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ASPIDODERIDAE FROM NORTH AMERICA, WITH THE DESCRIPTION OF A NEW SPECIES OF *ASPIDODERA* (NEMATODA: HETERAKOIDEA)

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ABSTRACT: Aspidodera sogandaresi n. sp. (Heterakoidea: Aspidoderidae) from Dasypus novemcinctus Linnaeus, 1758 is herein described. This nematode occurs in armadillos from as far south as the canal zone of Panama, north through central Mexico, and into the southern United States. Previously identified as Aspidodera fasciata (Schneider, 1866), this new species has blunt projections on the lips and lateral expansions at the distal tips of the spicules, whereas A. fasciata has conspicuous digitiform projections on the lips, and a terminal round expansion at the tips of the spicules. Other species of the family present in North America include Aspidodera binansata Railliet and Henry, 1913; Aspidodera vazi Proença, 1937; and Lauroia trinidadensis Cameron, 1939.

The Aspidoderidae, Skrjabin and Schikhobalova, 1947 (Ascaridida: Heterakoidea) currently includes 16 species divided among 4 genera. The worms occur in the cecum and large intestine of mammals with southern Nearctic and general Neotropical distributions. The known host range for species in the family includes xenarthrans, didelphiomorphs, and hystricognath and sigmodontine rodents.

Five species of the family have been recorded from armadillos north of the Isthmus of Panama, including Mexico and the United States (Chandler, 1946; Caballero, 1955; Flores-Barroeta, 1956); in opossums from Guatemala, Mexico, Panama, and the United States (Chandler, 1932; Foster, 1939; Caballero and Cerecero, 1944; Aldes, 1995); and in hystricognath and geomyid rodents from the United States, Mexico (Lamothe-Argumedo et al., 1997), and Central America. Species recorded include Aspidodera fasciata (Schneider, 1866) Railliet and Henry, 1913; Aspidodera raillieti Travassos, 1913; Lauroia dasypi Caballero, 1955; Lauroia intermedia Flores-Barroeta, 1956; and Paraspidodera uncinata (Rudolphi, 1819) Travassos, 1914.

Species assignable to *Aspidodera* Railliet and Henry, 1912 are diagnosed by the distinctive structure of the "hood" on the anterior-most end of the nematode, which has recurrent grooves covered by a cuticle; these structures are known as the cordons (Inglis, 1957). Characters used in combination to identify these nemas to the level of the species include the cordons, the shape and length of the spicules, the shape of the spinneret, and the number of caudal papillae (Santos et al., 1990). Herein, we describe a new species of *Aspidodera* and present 3 new records of *Aspidodera* in Central and North America.

MATERIALS AND METHODS

Thirteen nine-banded (or long-nosed) armadillos, *Dasypus novemcinctus* Linnaeus, 1758, were collected from 2001 through 2003 in Mexico and the United States (Fig. 1). Armadillos were obtained from local hunters and as road-kills in Morelos, Nayarit, Oaxaca, Veracruz, Florida, and Texas. Some specimens were captured alive and killed with chloroform in the field. Additional specimens collected from armadillos in the United States and Panama were borrowed from the United States National Parasite Collection (USNPC).

For this study, the large intestine was opened, washed in water, and aliquots were examined with a dissecting microscope. Nematodes found

were washed in water and immediately placed in 9% physiological saline prior to killing. Separate aliquots or samples of individual parasites were killed either in glacial acetic acid, 70% ethanol, or 10% formalin. Specimens were stored in either 70% ethanol or 10% formalin. Some specimens collected alive were washed in 9% saline solution and preserved in 95% ethanol for later study using molecular methods. Note that these specimens are deposited in the Harold W. Manter Laboratory of Parasitology (HWML) and will be available for DNA sequencing, and can be requested by referencing the HWML number. For examination via light microscopy, specimens fixed as above were cleared in lactophenol, mounted on a slide under a No. 1 coverslip, and studied with a light microscope. Specimens were identified using published descriptions and by direct comparison with type specimens. Specimens prepared for scanning electron microscopy (SEM) were treated with osmium-thiocarbohydrazide-osmium-thiocarbohydrazide-osmium (OTOTO), dehydrated in 100% ethanol, dried to a nonliquid state by critical-point drying using CO₂, attached to an SEM stub, and sputter coated with gold palladium.

Specimens examined were borrowed from and deposited into the following collections: Colección Helmintologica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil; Colección Nacional de Helmintos (CNHE), Mexico City, Mexico; Collection of Parasitology of the School of Veterinary Medicine of the University of Hokkaido (CPSVM), Sapporo, Japan; and the USNPC, Beltsville, Maryland. Species used for comparisons included *Aspidodera vazi* Proença, 1937 (CHIOC 9641, 14086, 18354); *Aspidodera binansata* Railliet & Henry, 1913 (CHIOC 8260, 9637, 9639, 9643, 18351, and USNPC 58363); *A. fasciata* (CHIOC 4119, 11190; USNPC 8550, 26644, 59968; CPSVM 2950); *Aspidodera scoleciformis* (Schneider, 1851) Railliet and Henry, 1912 (CHIOC 10, 5681, 5809, 8387, 9668, 11408, 14551, 15073, 15257, 18355, 19494, 19628, 20046, 34557, 34568); and *L. intermedia* (CNHE 2460).

Specimens were measured using an ocular micrometer or Sigmascan Pro Image Analyzer (Albinger et al., 1995) attached to a Zeiss ultraphot microscope. Measurements are given in micrometers. For each character studied, the range is given first, followed by sample mean, and coefficient of variation (as a percent value; Sokal and Rohlf, 1995) in parentheses. Drawings were made with a Wild microscope equipped with a drawing tube. Specimens imaged with SEM were exposed to a beam of 15 KV on both Hitachi field S-2460N and S-3000 scanning electron microscopes.

RESULTS

From the 11 armadillos infected, we identified 4 species of aspidoderid nematodes including 1 of *Lauroia* Proença, 1938 and 3 of *Aspidodera*. One of the species of *Aspidodera* was undescribed. Species found in *D. novemcinctus*, localities, and museum accession numbers are listed in Table I. This is the first record of a species of *Aspidodera* from armadillos in Mexico.

Redescription

Lauroia trinidadensis Cameron, 1939

Diagnosis: Nemas with slender bodies, sharp tail, red when alive. Cephalic plates with continuous cordons, velum around

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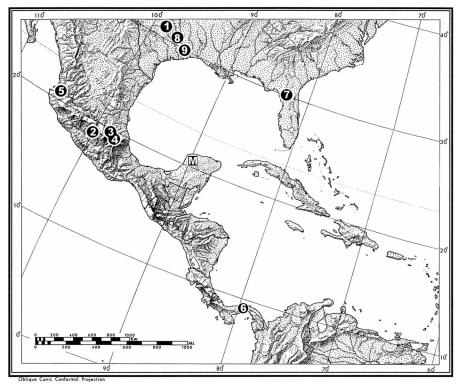


FIGURE 1. Collecting localities for *A. sogandaresi* n. sp. in North and Central America. (1) El Pedregal, 18 miles north by road (U.S. 281), Lampasas, Texas; (2) Teacalco; (3) Isla Limón Presa, Miguel Alemán; (4) Piscifactoria Temazcal; (5) Carretera Tepic-Aguamilpa Km 8; (6) Canal Zone; (7) Alachua County; (8) College Station; (9) Houston; M) Mérida.

lateral and posterior margins of plate; interlabium developed as a cuticular ridge at base of plates. Lateral longitudinal fields developed into thick and round lateral alae. Precloacal sucker without rim. Gubernaculum absent.

Taxonomic summary

Host: Dasypus novemcinctus Linnaeus, 1758.

Localities: Mexico: Oaxaca, Isla Limón Presa Miguel Alemán, 18°17'07"N, 96°34'55"W, 49 m elevation (22 May 2001; prevalence 50% 2/2). Piscifactoria Temazcal, 18°15'30"N, 96°25'14"W, 62 m elevation (24 May 2001). Yucatán, Mérida, 20°58'52"N, 89°36'36"W (19 November 2001) (Fig. 1).

Specimens deposited: Vouchers CMNPA2005-0025, CNHE5363 through CNHE5366, HWML48193 through HWML48195, HWML48244, CHIOC35432, USNPC97135, and USNPC97136.

Habitat: Attached to mucosa and in lumen of large intestine.

Aspidodera binansata Railliet and Henry, 1913

Diagnosis: Two recurrent branches of cordons on surface of dorsal plate, latero-ventral plates bearing 1 anterior and 1 posterior loop. Interlabium arising as a projection between plates. Lateral longitudinal fields developed in thin lateral alae. Spinneret whip-shaped.

Taxonomic summary

Host: Dasypus novemcinctus Linnaeus, 1758.

Localities: Mexico: Yucatán, Mérida, 20°58'52"N, 89°36'36"W

(19 November 2001). Panama: Canal Zone, 08°57′41″N, 79°33′54″W (Fig. 1).

Specimens deposited: Vouchers CNHE5367 and USNPC58363. *Habitat:* In lumen of large intestine.

Aspidodera vazi Proença, 1937

Diagnosis: Very elongated hood, posterior loops of hood widely separated on each plate. Interlabium arising as projection between plates. Lateral longitudinal fields simple or with lateral alae. Spinneret whip-shaped.

Taxonomic summary

Host: Dasypus novemcinctus Linnaeus, 1758.

Localities: Mexico: Nayarit, Carretera Tepic-Aguamilpa Km 8, 21°32'16"N, 104°52'25"W, 79 m elevation (16 June 2003). Oaxaca, Isla Limón Presa Miguel Alemán, 18°17'07"N, 96°34'55"W, 49 m elevation (22 May 2001; prevalence 50% 2/ 2). Piscifactoria Temazcal, 18°15'30"N, 96°25'14"W, 62 m elevation (24 May 2001) (Fig. 1).

Specimens deposited: Vouchers CNHE5358, HWML48191, HWML48192, and USNPC97134.

Habitat: In lumen of large intestine.

Description

Aspidodera sogandaresi n. sp.

(Figs. 2–6)

Diagnosis (358 worms collected from 8 localities in North America [Table I]; 21 additional specimens borrowed from

Locality	Georeference	Species	Collection number
Mexico			
Km 8, carretera Tepic-Aguamilpa,	21°32′16″N	Aspidodera sogandaresi	HWML48189
Nayarit	104°52′25″W (79 m)	Aspidodera vazi	CNHE5358
Teacalco, Morelos	18°37′12″N;	Aspidodera sogandaresi	HWML48184, CHIOC35429, CMNPA2005-0023, CNHE5359
	99°27′20″W		
Piscilfactoría Temazcal, Oaxaca	18°15′30″N	A. sogandaresi	HWML48190, CNHE5362,
	96°25′14″W (62 m)	-	CHIOC35431
		A. vazi	HWML48192
		Lauroia trinidadensis	CNHE5365
Isla Limón, Oaxaca	18°17′07″N 96°34′55″W	A. sogandaresi	HWML48185-7, CNHE5360, USNPC97133
		A. vazi	HWML48191, USNPC97134
		L. trinidadensis	HWML48193-5, HWML48244, CHIOC35432, CMNPA2005-0025, CNHE5363-4, USNPC97135-36
Mérida, Yucatán	20°58′52″N	Aspidodera binansata	CNHE5367
	89°36′36″W	L. trinidadensis	CNHE5366
Panama			
Canal Zone	08°57′41″N	A. sogandaresi	USNPC58605
	79°33′54″W	A. binansata	USNPC58363
United States			
El Pedregal, 18 miles north of Lam- pasas, Texas on U.S. 281	31°19'34"N 98°09'33"W (311 m)	A. sogandaresi	HWML48179,* HWML48180,† HWML48181-3, HWML48243, CHIOC35430, CMNPA2005-0024 CNHE5361, USNPC97132
College Station, Texas	30°35′59″N 96°18′42″W	A. sogandaresi	USNPC27135
Alachua County, Florida	29°40'N 82°20'W	A. sogandaresi	HWML48188

TABLE I. Collection data for aspidoderid nematodes from the nine-banded armadillo (*Dasypus novemcinctus* Linnaeus, 1758) across Central and North America.

* Holotype.

† Allotype.

USNPC): Nemas with slender bodies, sharp tail, white when alive. Cephalic cap or hood with anastomosing cordons, 6 anteriad and 6 posteriad loops; interlabium well developed (Fig. 2a, b). Lips simple with blunt projections laterally. Interlocking structures between latero-ventrals formed by blunt projection on both sinistro-ventral and dextro-ventral lips (Fig. 2a). Dorsal lip with 1 papilla on each side; latero-ventral lips with 1 papillae and amphid on dorsal side and circular medial papilla (Fig. 2b). Inner face of dorsal lip with 2 pairs of sockets (Fig. 2b). Lateral fields not forming lateral alae (Fig. 3a).

Males (based on measurements of 29 specimens unless otherwise indicated): Body length 4,400–7,009, 5,855 (10.6%); width at midbody 160–337, 268 (14.3%) (Fig. 3a). Cephalic hood 191–264, 221 (9.3%) long; 112–161, 138 (10%) wide. Nerve ring and excretory pore located 390–548, 455 (n = 25, 9.4%) and 552–775, 669 (n = 27, 9.46%), respectively, from anterior end. Stoma length 33–58, 44 (n = 28, 14.8%). Length of esophagus including bulb 1,052–1,502, 1,313 (8.5%). Pharynx length and width 43–88, 64 (n = 28, 13.3%) by 33–56, 44 (n = 28, 13.5%). Corpus of esophagus 891–1,327, 1,086 (10.6%) long. Width of esophagus at level of nerve ring 50–78, 61 (n = 28, 10.1%). Bulb of esophagus pyriform 167–229, 190 (n = 28, 7.3%) long by 148–209, 167 (n = 28, 8%) at maximum width. Length of left spicule 267–372, 331 (n = 25, 10.1%).

7.2%); width at calomus 16–26, 22 (n = 25, 11.1%). Length of right spicule 226–363, 320 (n = 25, 10.2%); width at calomus 16–26, 21 (n = 24, 12.9%). Gubernaculum 101–148, 118 (n = 25, 7.8%) long by 14–27, 21 (n = 22, 14.2%) wide (Fig. 3b, c). Rim of sucker 66–95, 75 (9.2%) in diameter.

With 23–29 pairs of caudal sessile papillae distributed in fields anterior, lateral, and posterior to cloaca. Anterior or precloacal papillae consisting of 3 subventral and 1 lateral pairs, 1 single papilla flanked by 2 papillae on posterior part of rim. Lateral or adcloacal papillae consisting of 3–5 pairs, 1 papilla each flanking cloacal opening, 2 or 4 pairs sublateral to cloaca. Papillae distributed posterior to cloaca (postcloacal) consisting of 10–12 subventral and 5–9 lateral pairs (Fig. 3c).

Tail length 268–393, 311 (9.1%) with needle-shaped spinneret 25–46, 36 (n = 28, 14.9%) gradually tapering to a sharp point (Figs. 3b, 5a).

Females (based on measurements of 29 individuals, unless otherwise indicated): Body length 4,711–6,886, 5,601 (10.3%); width at level of vulva 219–385, 297 (19.4%). Nerve ring and excretory pore 361–523, 457 (n = 26, 10.2%) and 549–757, 648 (n = 28, 9.14%), respectively, from anterior end (Fig. 4). Cephalic hood 213–312, 259 (n = 28, 10.9%) long by 114–258, 163 (n = 28, 17.7%) wide. Stoma 31–64, 51 (n = 27, 16.5%). Total length of esophagus including bulb 1,038–1,504,

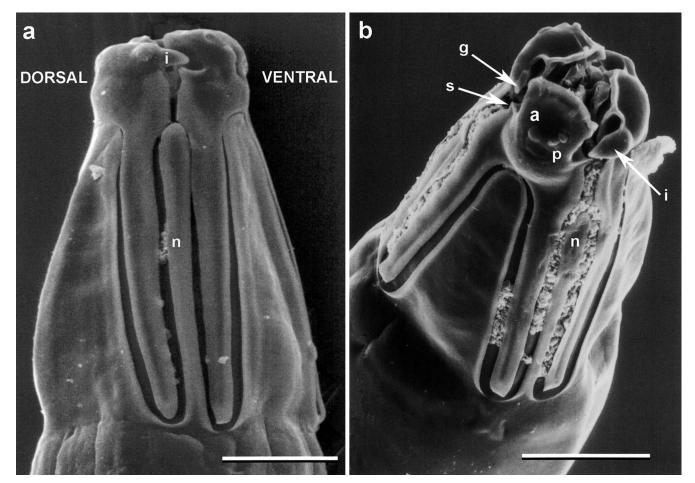


FIGURE 2. Hood of *A. sogandaresi* n. sp. (a) Detail of the right side female showing interlabium, "n"; cordons, and digitiform projection from the dorsal lip, "i." (b) Sinistroventral lip of male showing details of amphid "a"; 2 lateral papillae "p," the digitiform projection of the dextroventral lip, "g," and digitiform projection of the sinistroventral lip, "s." Scale bar = $50 \mu m$.

1,276 (n = 26, 9.0%). Pharynx 50–79, 64 (n = 27, 12.2%) long by 34–62, 49 (n = 27, 14.7%) wide. Corpus length 925–1,310, 1,071 (n = 26, 10.5%) by 41–94, 63 (n = 26, 19.9%) wide. Bulb of esophagus 158–221, 193 (n = 28, 8.4%) long by 123– 238, 168 (n = 27, 16.2%) wide (Fig. 4). Vulva located 1,811– 2,807, 2,265 (n = 24, 13.0%) from anterior end (Fig. 4). Uteri containing embryonated eggs 60–92, 71 (n = 508, 9.0%) by 40–70, 50 (n = 508, 12.9%). Tail 319–554, 418 (11.9%).

Taxonomic summary

Symbiotype: Dasypus novemcinctus Linnaeus, 1758, Museum of Southwestern Biology (MSB 145728).

Type locality: El Pedregal, 18 miles north by road (U.S. 281) from Lampasas, Texas, 31°19′34″N, 98°09′33″W; elevation 311 m (see map in Fig. 1).

Prevalence in type locality: 100% (3/3).

Date of collection of type specimens: 24 July 2001.

Other localities: Mexico: Morelos, Teacalco, 18°37'12"N, 99°27'20"W (22 May 2001; prevalence 100%, 1/2). Oaxaca, Isla Limón Presa Miguel Alemán, 18°17'07"N, 96°34'55"W, 49 m elevation (22 May 2001; prevalence 50% 2/2). Piscifactoria Temazcal, 18°15'30"N, 96°25'14"W, 62 m elevation (24 May 2001). Nayarit, Carretera Tepic-Aguamilpa Km 8, 21°32'16"N,

104°52′25″W, 79 m elevation (16 June 2003). Panama: Canal Zone, 08°57'41″N, 79°33'54″W. United States, Florida, Alachua County, 29°40'N, 82°20'W; Texas, College Station, 30°35'39″N; Texas, Houston, 96°18'42″W (Fig. 1).

Specimens deposited: Holotype, male HWML48179. Allotype, female HWML48180; paratypes HWML48181 through HWML48190, HWML48243, HWML48244, CNHE5359 through CNHE5362, CHIOC35429 through CHIOC35431, CMNPA 2005-0023, CMNPA 2005-0024, USNPC97132, and USNPC97133. Vouchers USNPC27135 and USNPC58605.

Habitat: Attached to mucosa and in lumen of large intestine. Etymology: The species is named after Dr. Franklin Sogandares-Bernal, our good friend, H. W. Baldwin Ward Medalist, and pioneer in the taxonomy and systematics of parasites from Latin American vertebrates.

Remarks

Aspidodera sogandaresi is unique in having a wide expansion at the tip of the spicules (Fig. 5a), blunt projections on the lips (Fig. 6a), and lateral fields without conspicuous lateral alae. Aspidodera sogandaresi is different from A. scoleciformis, Aspidodera ansirupta Proença, 1937, and A. binansata in the

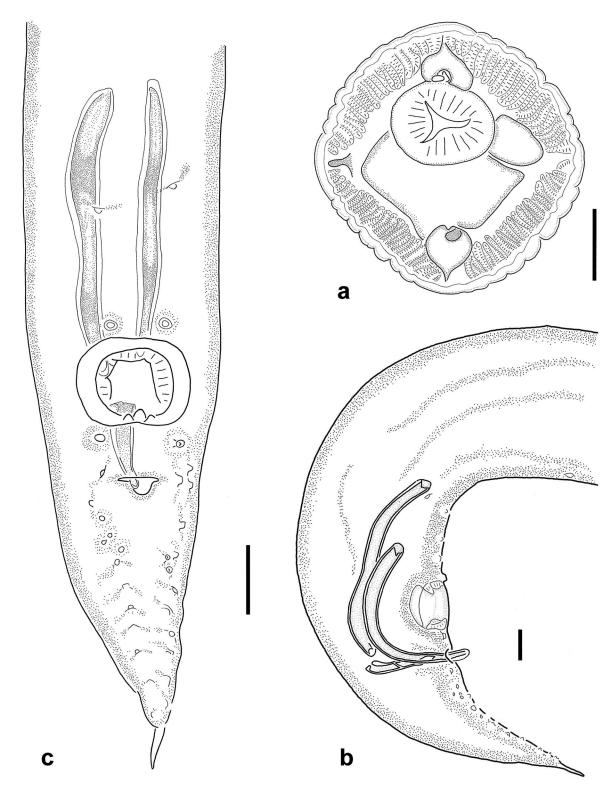


FIGURE 3. Details of the body of males of *A. sogandaresi* n. sp. (a) Cross-section showing smooth cuticle. (b) Detail of caudal end in lateral view. (c) Ventral view of caudal end showing genital papillae. Scale bar = $50 \mu m$.

structure of the cordons and in the digitiform projections of the lips. Additionally, the cephalic hood in *A. sogandaresi* is larger than that in *A. scoleciformis* and *A. ansirupta*, and has a shorter tail than both *A. scoleciformis* and *A. binansata*. It is also dif-

ferent from *Aspidodera lacombae* Vicente, 1964 in the size of the spicules and shape of the cordons.

Aspidodera sogandaresi has a shorter hood and shorter spicules as well as a needle-shaped spinneret in contrast with the

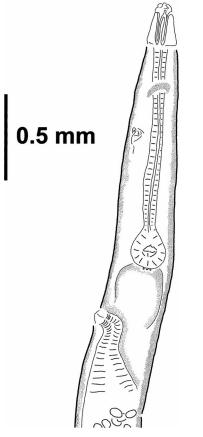


FIGURE 4. Anterior half of a female of *Aspidodera sogandaresi* n. sp. showing the relative distances of nerve ring, excretory pore, and vulva to the anterior end.

long hood, long spicules, and whip-shaped spinneret of *A. vazi*. Also, there is a long digitiform projection arising from the dextroventral lip of *A. sogandaresi* ("g" on Fig. 6a) relative to the homologous structures of *A. vazi* ("g" on Fig. 6c). The species most similar to *A. sogandaresi* is *A. fasciata*. Similarities include grooves on the hood, shape of spinneret, and size of body. However, *A. sogandaresi* can be separated from *A. fasciata* by the more blunt and simpler digitiform projections on the lips (Fig. 6a), a tail tapering gradually to a point of the spinneret, and spicules with an expansion at the tip (Fig. 5a).

DISCUSSION

Chandler (1946) reported *A. fasciata* in armadillos near Houston, Texas, and determined that his material differed from *A. fasciata* from South America by being smaller; however, he did not consider these differences sufficient to warrant a description of these specimens as a new species. Additional specimens of *A. sogandaresi* were also collected from a nine-banded armadillo by Emmet Price on 2 April 1926, from the vicinity of College Station, Texas (USNPC27135); later, these specimens were identified by E. A. Chapin as *A. fasciata*. Comparison of these worms with our samples and with specimens of *A. fasciata* from South America (USNPC17957 and USNPC59968) allowed us to identify the blunt projections on the lips of *A. sogandaresi* (Fig. 6a) in contrast to the heavily serrated lips of *A. fasciata* (Fig. 6b). Figure 6 a, b shows that

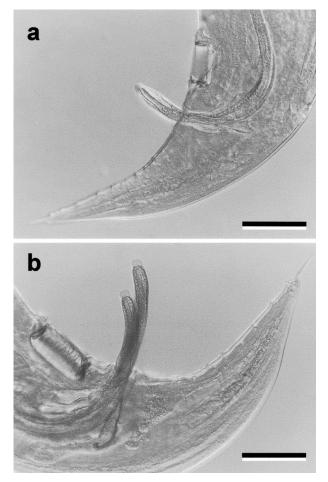


FIGURE 5. Comparison of caudal end and tip of spicules of 2 species of *Aspidodera* in lateral view. (a) *A. sogandaresi* n. sp. (b) *A. fasciata*. Scale bar = 100μ m.

the apparent simple interlocking lip system of *A. sogandaresi* is also evident on the sockets of the inner part of the dorsal lips. Figure 6a clearly shows 2 pairs of sockets on the inner part of the dorsal lip that complements the simple projections arising from the lateroventral lips. In contrast, the homologous sockets on the dorsal lip of *A. fasciata* (Fig. 6b) are apparently more complex, matching the heavily serrated projections arising from the latero-ventral lips.

The number of caudal papillae was used by Santos et al. (1990) to distinguish among species in the Aspidoderidae. However, it appears that the number of papillae is highly variable, as there is variation in the number of papillae even among worms found in the same individual host. Because of the high variability of this character within and among species, we do not recommend its use for identification of species of *Aspidodera*.

Finally, lateral alae are absent in *A. sogandaresi*; nevertheless, some specimens show a flat lateral field associated with the hypodermal cord as shown in cross-section (Fig. 3a). *A. vazi* may show a similar pattern in the lateral alae, in that Navone (1986) showed that lateral alae were present in some but not all of the individuals she examined in Argentina. It appears that lateral alae may be a polymorphic character in *A. vazi*.

Lauroia trinidadensis Caballero 1955 and L. dasypi Flores-

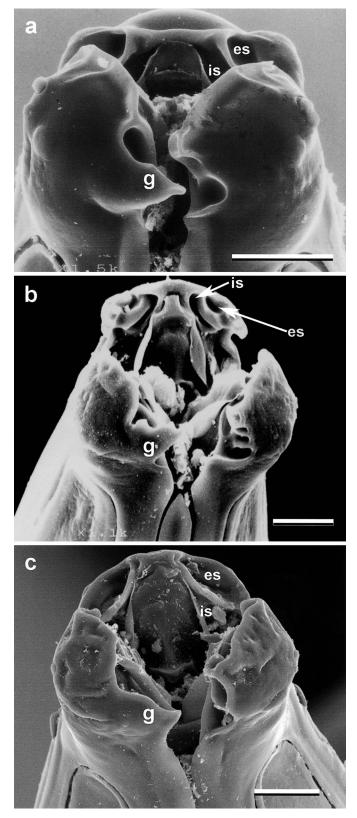


FIGURE 6. Comparison of the stoma and labial structures of 3 species of *Aspidodera* showing the digitiform projection of the dextroventral lip "g"; interior, "is"; and exterior sockets, "es." Scale bar = $20 \ \mu$ m. (a) *A. sogandaresi* n. sp. male (b) *A. fasciata* male (c) *A. vazi* female.

Barroeta 1956 were first described from nine-banded armadillos captured in Guatemala and Mexico, respectively (Caballero, 1955; Flores-Barroeta, 1956). Both species share several similarities with L. trinidadensis, including the shape of the lips, overall structure of the hood, and shape and size of spicules. Nevertheless specimens of L. intermedia show a spine between the latero-ventral lips, just at the base of the hood, that serves as the diagnostic character for the species. According to the original description, L. dasypi has 3 shields with rectangular shapes in the hood (Flores-Barroeta, 1956). The study of the specimens described by Flores-Barroeta (1956) was not possible because the type specimens and apparently the collection in which they were deposited have since disappeared. Because the dorsal lip of L. dasypi is described as being narrower and shorter than the latero-ventral lips, it is not possible that the latter can be rectangular. For these reasons, we consider L. dasypi to be a species inquirendae.

The discovery of A. vazi, A. binansata, and L. trinidadensis in Mexico represents a substantial extension of the known range of these species. While L. trinidadensis now appears to occur in armadillos only around the Caribbean region and in tropical Mexico, both A. vazi and A. binansata have been collected from armadillos from throughout the subtropical and tropical regions of South and Central America and Mexico. The geographic distribution of both A. vazi and A. binansata is nearly concordant with the known range of D. novemcinctus (see Taulman and Robbins, 1996). *Dasypus novemcinctus* has a wide geographic distribution, occurring from northern Argentina to the southcentral United States. This armadillo is capable of surviving in areas with relatively few days of freezing temperatures (Taulman and Robbins, 1996) and has been recently expanding its range to the north. Moreover, some populations of the same species show a continuous range expansion with documented long-distance migration by fertile individuals (Frutos and van den Bussche, 2002).

In a comparable manner, these factors may also explain the presence of *A. sogandaresi* in armadillos over a vast area of Central and North America. Up to the present time, *A. sogandaresi* appears to be the only sylvatic species of *Aspidodera* found in the United States. As summarized by Santos et al. (1990), the known host range for *A. vazi* includes both *D. novemcinctus* and *Tolypeutes matacus* (Desmarest, 1804), whereas *A. binansata* has been recorded in *D. novemcinctus*, *Euphractus sexcinctus* (Linnaeus, 1758), *Cabassous unicinctus* (Linnaeus, 1758), *Chaetophractus villosus* (Desmarest, 1804), and *Dasyprocta leporina* (Linnaeus, 1758).

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