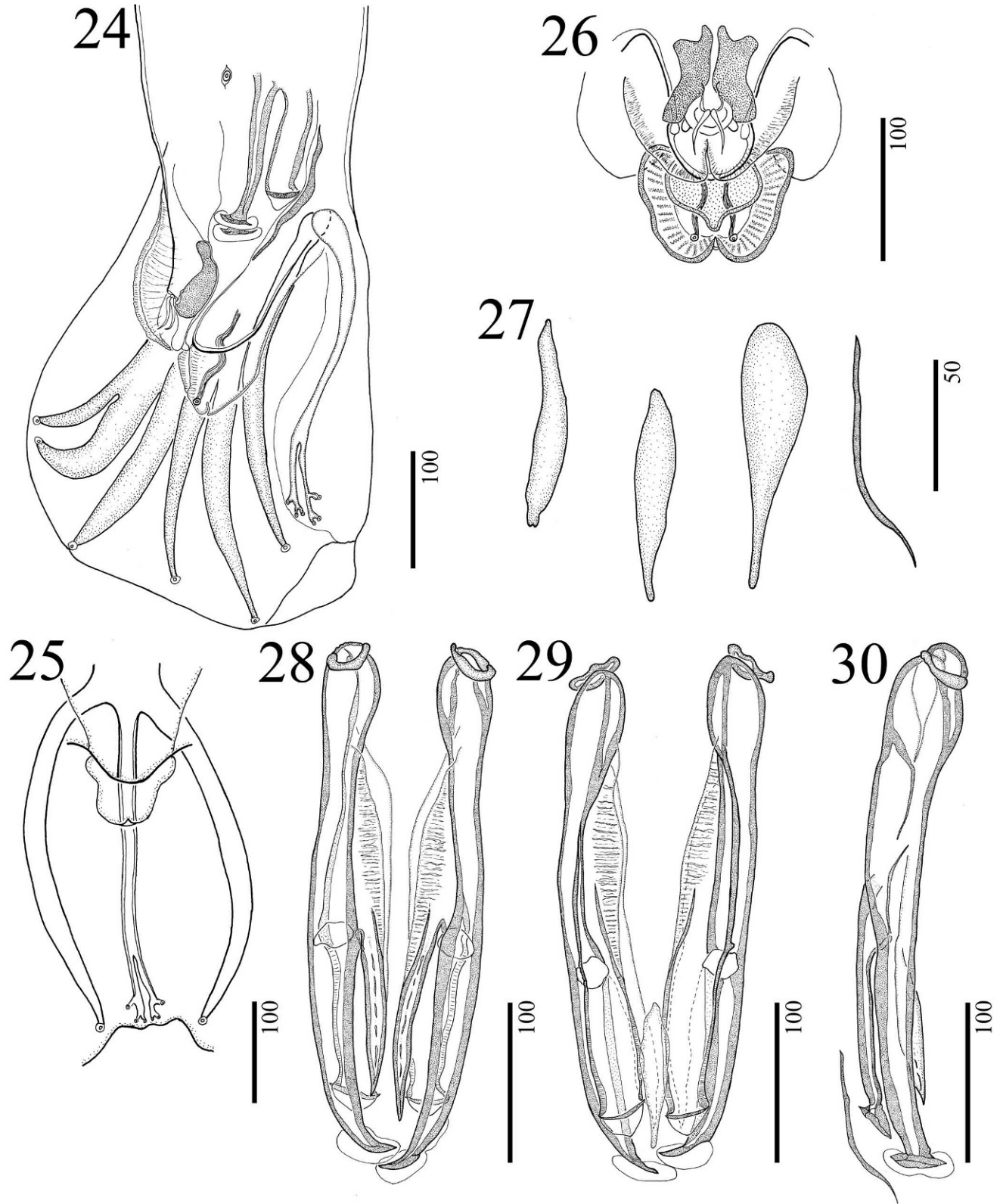
Marshallagia lichtenfelsi f. major resembles *M. dentispicularis* in the general structure of the spicules with a trifurcation near 72–78%; the dorsal and ventral processes are unequal (dorsal is near 50% of ventral); the ventral process is strongly chitinized throughout and terminates in a modified denticulate tip extending to near the distal extremity of the main shaft. A gubernaculum is present, weakly chitinized, conical, and supported by a transverse basal plate; this character had not been detected previously in *M.*



FIGURES 15–19. *Marshallagia lichtenfeldsi* sp. n. f. major male showing primary structural characters of the bursa. Scale bars in micrometers. (15) Copulatory bursa ventral view (Holotype, USNPC 104914). (16) Copulatory bursa, left lateral view (Paratype, USNPC 104774). (17) Dorsal ray in ventral view (Paratype, USNPC 46225), showing asymmetrical origins and structure. (18) Genital cone in ventral view (Holotype), showing structure and position of the “0” papillae, and rectangular accessory bursal membrane containing divergent “7” papillae and medial chitinized support. (19) Genital cone in right lateral view (Paratype, USNPC 46225), showing relative positions and dimensions of the dorsal (rays 9/10) and externodorsal rays (rays 8).



FIGURES 20–23. *Marshallagia lichtenfelsi* sp. n. f. major male showing primary structural characters of the spicules and gubernaculum. Scale bars in micrometers. (20) Spicules in ventral view (Paratype, USNPC 46225). (21) Spicules and conical gubernaculum in dorsal view (Paratype, USNPC 104917). (22) Spicule (right) and sinuous gubernaculum in lateral view (Paratype, USNPC 104774). (23) Gubernaculum in dorsal and lateral views (Paratype, USNPC 104917) showing variation in form.



FIGURES 24–30. *Marshallagia lichtenfelsi* sp. n. f. minor male showing primary structural characters. Scale bars in micrometers. (24) Bursa and genital cone in left lateral view. (25) Dorsal ray in ventral view (Paratype, USNPC 104776) showing symmetrical origin. (26) Genital cone in ventral view (Paratype, USNPC 104916) showing position of the “0” papillae, prominent ventral membrane and trapezoidal Sjöberg’s organ containing sinuous “7” papillae. (27) Gubernaculum in dorsal and lateral views (Paratypes, USNPC 46575 and USNPC 104917). (28) Spicules in ventral view (Paratype, USNPC 104916). (29) Spicules and gubernaculum in dorsal view (Paratype, USNPC 104917). (30) Spicule in right lateral view, showing position of gubernaculum (Paratype, USNPC 46575).



FIGURES 31–32. *Marshallagia lichtenfelsi* sp. n. showing details of the genital cone in male specimens. Scale bars in micrometers. (31) Genital cone in major morphotype (Paratype, USNPC 104917) showing structure and position of prominent “0” papillae (0), rectangular accessory bursal membrane (abm) and straight and divergent “7” papillae (7). (32) Genital cone in minor morphotype (Paratype, USNPC 104916) showing structure of trapezoidal and weakly bilobed Sjöberg’s organ (sjö) and sinuous “7” papillae (7).

dentispicularis (based on KIS 19478; E. P. Hoberg, A. A. Abrams, and P. A. Pilitt, unpubl. obs.). In specimens of *M. dentispicularis*, the esophageal valve is prominent ($n = 10$, 104–135 μm in length) and similar to that in *M. lichtenfelsi*. Most primary meristic characters from the major morphotypes of these respective species overlap (Tables III, IV; Appendix 1; Asadov, 1954b; Boev, 1963). Specimens of *M. lichtenfelsi* differ, however, in the absence of angular denticulate structures on the ventral process of the spicules and in the presence of a transverse chitinized bar in the dorsal ala (Figs. 20–21). In *M. lichtenfelsi*, the ABM is strongly rectangular, wider than long (contrasting with longer than wide), and contains straight and highly divergent (contrasting with curved) “7” papillae (Asadov, 1954b; Boev et al., 1963) (Figs. 18, 31). Further, the structure of the cervical synlophe, as defined above, serves to distinguish these species. Neither the minor morphotype male nor the female for *M. dentispicularis* are currently known.

Other species and characters

Specimens of *M. lichtenfelsi* f. major are distinct from males and females of *M. brevicauda* Hu and Jiang, 1984. In *M. brevicauda*, the spicule trifurcation is near 76% and the ventral process terminates in a simple bent point; the ABM is rectangular, and slightly wider than long, containing relatively straight and divergent “7” papillae; females are characterized by a short tail

near 170–209 μm in length (Hu and Jiang, 1984). Specimens of *M. lichtenfelsi* contrast in the structure of the ventral process of the spicule tip (Figs. 20–21; Appendix 1) and in a substantially longer, narrow, sinuous tail with a bulbous tip (280–375) in the female (Figs. 8, 14; Tables III, IV). A minor morphotype for *M. brevicauda* is currently unknown.

Marshallagia lichtenfelsi f. major is distinguished from *M. mongolica* by the structure of the spicule tips and the relative dimensions and form of the ABM (Figs. 15–23; Appendix 1). In the latter species, the trifurcation occurs in the range of 63–68%; the ventral process is strongly chitinized, straight, extends to near the termination of the main shaft, and ends in a smooth, expanded cap (resembling a Morell mushroom); the dorsal process is recurved, about 50% of the length of the ventral. The gubernaculum is present and has been depicted as ovoid with a narrow, anteriorly directed extension and lacking a chitinized transverse base (Skrjabin et al., 1954; Boev et al., 1963). This structure, however, contrasts with that shown by Andreeva (1958), which is more typical (transverse basal plate and weakly chitinized body) and seen in specimens of *M. lichtenfelsi*, *M. brevicauda*, *M. marshalli*, *M. qilianensis*, and *M. sinkiangensis*. The ABM in *M. mongolica* is elongate, with length > width, and has rounded margins in the posterior with curved divergent “7” papillae (Andreeva, 1958; Boev et al., 1963). The female of *M. mongolica* is currently unknown.

Marshallagia lichtenfelsi f. minor can also be distinguished from *M. grossospiculum*, the putative minor morphotype for *M. mongolica* (Figs. 24–30, 32; Appendix 1). Although meristic data for *M. lichtenfelsi* f. minor and *M. mongolica*/*M. grossospiculum* overlap, the minor morphotypes can be differentiated relative to the structure of the Sjöberg's organ and configuration of the ventral process of the spicules (Li et al., 1987). In the latter morphotype, the spicules are 290–350 µm in length with a trifurcation near 59%; ventral and dorsal processes are equal in length, straight, not extending to the tip of main shaft, about 80% of spicule tip from trifurcation. The ventral process broadens near the tip, ending in a sharp point. The Sjöberg's organ is ovoid, not elongate, and contains sinuous and convergent “7” papillae (Li et al., 1987).

Marshallagia lichtenfelsi f. major differs from *Marshallagia petrovi* Asadov, 1959 in the placement of the trifurcation and in the structure of the dorsal and ventral processes of the spicule tips and disposition of the “7” papillae in the ABM (Tables III, IV; Figs. 15–22, 31; Appendix 1). In the latter species, the trifurcation is near 67% and the dorsal and ventral processes are similar, of equal length, straight, pointed, and thin and do not attain the tip of the main shaft (extending about 56% of the distance from the trifurcation to the spicule tip) (Asadov, 1959). The ABM is elongate, containing divergent, curved “7” papillae. A minor morphotype and female for *M. petrovi* are currently unknown.

Marshallagia lichtenfelsi f. major is distinguished from *M. qilianensis* based primarily on the structure of the dorsal and ventral processes of the spicules and the position of the “7” papillae in the ABM (Figs. 15, 18, 20–22, 31; Appendix 1). In the latter species, spicule length ranges from 237–280 µm, the trifurcation is near 74%, ventral and dorsal processes are near equal and end in acute points; a gubernaculum is present (Luo et al., 1993). The ABM is somewhat elongate and rounded along the posterior margin and contains “7” papillae that are parallel throughout their length. A minor morphotype for *M. qilianensis* is currently unknown.

Marshallagia lichtenfelsi f. major is separated from *M. qinghaiensis* based on the structure of the ABM, length of the dorsal ray, length and configuration of the spicules, and body length in both males and females (Figs. 6–22; Appendix 1). In specimens of the latter, the ABM is oval, rounded, and the “7” papillae are curved and divergent within the membrane. The dorsal ray is relatively short (119–188 µm in length). The spicules are substantially smaller (175–208 µm), with relatively similar dorsal and ventral branches lacking chitinized modifications (Luo et al., 1993). Overall, these are among the smallest nematodes referred to *Marshallagia*, with a mean length of 7 mm in males and 8.5 mm in females. A minor morphotype for *M. qinghaiensis* is currently unknown.

Marshallagia lichtenfelsi f. major differs from *M. schikobalovi* Altaev, 1953 in the structure and termination of the dorsal ray and in the relative dimensions of the ABM (Figs. 15–19). In the latter species, the dorsal ray terminates in a knob-like bifurcation that is unique within the genus (Altaev, 1953; Kadyrov, 1959; Boev et al., 1963). The ABM is rectangular, slightly longer than wide, and with rounded margins along the posterior extremity; the “7” papillae are curved and divergent at their tips (Kadyrov, 1959). A minor morphotype and female for *M. schikobalovi* are currently unknown.

Marshallagia lichtenfelsi f. major differs from *M. schumakovitschi* in the structure of the spicule tips and ABM, among other characters (Figs. 18–22; Appendix 1). In the latter species, the

trifurcation is placed at 78–83%, the ventral process is narrow, and terminates in a simple point that may be bent. The dorsal process is weakly chitinized, not strongly recurved, and terminates in a slightly expanded, spoon-shaped tip which extends to near the distal extremity of the main shaft (Kadyrov, 1959; E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.). The ABM is longer than wide and contains curved, divergent “7” papillae (Kadyrov, 1959; Boev et al., 1963). A female for *M. schumakovitschi* is currently unknown.

Marshallagia lichtenfelsi f. minor can also be distinguished from *M. trifida*, the putative minor morphotype for *M. schumakovitschi*, based on the structure of the Sjöberg's organ, configuration of the “7” papillae, and structure of the spicules (Figs. 24–30, 32; Appendix 1). In specimens of *M. schumakovitschi*/*M. trifida*, the spicules are 245–340 µm in length with a trifurcation near 54%. The ventral process is strongly curved, terminating in a point without expansion (Shul'ts and Andreeva, 1953). The Sjöberg's organ is ovoid, slightly elongate, and contains convergent “7” papillae (Boev et al., 1963).

Marshallagia lichtenfelsi f. major differs from *M. sinkiangensis* in the structure of the spicule tips among other characters (Figs. 20–22; Appendix 1). In the latter species, the ventral process is narrow, terminating in a sharply pointed, bent tip without chitinized modifications (Wu and Shen, 1960). A minor morphotype for *M. sinkiangensis* is currently unknown.

Marshallagia lichtenfelsi f. major differs from *M. skrjabini* in the structure of the spicule tips and gubernaculum and in the form of the ABM (Figs. 18–23; Appendix 1). In the latter species, the dorsal and ventral processes are nearly equal in length. The dorsal process terminates in a triangular thickening whereas the ventral is a simple point lacking chitinized modifications. The gubernaculum is narrow and elongate and does not originate from a strongly chitinized transverse base. The ABM, although rectangular, is considerably longer than wide (Asadov, 1954a). A female for *M. skrjabini* is currently unknown.

Marshallagia lichtenfelsi f. minor can also be distinguished from *M. belockani*, the putative minor morphotype for *M. skrjabini* (Figs. 24–30; Appendix 1). Further, we suggest that *Marshallagia sogdiana* (Pulatov, 1985) be reduced as a synonym of *M. belockani* (Appendix 1) based on a comparison of data from the original descriptions (see Asadov, 1954c; Boev et al., 1963; Pulatov, 1985). Specimens of *M. skrjabini*/*M. belockani* (including *M. sogdiana*) are characterized by an elongate, weakly rectangular Sjöberg's organ containing “7” papillae which are divergent throughout their length (Asadov, 1954c; Pulatov, 1985).

Currently, we have no basis for comparison to *Marshallagia hsui* Qi and Li, 1963, *Marshallagia lasaensis* Li and K'ung, 1965, and *Marshallagia tarimanus* Qi, Li, and Li, 1963. Following an extensive search, the original descriptions could not be located. We determined that descriptions of these nominal taxa were never formally published, although each is mentioned in papers that present descriptions of other valid species of *Marshallagia* (Hu and Jiang, 1984; Luo et al., 1993). As the respective descriptions were contained in institutional reports with limited circulation in China, we regard these species as nomina nuda.

Comments on 2 characters

There are apparently 2 different forms recognized for the gubernaculum among major morphotypes of *Marshallagia*. It

appears that the most common form is a poorly chitinized conical structure supported by a prominent transverse basal plate (Fig. 23), as exemplified in *M. lichtenfelsi*, *M. brevicauda*, *M. marshalli*, *M. qilianensis*, and *M. sinkiangensis*. A second form, apparently only seen in *M. skrjabini*, is a narrow, elongate structure more typical of other ostertagiines such as species of *Teladorsagia* (Asadov, 1954a). The gubernaculum is reported to be absent among many species of *Marshallagia*; however, it is more likely that this particularly cryptic structure has been overlooked in many original descriptions (e.g., Ransom, 1907, 1911).

The relative length of the dorsal and ventral process, particularly in the major morphotypes, appears to be an important attribute in distinguishing among species. Boev et al. (1963) indicated that the ventral process in *M. marshalli* and *M. schumakovitschi* is shorter than the dorsal. Based on our examination of specimens, this does not appear to be correct. We found that the ventral process is consistently greater than the dorsal in *M. marshalli* and that, in the latter species, the 2 processes are near equal in length although asymmetric in structure.

DISCUSSION

Defining species limits

Marshallagia lichtenfelsi sp. n. differs from 11 nominal species of *Marshallagia* based on a suite of morphological characters associated with males and females (Figs. 1–32). Species diversity within *Marshallagia* remains, however, incompletely known and reflects the challenges of dealing with and recognizing conspecific polymorphic males and females. Few of the currently recognized species have been fully characterized in this regard (Appendix 1). It is further apparent that there are relatively few diagnostic characters that immediately distinguish among the known species and, for the most part, these are based on the structure of the genital cone and the spicules. There is extensive overlap in most morphometric characters among females, although this is less of a problem for respective major and minor morphotypes among male nematodes (Appendix 1). The synlophe may most appropriately be used in making decisions about conspecificity for males and females, but among *Marshallagia* may not generally be of utility in distinguishing among a relatively large array of related species. This is suggested by the apparent uniformity in the parallel cervical and whole-body patterns demonstrated among the 5 species, where it has been possible to explore the structure of the synlophe. Conserved patterns for the synlophe are also known among species of *Teladorsagia* Andreeva and Satubaldin, 1954, *Mazamastrongylus* Cameron, 1935, and *Spiculopteragia* (Orloff, 1933) (Hoberg et al., 2009b). Ridge counts, shown to be useful among other ostertagiines, may eventually be found to be applicable for differentiation among species of *Marshallagia* (Hoberg et al., 2009b).

Clear definitions of diversity and species limits for *Marshallagia* may emerge only through new geographically extensive field collections and integrated approaches that link comparative morphology and molecular systematics (Hoberg et al., 1999; Pérez-Ponce de Leon and Nadler, 2010). We note for the purposes of the present study that *M. marshalli*/*M. occidentalis* is regarded as a morphospecies, which is partitioned across a number of

geographically widespread, but isolated, host species and populations. Until recently, specimens now regarded as *M. lichtenfelsi* were considered conspecific with *M. marshalli*, and the current study indicates that these nominal taxa are poorly differentiated morphologically. Molecular-based comparisons across this assemblage spanning the Holarctic will be required to explore the possibility that a species complex exists, similar to that being revealed for *Teladorsagia* among free-ranging and domesticated ungulates (Hoberg, et al., 1999; Leignel et al., 2002).

Standardizing descriptions

The difficulty of completing direct comparisons that serve to distinguish among morphologically similar species (respective major and minor morphotypes and females) is highlighted in the current study. Morphological homogeneity and the occurrence of subtle structural differences confuse separation and reliable identification for many of these species. This challenge has been confounded by a lack of standardization and detail for descriptions with respect to the range of characters which may be diagnostic for species of *Marshallagia* and, perhaps, other ostertagiines.

Building on prior comparative morphological studies among species of *Marshallagia* (e.g., Asadov, 1954a, 1954b; Kadyrov, 1959; Boev et al., 1963; Hu and Jiang, 1984; Lichtenfels and Pilitt, 1989; Luo et al., 1993), we propose that uniform standards be applied to future descriptions among *Marshallagia* and other ostertagiines. For example, although many authors have included some details of the genital cone and spicules, most have not provided any meaningful insights about the structure (pattern and configuration in the cervical zone and through the body) and numbers of ridges comprising the synlophe in various regions of the body. Where ridge counts are presented, there is seldom any indication of the level of body or if counts represent 1 surface, or the circumference of the worm, or if these were based on transverse sections (e.g., Altaev, 1953; Boev et al., 1963; Hu and Jang, 1984; Luo et al., 1993). The synlophe is demonstrably one of the most important characters for recognition of species across the diversity represented by the Ostertagiinae and other Trichostrongyloidea (Durette-Desset, 1983; Lichtenfels et al., 1988; Lichtenfels and Hoberg, 1993; Hoberg et al., 2009b).

The synlophe represents a general character to be considered for males and females (Durette-Desset, 1983, 1985). Characteristic patterns are evident and have been defined at the generic level and are also often sufficient, with some recognized exceptions, to differentiate among a number of closely related species of the Ostertagiinae (e.g., Lichtenfels and Hoberg, 1993; Hoberg et al., 2009b). Further, the synlophe has proven important in the recognition of conspecific polymorphic males and females in such genera as *Ostertagia*, *Marshallagia*, and *Teladorsagia* (Lichtenfels et al., 1988; Lichtenfels and Pilitt, 1989). The following aspects of the synlophe should be incorporated in descriptions: (1) pattern, particularly the relationship of ridges in lateral and dorso-ventral fields (parallel vs. tapering) in the cervical zone anterior to the EIJ (Lichtenfels et al., 1988); (2) orientation and gradients of size for ridges as determined in transverse section (Durette-Desset, 1983); (3) cuticular structure and the presence of inflations and struts (Hoberg et al., 1993); (4) distribution and extent of synlophe on body, including termination in the posterior and the presence of gaps; and (5) numbers of ridges at specific levels of the body as

determined in transverse section (minimally at the base of esophagus, mid-body, and at termination of the synlophes in the posterior).

An additional general character for males and females is the structure and dimensions of the esophageal valve. Valve length can provide another adjunct to recognizing conspecific male morphotypes and females (Lichtenfels and Pilitt, 1991).

Essential characters among males include the following: (1) bursal formula and general disposition of the rays (Durette-Desset, 1983), with length and position (%) of the primary bifurcation of the dorsal ray (rays 9/10); (2) structure of the genital cone including the configuration (relative length, width, and shape) of the ABM in major morphotypes, and of the Sjöberg's organ in minor morphotypes, and the disposition of the "7" papillae; and (3) spicule morphology in major and minor morphotypes, focusing on overall shape and relationships of the three processes, position of the trifurcation (%), form, e.g., curved, straight, broad, or narrow, and relative length of the dorsal and ventral processes (%), and distally the presence or absence of chitinized modifications (caps, denticles, barbs, hyaline membranes). Descriptions should be accompanied by high-magnification figures depicting the processes of the spicules.

Essential characters among females have generally been widely recognized in prior descriptions. Where possible, we suggest application of the terminology proposed for the structure of the ovejectors, with measurements presented when possible, for each of the components in a didelphic system (infundibulum, sphincter-1, sphincter-2, and vestibule) (Lichtenfels et al., 2003). Further, detailed descriptions of the structure of the vulva and disposition of flaps (%), fans, or cuticular expansions can be useful in some situations (Hoberg et al., 1993).

Specificity and occurrence of *M. lichtenfelsi*

Current evidence based on survey and inventory suggests that *M. lichtenfelsi* is a relatively host-specific parasite limited in distribution to mountain goats. Prior records of *Marshallagia* were, of course, limited to those reported as *M. marshalli* in this rupicaprine (e.g., Kerr and Holmes, 1966; Boddicker et al., 1971; Samuel et al., 1977; Jenkins et al., 2004). Examination of all materials held in the USNPC from *O. americanus*, and substantial material in other free-ranging and domesticated ungulates from North America (Table I), revealed minimal evidence for sharing of *Marshallagia* spp. Except for mixed infections in 2 hosts from Alberta in which *M. marshalli*/*M. occidentalis* was rare, all nematodes in mountain goats were referable to *M. lichtenfelsi*; those in other ungulates were invariably *M. marshalli*/*M. occidentalis*. In zones of contact for mountain goats and bighorn sheep, there was no indication of mixed infections in the latter caprine; insufficient collections are available to understand the potential for exchange between mountain goats and Dall's sheep at higher latitudes, but all records from the latter are attributable to *M. marshalli* (Hoberg et al., 2001). Such a narrow level of host fidelity for a species of ostertagiine nematode, as apparently indicated for *M. lichtenfelsi*, is somewhat unexpected (Suarez and Cabaret, 1991).

Specimens we examined from *O. americanus* were morphologically consistent and represented apparently natural populations in Idaho, Montana, Wyoming, Alberta, and British Columbia. We did not have materials available from coastal British

Columbia nor from localities in Alaska, the Northwest Territories, and the Yukon Territories, although we would suggest that *M. lichtenfelsi* may have a distribution that coincides with its apparently primary host, *O. americanus*. Mountain goats are endemic in a series of discontinuous populations extending from 63°N to 44°S across southeastern Alaska into the southern Yukon and Northwest Territories (southwestern Mackenzie Mountains) through the Western Cordillera to north-central Oregon, central Idaho, Montana, and Wyoming (Côté and Festa-Bianchet, 2003). Translocation and introduction onto historical range, and areas considered to be suitable for mountain goats, have been major considerations in management for this species (Côté and Festa-Bianchet, 2003). Thus, mountain goats were introduced and established at various times on Kodiak, Chichigof, and Baranoff Islands, Alaska, the Olympic Peninsula, Washington, central Montana, the Black Hills, South Dakota, and Colorado (Côté and Festa-Bianchet, 2003; MacDonald and Cook, 2009). As a consequence, *M. lichtenfelsi* may have been introduced with the translocation of mountain goats in some geographic areas, potentially obscuring or confusing historical biogeographic associations in some instances.

In addition to established records linked to voucher and type specimens, fecal-based surveys demonstrated the occurrence of *Marshallagia* in mountain goats from the Mackenzie Mountains, Northwest Territories, coastal British Columbia, central British Columbia, and Idaho (Brandborg, 1955; Jenkins et al., 2004). It is probable that these populations, some outside of the range documented by type and voucher specimens in the current description, are consistent with *M. lichtenfelsi*. *Marshallagia* has not been recognized as a parasite in translocated mountain goats that were established in South Dakota in the 1960s from the region near Banff, Alberta, although *M. marshalli* is known in bighorn sheep (Boddicker and Huggins, 1969; Boddicker et al., 1971).

In contrast to the apparent specificity of *M. lichtenfelsi*, infections of *M. marshalli*/*M. occidentalis* appear to be a common feature of helminth faunas for both free-ranging ungulates and domesticated sheep spanning the Western Cordillera (Becklund and Senger, 1967; Uhazy and Holmes, 1971; Hoberg et al., 2001). In this zone extending into the Arctic, the morphospecies *Marshallagia marshalli* is a characteristic parasite across a disparate host assemblage including muskoxen, bighorn sheep, Dall's sheep, and pronghorn (Luckner and Dikmans, 1945; Bergstrom 1975a, 1975b; Hoberg et al., 2001). *Marshallagia marshalli* is relatively rare in cervids from North America and occurrence in these hosts (*Odocoileus hemionus*, *Cervus elaphus*, and *Rangifer tarandus*) may reflect colonization from caprine sources (Hoberg et al., 2001; Kutz et al., 2012). Our current understanding of distribution is consistent with the contention that the occurrence of *M. marshalli* in domesticated sheep is related to host switches in zones of sympatry for source populations of parasites circulating in local, free-ranging ungulates, particularly caprines and possibly *Antilocapra americana* (Luckner and Dikmans, 1945; Bergstrom 1975a, 1975b). There is no indication, as with other components of mosaic parasite faunas in ungulates, that species of *Marshallagia* were introduced to North America with domesticated sheep following European contact in the 1500s (Hoberg, 2010).

Marshallagia marshalli/*M. occidentalis* is considered to have a substantially broader geographic distribution that extends at high

latitudes across the entire Holarctic region and into Central Asia among Caprini and Rupicaprini (Govorka et al., 1988; records summarized in Suarez and Cabaret, 1991). It is suggested, however, that this apparent broad host and geographic distribution, indicative of a widespread species, receive scrutiny in the context of molecular-based studies to explore diversity and population structure (e.g., Hoberg et al., 1999; Dallas et al., 2001; Pérez-Ponce de Leon and Nadler, 2010).

History, hosts, and geographic distribution

Species of *Marshallagia* are known from a diverse assemblage of artiodactyls primarily comprising the Bovidae (Caprinae–Caprini, Rupicaprini, and “Ovibovini” and, to a lesser extent, Antelopinae), although some Cervidae and Antilocapridae are also recognized as hosts. Diversification of the Caprinae and origins of the modern tribes dates to 14.7–14.5 Mya (summarized in Hernández Fernandez and Vrba, 2005). Independent events of geographic expansion and diversification for respective caprines from Eurasia into the Nearctic during the Pliocene–Pleistocene coincided with climate fluctuations, episodic glaciations, and habitat perturbation that unfolded near 3.0–2.5 Mya. These processes of successive expansion and isolation on local to regional scales have been considered as central drivers in the diversification of an associated strongylate nematode fauna among Holarctic artiodactyls (Hoberg et al., 1995, 1999, 2004, 2012; Hoberg, 2005).

The center of diversity for species of *Marshallagia* is the mountain–steppe region of central Eurasia, where 11 species (including the Holarctic *M. marshalli*) are recognized in association with Caprini, Rupicaprini, and Antelopinae (only *Saiga tatarica*) (Skrjabin et al., 1954; Boev, 1963; Appendix 1). Only *M. marshalli* is represented in the African fauna, but is apparently unknown in free-ranging Antelopinae and associated subfamilies of free-ranging Bovidae and is considered to have been introduced with domesticated sheep (Hoberg et al., 2008). Further, the morphospecies *M. marshalli* exhibits the broadest spectrum of hosts, and greatest geographic extent latitudinally, extending into the sub-Arctic and Arctic in muskoxen (*Ovibos moschatus*) and reindeer–caribou (*Rangifer tarandus*) (Suarez and Cabaret, 1991; Halvorsen and Bye, 1999; Hoberg et al., 2001).

In contrast to Eurasia, the diversity of the *Marshallagia* fauna in North America appears minimal. This observation is consistent with Eurasian origins and limited expansion with Caprinae or Antelopinae into the Nearctic during the Quaternary. Timing of different expansion events for wild sheep or paleo-goats would serve as a determinant of the potential for secondary diversification through episodic isolation of hosts and parasites (Hoberg et al., 1999; Hoberg, 2005).

Among extant rupicaprines, mountain goats are the sister of chamois, species of *Rupicapra* de Blainville, from mountainous regions of the central Palearctic (Hernández Fernandez and Vrba, 2005). Species resembling mountain goats were represented by *Neotragoceros* in western North America during the Hemphillian and Blancan mammal stages extending to the early and middle Pliocene, and a relationship with *Oreamnos* has been postulated (Kurtén and Anderson, 1980). The first occurrence of *Oreamnos*, however, is known in western North America from the late Pleistocene, with the earliest fossil record from British Columbia

attributed to the Sangamonian interglacial near 90 Kya (Kurtén and Anderson, 1980). Such is consistent with establishment of rupicaprines in the Nearctic following expansion from Eurasia across Beringia prior to the Wisconsinan. Phylogeographic analyses identify northern and southern clades of mountain goats and estimate divergence near 224 Kya, indicating their occurrence in restricted northern and southern refugia (and micro-refugia) along with mountain sheep through multiple glacial–interglacial cycles in the late Pleistocene (Loehr et al., 2006; Shafer et al., 2010, 2011).

Late Pleistocene assemblages of herbivores linking the Palearctic and Nearctic through Beringia were associated with high sympatry, greater density, and higher diversity than those which have characterized the Holocene (e.g., Guthrie, 1982, 1984, 2001; Vereschagin and Baryshnikov, 1982). These faunal characteristics, in part, determine the potential for sequential host colonization as well as the influence of episodic fragmentation and isolation in the diversification of parasites in these large ungulates and other mammals (e.g., Hoberg et al., 1999; Hoberg, 2005; Hoberg and Brooks, 2008; Durette-Desset et al., 2010).

Morphological similarity of *M. lichtenfelsi* and *M. marshalli*, and their distribution in the Western Cordillera of North America, may indicate a close genealogical relationship for these ostertagiines, although considerable similarity to *M. dentispicularis* is apparent. The former relationship would assume a single colonization event of North America by *M. marshalli*/*M. occidentalis* from Eurasia and subsequent origin of *M. lichtenfelsi* by a process of peripheral isolates speciation. In this instance, *M. marshalli* would occupy a broad ancestral distribution relative to *M. lichtenfelsi*. Interpretation of this history hinges on the conspecificity of *M. marshalli* in the Nearctic and Palearctic, e.g., *M. marshalli* and *M. lichtenfelsi* could be sisters, and related to a single event of geographic colonization, but the former species may also be endemic to North America and with a more limited distribution than currently considered. Such a conclusion would imply identification of *M. marshalli* in Eurasia to be incorrect. Alternatively, the distribution of *Marshallagia* in the Nearctic may reflect multiple expansion events for hosts and parasites from Eurasia and genealogical relationships for either *M. marshalli* or *M. lichtenfelsi* linked to other congeners.

The geographic range for *Marshallagia* in mountain goats suggests that *M. lichtenfelsi* may have been present in both the northern and southern refugia and, possibly, the unglaciated coastal zone during the terminal Pleistocene (Shafer et al., 2011). Consequently, if *M. lichtenfelsi* was a parasite of the common ancestor of the northern and southern clades of *Oreamnos*, some level of population differentiation for these nematodes would be predicted; a signature for secondary expansion from northern and southern refugia and contact for parasite populations might also be postulated. Alternatively, a shallow evolutionary association with mountain goats, and isolation and differentiation in either the northern or the southern refugial zones alone during the Wisconsinan (following colonization from a caprine source), would be associated with lower levels of genetic diversity and putative signatures for secondary post-glacial expansion. Diminished genetic diversity would also result from post-Pleistocene expansion–contraction in ranges and sequential founder events, depending on the initial population density for hosts and parasites and slow versus rapid patterns of dispersal (Hewitt, 1996; Arenas et al., 2012). Clear, testable hypotheses are apparent

for exploring the history of this host–parasite association but require new geographically extensive collections suitable for integrated approaches.

The intricate history for refugial isolation and population fragmentation demonstrated for mountain goats and wild sheep (Loehr et al., 2006; Shafer et al., 2010, 2011) indicate the potential for considerable cryptic diversity for *Marshallagia*, *Teladorsagia*, and perhaps other nematodes (Hoberg et al., 1999, 2012). Shifting patterns of contact and sympatry among assemblages of ungulates are consistent with geographic and host colonization as a process involved in diversification of these parasites (Hoberg and Brooks, 2008). Understanding and establishing the limits of species and population diversity for *Marshallagia* in this complex historical arena will rely on the application of molecular–phylogeographic protocols to explore the cryptic connections for hosts and parasites (Nieberding and Olivieri, 2007; Nieberding et al., 2008; Koehler et al., 2009).

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APPENDIX 1. Diversity for *Marshallagia* spp. in ungulates, including nominal taxa referred to this and related genera (valid species of **Marshallagia* based on major morphotype or minor morphotype).

Major morphotype	Minor morphotype
* <i>Marshallagia marshalli</i> (type for genus) = <i>Marshallagia</i> sp. 3 of Drózdź (1995)	* <i>M. occidentalis</i> = <i>Marshallagia</i> sp. 4 of Drózdź (1995) Currently unrecognized
* <i>Marshallagia brevicauda</i>	Currently unrecognized
* <i>Marshallagia dentispicularis</i>	Currently unrecognized
* <i>Marshallagia lichtenfelsi</i> sp. n. forma major	* <i>Marshallagia lichtenfelsi</i> sp. n. forma minor
* <i>Marshallagia mongolica</i>	* <i>Marshallagia grossospiculum</i> = <i>Marshallagia</i> sp. 1 of Drózdź (1995) Currently unrecognized
* <i>Marshallagia petrovi</i>	Currently unrecognized
* <i>Marshallagia qilianensis</i>	Currently unrecognized
* <i>Marshallagia quinghaiensis</i>	Currently unrecognized
* <i>Marshallagia schikobalovi</i>	Currently unrecognized
* <i>Marshallagia schumakovitschi</i>	* <i>Marshallagia trifida</i> nov. comb = <i>Marshallagia</i> sp. 2 of Drózdź (1995) Currently unrecognized
* <i>Marshallagia sinkiangensis</i>	Currently unrecognized
* <i>Marshallagia skrjabini</i>	* <i>Marshallagia belockani</i> = <i>Marshallagia sogdiana</i> nov. comb.?

Annotation for major morphotypes attributed to *Marshallagia*—

Marshallagia marshalli* (Ransom, 1907) Orloff, 1933—type for genus (synonyms: *Ostertagia tricuspis* Marotel, 1912; *Ostertagia brigantica* Blanchard, 1909; *Ostertagia orientalis* (Bhalerao, 1932)). Ransom (1907, 1911) described this species and the minor morphotype, *M. occidentalis*, based on specimens in domesticated sheep (*Ovis aries* L.) from Montana. **Morphology: Spicules strongly curved in lateral view, 224–340 µm in length (North American); trifurcation 70–75%; eyelet at trifurcation prominent; with dorsal < ventral process in length, to near equal; ventral process straight, terminates in asymmetrical knob; dorsal process recurved, broad, blunt membranous tip; gubernaculum with strongly chitinized transverse base and granular, conical anterior extension (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs. based on USNPC 56743). ABM is longer than wide, rounded posteriorly, containing curved divergent “7” papillae. Mönning (1940) reported 28 ridges at mid-body (single field?). Lichtenfels and Pilitt (1989) reported 51–56 ridges near the mid-body in males. Synlophe in cervical zone is a 3-ridge parallel lateral system, grading to 5 or more ridges posterior to EIJ.

Marshallagia sp. 3— in *Ovis canadensis* Shaw. Drózdź (1995) considers this to represent an undescribed major morphotype, distinct from *M. marshalli*. This conclusion is apparently an error. Based on an examination of type specimens of *M. marshalli* in domesticated sheep, and vouchers in bighorn, Dall’s sheep (*O. dalli* Nelson), muskoxen (*Ovibos moschatus* (Zimmermann)) and pronghorn (*Antilocapra americana* (Ord)), there appears to be a single morphospecies in North America (E. P. Hoberg, A. Abrams, and P. A. Pilitt, observations of present study); this species is attributable to *M. marshalli*. The original description of *M. marshalli*/*M. occidentalis* was based on specimens from the Nearctic and only later was it reported in central Eurasia and Africa (e.g., Boev et al., 1963; Mönning, 1940); conspecificity of these latter nematodes requires confirmation.

Specimens depicted by Drózdź (1995) (designated as *Marshallagia* sp. 3) in bighorn are identical with *M. marshalli*; those depicted as “*M. marshalli*” from Romania do not represent this species. *Marshallagia marshalli* was originally described based on parasites

in *Ovis aries*, but it has been demonstrated that populations of *Marshallagia* are shared among free-ranging bighorn, pronghorn, and domestic sheep on common range. Populations in the Nearctic are consistent with *M. marshalli*, a contention supported by studies by Lichtenfels and Pilitt (1989), who demonstrated no morphometric or structural differences in parasites in bighorn or domesticated sheep. Specimens depicted by Lichtenfels and Pilitt (1989) and Drózdź (1995) in *Ovis canadensis* appear to be identical. Consequently, it is probable that the Palearctic specimens of “*M. marshalli*” do not represent that species, but are either already named or represent another species remaining to be named. Alternatively, *M. marshalli* may have a Holarctic distribution (see Andreeva, 1958; Boev et al., 1963) and may be distinct from “*M. marshalli*” of Drózdź (1995) in the Palearctic.

Marshallagia brevicauda* Hu and Jiang, 1984—Appears consistent with a major morphotype of *Marshallagia*. Originally reported in domesticated sheep from Xinjiang, China and is considered to resemble *M. tarimanus* (see Hu and Jiang, 1984). **Morphology: Specimens are reported to have 51 ridges; spicules 268–310 µm with trifurcation near 76%; dorsal process recurved, longer than ventral; ventral process ends in simple bent point; presence of a weakly chitinized gubernaculum with a conical granular body arising from a basal transverse plate; long dorsal ray 270–360 µm in length; ABM rectangular, wider than long, with straight divergent “7” papillae. In females the tail is exceptionally short, 170–209 µm (a definitive character), and eggs are 155–180. Minor morphotype male currently unknown.

Marshallagia brevispiculum Mönning, 1940—Appears to have been found only once, and the description was based on a single male with aberrant (?) spicules; found with *M. marshalli* in domesticated sheep from South Africa. **Morphology:** Reported to have 42 ridges at mid body; dorsal ray = 250 µm; spicules short about 150 µm (Mönning, 1940). Minor morphotype male and female unknown.

Marshallagia dentispicularis* Asadov, 1954—Typical major morphotype for *Marshallagia*. Originally based on specimens in domesticated goats (*Capra hircus* L.) and later domesticated sheep (*Ovis aries*) from Azerbaijan and Kazakhstan. **Morphology: Spicules 230–275 µm with trifurcation at 72–78%; dorsal-ventral processes of spicules are unequal; ventral process with irregular,

sharply denticulate tip; eyelet at trifurcation prominent; dorsal process recurved about 50% length of ventral; gubernaculum present as a transverse plate and conical granular extension (KIS 19478; E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.). Dorsal ray 251–329 μm . ABM rectangular, considerably longer than wide, “7” papillae strongly divergent, curved (Asadov, 1954b; Boev et al., 1963). Synlophe, parallel, continuous to near PBP; 1–3 ridge lateral in cervical zone, grading to 5+ lateral extending beyond EIJ (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.). Minor morphotype male and female unknown.

***Marshallagia hsui* Qi and Li, 1963?**—Considered as nomen nudum. Unknown status. Original description was not published but represented an internal institutional document, although this species was listed in Hu and Jiang, (1984) and Luo et al. (1993).

***Marshallagia lasaensis* Li and K’ung, 1965?**—Considered as nomen nudum. Unknown status. Original description was not published but represented an internal institutional document, although this species was listed in Hu and Jiang, (1984) and Luo et al. (1993).

****Marshallagia lichtenfelsi* sp. n. forma major Hoberg, Abrams, Pilitt and Jenkins**—Typical polymorphic species in *Marshallagia*, based on specimens in mountain goats (*Oreamnos americanus* (de Blainville)) from northwestern North America. Originally considered conspecific with *M. marshalli* (see Lichtenfels and Pilitt, 1989).

****Marshallagia mongolica* Schumakovitsch, 1938**—Typical major morphotype of *Marshallagia*. Originally described based on specimens in free-ranging caprines and antelope from Mongolia. **Morphology:** Spicule trifurcation at 63–68%; dorsal-ventral processes of spicules unequal (dorsal approximately 50% of ventral); ventral process terminates in expanded cap; dorsal process blunt, strongly recurved; gubernaculum present, with transverse basal plate and poorly chitinized conical extension to anterior (see Andreeva, 1958; Boev et al., 1963). ABM elongate, length > width, rounded along posterior margin. Synlophe parallel, continuous to near PBP; 3 ridge lateral in cervical zone, grading to 5+ lateral extending beyond EIJ (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.). Female unknown.

****Marshallagia petrovi* Asadov, 1959 nec Pushmenkov, 1937**—Typical major morphotype of *Marshallagia*. Described based on specimens in domesticated sheep from Buriatia (Russia) (Asadov, 1959). **Morphology:** Dorsal ray 212–260 μm ; Spicules 245–270 μm ; trifurcation estimated at 67%; dorsal and ventral processes of the spicules are similar, of equal length, pointed and thin, extending about 56% of distance from trifurcation. ABM is elongate, containing divergent, curved “7” papillae and dorsal ray is 212–260. Minor morphotype male and female unknown.

****Marshallagia qilianensis* Luo, Chen, Zhang, Wu and Bai, 1993**—Typical major morphotype of *Marshallagia*. Described based on specimens in Tibetan gazelle (*Procapra picticaudata* Hodgson) from Qinghai Province, China (Tibet). **Morphology:** Reported to have 38 ridges. In male, spicules 237–280 μm ; trifurcation estimated at 74%; dorsal and ventral processes near-equal length, ending in sharp points; gubernaculum present, 45–49 in length, appears poorly chitinized, and with anteriorly directed extension arising from a basal plate; dorsal ray 244–366; ABM rounded with parallel “7” papillae. In female, length of tail 237–333 μm , and eggs, 175–204. Considered similar to *M. tarimanus*, *M. dentispicularis*, *M. lasaensis*, *M. quinghaiensis*, and *M. marshalli* (English summary in Luo et al., 1993). Minor morphotype male unknown.

****Marshallagia quinghaiensis* Luo, Chen, Zhang, Wu and Bai 1993**—Typical major morphotype of *Marshallagia*. Described based on specimens in bharal (*Pseudois nayaur* (Hodgson)) from Qinghai Province, China (Tibet). **Morphology:** Overall, very small nematodes in male (7 mm) and female (8.5 mm), reported to have 32 ridges. In male, spicules 175–208 μm , trifurcation estimated at 72%; gubernaculum not seen; dorsal ray relatively short, 119–188. In female, length of tail 181–254 μm , and eggs 165–235. Considered similar to *M. tarimanus*, *M. dentispicularis*, *M. lasaensis*, and *M. marshalli* (English summary in Luo et al., 1993). Minor morphotype male unknown.

****Marshallagia schikhobalovi* Altaev, 1953**—Typical major morphotype, in most respects, for *Marshallagia* based on specimens in domesticated sheep from Eurasia (Altaev, 1953; Skrjabin et al., 1954). **Morphology:** Synlophe with ridges 16 (on a side?) in number. Spicules 243 μm in length; trifurcation about 78% of spicule length from anterior. Dorsal and ventral processes near equal in length, extending to near level of termination of main shaft. ABM with rounded margins. Dorsal ray terminates in knob-like bifurcation, atypical of any species in the genus. Minor morphotype male and female unknown.

****Marshallagia schumakovitschi* Kadyrov, 1959**—Typical major morphotype for *Marshallagia*. Original description based on specimens in domestic sheep from northern Kazakhstan. **Morphology:** Spicules 238–285 μm ; trifurcation 78–83%; dorsal and ventral processes near equal in length; ventral process terminates in simple point, which may be bent; eyelet at trifurcation indistinct or absent; dorsal process, weakly chitinized, blunt, not strongly recurved, extends to near termination of main shaft. Dorsal ala of spicule with chitinized bar articulated to main shaft. No discernable gubernaculum observed. ABM slightly longer than wide, containing divergent, curved “7” papillae. Dorsal ray 252–350 (Kadyrov, 1959; Boev et al., 1963). There are 36–40 ridges at the mid-body of males based on 3 specimens (KIS 14777) (E. P. Hoberg and P. A. Pilitt, unpubl. obs.); laterally a single-ridge system (seldom 3), 1–2 pairs of ridges terminate anterior to EIJ outside of lateral-most fields, but not conspicuously tapering, parallel throughout extending to PBP. Posterior to EIJ, entirely parallel and continuous, grading to a 5+ ridge system laterally. Putative major morphotype for *M. trifida*; female unknown.

****Marshallagia sinkiangensis* Wu and Shen, 1960**—Typical major morphotype for *Marshallagia*. Specimens found in Siberian ibex (*Capra sibirica* (Pallas)) from Uigur Autonomous Region, Sinkiang, China (Wu and Shen, 1960). **Morphology:** Reported to have 36 ridges. Spicules 221–244 μm with trifurcation near 67%; ventral process with sharply pointed, bent tip; dorsal process tapers distally to end in spoon-shaped tip; length dorsal > ventral process. Dorsal ray 264. ABM with width \geq length. Gubernaculum obscure, conical, arising from chitinized transverse basal plate. Female with tail 181–270 μm ; vulval flap present; eggs 171–201 μm in length. This species was described in a paper also reporting *M. mongolica* and *M. marshalli* in domesticated sheep (English summary in Wu and Shen, 1960). Minor morphotype male unknown.

****Marshallagia skrjabini* Asadov, 1954**—Typical major morphotype for *Marshallagia*. Specimens in tur (*Capra caucasica* Gldenstaedt and Pallas = *C. cylindricornis* Blyth) and alpine chamois (*Rupicapra rupicapra* (Linnaeus)) from Azerbaijan (Asadov, 1954a). **Morphology:** Spicules 280–317 μm ; trifurcation at 76%, processes of near-equal length; dorsal process terminating in triangular chitinized foot with dorsally directed barb; ventral process ending in a simple point; ABM considerably longer than

wide, rectangular; gubernaculum narrow, elongate, lacking chitinized transverse base; dorsal ray 350–427. Putative major morphotype for *M. belockani*, and see *M. sogdiana* (outlined below); female unknown.

***Marshallagia tarimanus* Qi, Li and Li, 1963?**—Considered as nomen nudum. Unknown status. Original description was not published but represented an internal institutional document, although this species was listed in Hu and Jiang, (1984) and Luo et al. (1993).

***Marshallagia uzbekistanica* Azimov and Dadaev, 2001**—A morphologically atypical form referred to *Marshallagia* in the original description. Originally described based on male nematodes in domesticated sheep and goats from Uzbekistan (Azimov and Dadaev, 2001). **Morphology:** There is some suggestion, based on spicule structure, that these are teratological forms; however, the description reports 12 specimens from multiple hosts. These would be referred to *Ostertagiinae* based on the paired “0” papillae and the accessory bursal membrane. Spicules are asymmetric, right 121–132 μm , left 104–110 (asymmetry not seen among species of *Marshallagia*); dorsal ray relatively short 158–163. Female unknown. Considered to have been incorrectly referred to *Marshallagia* in original description and in online databases.

Annotation for minor morphotypes of *Marshallagia*, established and putative—

****Marshallagia occidentalis* (Ransom, 1907)**—Minor morphotype of *M. marshalli* (Ransom, 1907, 1911; Drózd, 1995). Synonym: *Ostertagia skrjabini* Kamensky, 1929, nec Shen Wu and Yen, 1959 as determined by Skrjabin et al. (1954); *O. trifida* (Guille, Marotel and Panisset, 1911) is considered valid (see below) although often included among synonyms for *O. occidentalis*. Along with the major morphotype, *M. occidentalis* was originally described based on specimens in domesticated sheep from Montana (Ransom, 1907, 1911).

****Marshallagia grossospiculum* Li, Yin, Kong and Jang, 1987**—Appears consistent with a typical minor morphotype for *Marshallagia*. Specimens were found in association with putative *M. mongolica* in both natural and experimental infections; in domesticated sheep from Gansu Province, China (Li et al., 1987). **Morphology:** Synopse appears parallel based on figures from the cervical region in the original description. Spicules 290–350 μm ; trifurcation near 59%; ventral and dorsal processes equal in length, not extending to tip of main shaft, about 80% of spicule tip from trifurcation; ventral process broadens near tip, ending in sharp point. Gubernaculum reported as absent. The “7” papillae in Sjöberg’s organ are sinuous and convergent.

****Marshallagia lichtenfelsi* sp. n. forma minor Hoberg, Abrams, Pilitt and Jenkins**—Typical minor morphotype of a polymorphic species in *Marshallagia*, based on specimens in mountain goats (*Oreamnos americanus* (de Blainville)) from northwestern North America. Originally considered conspecific with *M. occidentalis* (see Lichtenfels and Pilitt, 1989).

***Marshallagia* sp. 1**—Associated with *M. mongolica* in Siberian ibex from Mongolia (see Drózd, 1995). It was indicated that this minor morphotype had not been described; however, see *M. grossospiculum*.

****Marshallagia* sp. 2**—Associated with *M. schumakovitschi* in Siberian ibex from Mongolia (see Drózd, 1995). Not apparently described, but see comments under *M. trifida*.

***Marshallagia* sp. 4**—In *Ovis canadensis*. Drózd (1995) considers this to represent an undescribed minor morphotype (counterpart for *Marshallagia* sp. 3), distinct from *M. occidentalis*. This raises the question of the original description of *M. marshalli*/*M. occidentalis* in the Nearctic and of what has been subsequently reported as this species from Eurasia. Figures in Drózd (1995) show what appear to be distinct species. *Marshallagia marshalli* was originally described based on parasites in domesticated sheep, but it has been demonstrated that populations of *Marshallagia* are shared among free-ranging bighorn (and some crevids, antilocaprids and caprines) and domesticated sheep on common range. Thus, these should be *M. marshalli*, a contention supported by studies by Lichtenfels and Pilitt (1989) who demonstrated no morphometric or structural differences in parasites from bighorn or domesticated sheep (confirmed by E. P. Hoberg, A. Abrams, and P. A. Pilitt in the present study). Consequently, it is probable that the Palearctic specimens of *M. marshalli* do not represent that species, but are either already named or represent another species remaining to be named.

****Marshallagia belockani* (Asadov, 1954)**—Appears consistent with a minor morphotype for *Marshallagia* and is now transferred to that genus as a new combination. Originally established in *Ostertagia* (*Grosspiculagia*) based on specimens in *Rupicapra rupicapra* and *Capra caucasica* (reported as *C. cylindricornis*) from Azerbaijan. Indicated to be similar to *O. occidentalis* and *O. trifida* by Asadov (1954c). **Morphology:** In original description: spicule length 305–317 μm , trifurcation 55%, ventral process with blunt point, about 80% length of dorsal process; dorsal process broad, with transverse bar, recurved, not attaining point of main shaft; “7” papillae contained in elongate Sjöberg’s organ, divergent throughout length; dorsal ray 268–280. In 2 specimens (KIS 17314): bursa 367–416, dorsal ray 171–174, spicules 247–283, gubernaculum present; Sjöberg’s as depicted for *M. occidentalis* (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.). Referred to *Marshallagia* by Durette-Desset (1989); may represent minor morphotype for *M. skrjabini*.

***Marshallagia sogdiana* (Pulatov, 1985) nov. comb.**—Consistent with a minor morphotype of *Marshallagia*, based on spicule structure, and now transferred to that genus as a new combination. Originally described in *Ostertagia* based on specimens in domesticated goats from Uzbekistan; found with *T. circumcincta* and *T. trifurcata*. **Morphology:** Spicules 280–320 μm ; trifurcation about 57%; ventral process about 82% of dorsal process which does not attain end of spicule tip. Gubernaculum is present. Dorsal ray length 230–300. The “7” papillae embedded in the Sjöberg’s organ are divergent according to Pulatov (1985). This species was considered similar to *O. occidentalis* and *O. trifida*, but was not compared to *M. belockani*, and is a possible synonym of the later based on direct comparisons of meristic data (see Asadov, 1954c; Boev et al., 1963; Pulatov, 1985). Pulatov (1985) used, as a basis for comparison, the data presented in Shul’ts and Andreeva (1953); in that paper the figures for *O. occidentalis* and *O. trifida* are reversed.

****Marshallagia trifida* (Guille, Marotel and Panisset, 1911) nov. comb.**—Consistent with a minor morphotype of *Marshallagia*, based on spicule structure, and now transferred to this genus as a new combination. Originally described in *Ostertagia* based on specimens in steppe saiga (*Saiga tatarica* (Linnaeus)), argali (*Ovis ammon* (Linnaeus)), domesticated sheep, and goats from

Kazakhstan (Boev et al., 1963). **Morphology:** Spicules 245–340 μm ; trifurcation 54%; ventral process, strongly curved, 91% of dorsal process; dorsal process extends to tip of main shaft of spicule. “7” papillae in Sjöberg’s organ convergent; gubernaculum present; dorsal ray length 244–320 μm . NOTE: J. R. Lichtenfels studied specimens attributed to *O. trifida* in *C. hircus* from Pakistan and described (unpubl.) a single-ridge lateral system with irregular pairs dropping out anterior to EIJ; posterior to EIJ 3–5+ ridges, continuous and parallel (confirmed by E. P. Hoberg, A. Abrams, and P. A. Pilitt). Consequently, it is apparent that *M. occidentalis* and *M. trifida* cannot be synonyms (see Lichtenfels and Pilitt, 1989). Cervical synlophe in *O. trifida* appears identical to males and females of *M. schumakovitschi*, suggesting these are minor and major morphotypes of a single species (E. P. Hoberg, A. Abrams, and P. A. Pilitt, unpubl. obs.).

Annotation for indeterminant minor morphotypes

The following species are not *Marshallagia* or must be designated as being of indeterminant generic placement. These species were originally referred to *Grosspiculagia* or were subsequently referred to this genus following description. The genus *Grosspiculagia* is indicative of putative status as a minor morphotype, and Drózdź (1995) considers the *Grosspiculagia*-forms to represent the minor morphotypes of *Marshallagia* spp. A number of species originally established in *Grosspiculagia*, including 11 of 13 nominal taxa listed in K’ung and Li (1965) (see also, Skrjabin et al., 1954; Andreeva, 1956; Durette-Desset, 1989), are not compatible with *Marshallagia*. Some errors are perpetuated in online taxonomic databases. Where possible, we attempt to clarify some of these records relative to *Marshallagia*.

***Mouflongia podjapolskyi* Schulz, Andreeva and Kadenazii, 1954**—Originally in *Mouflongia*, later to *Grosspiculagia* by Jansen (1958); based on specimens in mouflon from Kazakhstan. Not consistent with *Marshallagia* (see Skrjabin et al., 1954; Andreeva, 1958). This nematode represents a minor morphotype for a species of *Ostertagia*. Incorrectly referred to *Marshallagia* in some online authoritative databases.

***Orloffia buriatica* (Konstantinov, 1933)**—Originally described under *Ostertagia* based on specimens in domesticated sheep from Mongolia and Buriatia. The minor morphotype was associated with *O. dahurica* (Orloff, Belova and Gnedina, 1931) according to Drózdź (1995). *Ostertagia hsiunga* Hsu, Ling, and Liang, 1957 is a synonym of this morphotype according to Yen (1963). Incorrectly referred to *Marshallagia* in some online authoritative databases.

***Ostertagia aegagri* Grigorian, 1951**—Originally *Ostertagia* (*Grosspiculagia*), based on male specimens in Bezoar goat (*Capra aegagrus*) from Armenia. Specimens have a short dorsal ray (135), incompatible with *Marshallagia*, and probably represent a minor morphotype for a species of *Ostertagia* (see Skrjabin et al., 1954).

***Ostertagia butschnevi* (Rudakov, 1937)**—Originally *Ostertagia* (*Marshallagia*), later transferred to *Ostertagia* (*Skrjabinagia*), later to *Camelostrongylus*; considered a species of *Marshallagia* by Boev et al. (1963). Originally described based on specimens in domesticated sheep from Eurasia. Specimens have a short dorsal ray, incompatible with *Marshallagia*, and probably represent a minor morphotype for a species of *Ostertagia* (see Skrjabin et al., 1954; Boev et al., 1963; Durette-Desset, 1989).

***Ostertagia gansuensis* Chen, 1981**—Originally described under *Ostertagia* (*Grosspiculagia*) based on specimens in domesticated

sheep from China. Indicated to be similar to *Ostertagia arctica*, *Ostertagia ningshaanensis*, and *Ostertagia lanceata*; not consistent with *Marshallagia* (?). Seen in abstract only, but discussed by Liu and Chen (1988) and Luo, Chen, and Wu (1991). Incorrectly referred to *Marshallagia* in some online authoritative databases.

***Ostertagia lanceata* Luo, Chen and Wu, 1991**—Originally described under *Ostertagia* (*Grosspiculagia*) based on specimens in bharal from Qinghai Province, China (Tibet). Indicated to resemble *O. (G.) gansuensis* and *O. arctica*; not consistent with *Marshallagia* (?). The bursa is not elongate and the rays are relatively robust rather than narrow and long. There is a narrow, elongate gubernaculum and a relatively short dorsal ray, 96–149 μm in length; “7” papillae are relatively parallel with convergent or medially directed tips; spicules about 210 in length, dorsal and ventral processes of equal length, not attaining tip of main shaft; trifurcation at 55% (Luo, Chen, and Wu, 1991). Incorrectly referred to *Marshallagia* in some authoritative online databases.

***Ostertagia lasensis* (Asadov, 1953)**—Originally described under *Ostertagia* (*Skrjabinagia*) based on specimens in roe deer (*Capreolus capreolus* Linnaeus) from Eurasia. The Sjöberg’s organ is typical of *Ostertagia* rather than *Marshallagia*. This species is considered a synonym of *Ostertagia kolchida* and *Ostertagia popovi*; recognized as the minor morphotype of *Ostertagia leptospicularis* Asadov, 1953 according to Drózdź (1965, 1995); see also *Ostertagia rubricervi* Andrews, 1963.

***Ostertagia nemorhaedi* Schulz and Kadenazii, 1950**—Originally described under *Ostertagia* (*Grosspiculagia*) based on specimens in Himalayan goral (*Naemorhedus goral* (Hardwicke)) from southern Eurasia. The Sjöberg’s organ is not typical of *Marshallagia*; short dorsal ray (see Skrjabin et al., 1954). Minor morphotype of *Ostertagia muraschkinzevi* Schulz and Kadenazii, 1950 according to Drózdź (1995).

***Ostertagia nianquingtanggulaensis* K’ung and Li, 1965**—Originally described under *Ostertagia* (*Grosspiculagia*) based on specimens in domesticated sheep from Tibet (K’ung and Li, 1965); later redescribed based on specimens in domesticated sheep and goats from western Nepal (Johsi, Gibbons, and Jacobs, 1997). Based on the structure of the 2-2-1 bursa, presence of a proconus, small eggs, and other characters, it is not compatible with *Marshallagia* and appears to be a major-morphotype form; possibly referable to *Sarwaria*.

***Ostertagia ningshaanensis* Liu and Chen, 1988**—Originally described under *Ostertagia* (*Grosspiculagia*) based on specimens in takin (*Budorcas taxicolor* Hodgson) from Ningshaan, China. Indicated to be similar to *O. arctica* and *O. gansuensis*; not consistent with *Marshallagia* in having a short dorsal ray and 2-2-1 bursa (Liu and Chen, 1988). Incorrectly referred to *Marshallagia* in some authoritative online databases.

***Ostertagia petrovi* Pushmenkov, 1937**—Originally reported as an undescribed species of *Ostertagia* in reindeer (*Rangifer tarandus* (Linnaeus)) from Russia. Bursa is incorrect for *Marshallagia*, with short dorsal ray; considered teratological specimen (Drózdź, 1965). Transferred to *Ostertagia* (*Grosspiculagia*) in Skrjabin et al. (1954).

***Ostertagia rubricervi* Andrews, 1963**—Originally described in *Ostertagia* (*Grosspiculagia*) based on specimens in red deer (*Cervus elaphus* L.) from New Zealand (Andrews, 1963). Bursa and genital cone consistent with a minor morphotype of *Ostertagia*, excluded from *Marshallagia* based on structure of

dorsal ray, Sjöberg's organ, and genital cone. Apparently a synonym of *Ostertagia kolchida*, the minor morphotype for *Ostertagia leptospicularis*.

***Ostertagia skrjabini* Shen, Wu and Yen, 1959**—Established as *Ostertagia* (*Grosspiculagia*) based on specimens in *Capra hircus* from Kweiyang and Tsinan, China. Minor morphotype consistent with *Ostertagia*, excluded from *Marshallagia* based on short

dorsal ray, structure of Sjöberg's organ, and small eggs (Shen, Wu, and Yen, 1959).

***Ostertagia volgaensis* Tomskich, 1938**. Originally described in *Ostertagia* (*Grosspiculagia*) based on specimens in domesticated sheep from central Russia. Incompatible with *Marshallagia* in the form of the bursa, short dorsal ray, and small eggs (see Skrjabin et al., 1954).

ERRATUM

Due to a series of errors, none of which were the authors', this portion of Table I, in Volume 98, page 819–820, was printed incorrectly. The corrected portion is in bold font.

USNPC*	Species	Host	Locality	Specimens†
4691 (type)	<i>M. occidentalis</i>	<i>O. aries</i>	Montana, USA	0/ 2/ 0
14467	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	8/ 0/ 2
14488	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	1/ 0/ 0
14878	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	0/ 0/ 9
15587	<i>M. occidentalis</i>	<i>O. aries</i>	Montana, USA	0/ 1/ 0
15864	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	1/ 0/ 1
16219	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 1
16315	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	1/ 0/ 0
16320	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 3
16322	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 1
16324	<i>M. occidentalis</i>	<i>O. aries</i>	Colorado, USA	0/ 1/ 0
29493	<i>M. marshalli</i>	<i>O. aries</i>	Idaho, USA	2/ 0/ 0

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USNPC*	Species	Host	Locality	Specimens†
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14467	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	8/ 0/ 2
14488	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	1/ 0/ 0
14878	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	0/ 0/ 9
15587	<i>M. occidentalis</i>	<i>O. aries</i>	Montana, USA	0/ 1/ 0
15864	<i>M. marshalli</i>	<i>O. aries</i>	Montana, USA	1/ 0/ 1
16219	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 1
16315	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	1/ 0/ 0
16320	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 3
16322	<i>M. marshalli</i>	<i>O. aries</i>	Colorado, USA	0/ 0/ 1
16324	<i>M. occidentalis</i>	<i>O. aries</i>	Colorado, USA	0/ 1/ 0
29493	<i>M. marshalli</i>	<i>O. aries</i>	Idaho, USA	2/ 0/ 0