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Systematics of the genus *Gnathostoma* (Nematoda: Gnathostomatidae) in the Americas

Sistemática del género *Gnathostoma* (Nematoda: Gnathostomatidae) en América

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Abstract. To date, more than 20 species of the genus *Gnathostoma* have been described as parasites of mammals, 9 of them in the Americas. However, the taxonomic status of some of these species has been questioned. The main goal of this study is to clarify the validity of the American species included in the genus. In order to complete this objective, we analyze type and/or voucher specimens of all these species deposited in 6 scientific collections, through morphometric and ultrastructural studies. Based on diagnostic traits as host specificity, site of infection, body size, cuticular spines, presence of 1 or 2 bulges in the polar ends of eggs, as well as eggshell and caudal bursa morphology, we re-establish *Gnathostoma socialis* (Leidy, 1858) and confirm the validity of other 6 species: *Gnathostoma turgidum* Stossich, 1902, *Gnathostoma americanum* Travassos, 1925, *Gnathostoma procyonis* Chandler, 1942, *Gnathostoma miyazakii* Anderson, 1964, *Gnathostoma binucleatum* Almeyda-Artigas, 1991, and *Gnathostoma lamothei* Bertoni-Ruiz, García-Prieto, Osorio-Sarabia and León-Régagnon, 2005. *Gnathostoma didelphis* Chandler, 1932 and *Gnathostoma brasiliensis* Ruiz, 1952 are considered synonyms of *G. turgidum*. Finally, based on a wide revision of specimens deposited in 6 American collections, we conclude that records of *Gnathostoma spinigerum* Owen, 1836 in the Americas are invalid.

Key words: systematics, taxonomy, *Gnathostoma*, Americas, Mexico, synonyms.

Resumen. A la fecha, se han descrito más de 20 especies del género *Gnathostoma* parásitas de mamíferos, 9 de ellas en América. Sin embargo, el estado taxonómico de algunas ha sido cuestionado. El objetivo de este estudio es aclarar la validez de las especies americanas incluidas en el género. Para ello, se analizaron ejemplares tipo o de referencia de todas las especies, depositados en 6 colecciones científicas, mediante estudios morfométricos y ultraestructurales. Con base en rasgos diagnósticos como especificidad hospedatoria, sitio de infección, dimensiones corporales, espinas cuticulares (número de puntas, densidad, forma y distribución), presencia de uno ó dos tapones polares en los huevos, así como morfología de la bursa, patrón papilar y de la cubierta de los huevos, se re-establece a *Gnathostoma socialis* (Leidy, 1858) y se confirma la validez de otras 6 especies: *Gnathostoma turgidum* Stossich, 1902, *Gnathostoma americanum* Travassos, 1925, *Gnathostoma procyonis* Chandler, 1942, *Gnathostoma miyazakii* Anderson, 1964, *Gnathostoma binucleatum* Almeyda-Artigas, 1991 y *Gnathostoma lamothei* Bertoni-Ruiz, García-Prieto, Osorio Sarabia y León-Régagnon, 2005. *Gnathostoma didelphis* Chandler, 1932 y *Gnathostoma brasiliensis* Ruiz, 1952 son consideradas sinónimos de *G. turgidum*. Basados en una amplia revisión de material depositado en 6 colecciones Americanas, se invalidan los registros de *Gnathostoma spinigerum* Owen, 1836 en América.

Palabras clave: sistemática, taxonomía, *Gnathostoma*, América, México, sinónimos.

Introduction

Gnathostoma spinigerum Owen, 1836, type species of the genus, was described as a stomach parasite of a tiger (*Panthera tigris*) at the London Zoo. Thereafter, more than

twenty species parasitizing mammals (rodents, domestic and wild swine, felids, otters, raccoons, marsupials, and weasels), have been described mainly in Asia and America (Miyazaki 1991; Bertoni-Ruiz et al., 2005) (Table 1).

Adult worms of most species inhabit the gastric wall of definitive hosts; however, some species parasitize esophagus, kidneys or the urinary bladder (Table 1).

The advanced third stage larvae (A₃L) of some species in the genus (*Gnathostoma binucleatum* Almeyda-Artigas,

Table 1. Current composition of the genus *Gnathostoma*

Species	Definitive host	Miyazaki (1961)	Daengsvang (1980)	Miyazaki (1991)
<i>Gnathostoma spinigerum</i> Owen, 1836 ^{1, As}	<i>Panthera tigris</i>	Valid species	Valid species	Valid species
<i>Gnathostoma socialis</i> (Leidy, 1858) ^{1, Am}	<i>Mustela vison</i>	<i>Species inquirenda</i>	Not included	Not included
<i>Gnathostoma hispidum</i> Fedtschenko, 1872 ^{1, As, Eu}	<i>Sus scrofa</i>	Valid species	Valid species	Valid species
<i>Gnathostoma turgidum</i> Stossich, 1902 ^{1, Am}	<i>Didelphis azarae</i>	Valid species	Valid species	Valid species
<i>Gnathostoma americanum</i> Travassos, 1925 ^{1, Am}	<i>Leopardus tigrinus</i>	Valid species	Valid species	Valid species
<i>Gnathostoma doloresi</i> Tubangui, 1925 ^{1, As}	<i>Sus scrofa</i>	Valid species	Valid species	Valid species
<i>Gnathostoma didelphis</i> Chandler, 1932 ^{2, Am}	<i>Didelphis virginiana</i>	Synonym of <i>G. turgidum</i>	Valid species	Synonym of <i>G. turgidum</i>
<i>Gnathostoma brasiliensis</i> Ruiz, 1952 ^{2, Am}	<i>Lutreolina crassicaudata</i>	Synonym of <i>G. turgidum</i>	Valid species	Not included
<i>Gnathostoma nipponicum</i> Yamaguti, 1941 ^{3, As}	<i>Mustela sibirica</i>	Valid species	Valid species	Valid species
<i>Gnathostoma procyonis</i> Chandler, 1942 ^{1, Am}	<i>Procyon lotor lotor</i>	Valid species	Valid species	Valid species
<i>Gnathostoma miyazakii</i> Anderson, 1964 ^{4, Am}	<i>Lutra canadensis</i>	Not included	Valid species	Valid species
<i>Gnathostoma malaysiae</i> Miyazaki and Dunn, 1965 ^{1, As}	<i>Rattus surifer</i>	Not included	Valid species	Valid species
<i>Gnathostoma vietnamicum</i> Le-Van-Hoa, 1965 ^{4, As}	<i>Lontra elioti</i>	Not included	Valid species	Valid species
<i>Gnathostoma binucleatum</i> Almeyda-Artigas, 1991 ^{1, Am}	<i>Leopardus pardalis</i>	Not included	Not included	Not included
<i>Gnathostoma lamothei</i> Bertoni-Ruiz, García-Prieto, Osorio-Sarabia and León-Règagnon, 2005 ^{1, Am}	<i>Procyon lotor hernandezi</i>	Not included	Not included	Not included

1= Stomach; 2= Liver 3=Esophagous; 4= Kidney; As= Asia; Eu= Europe; Am=American continent.

1991, *Gnathostoma doloresi* Tubangui, 1925, *Gnathostoma hispidum* Fedtschenko, 1872, *Gnathostoma nipponicum* Yamaguti, 1941, and *G. spinigerum*) may infect humans causing the disease called gnathostomiasis; this infection is considered to be an injurious health problem in some countries as Thailand, Vietnam, and Mexico. Due to the medical importance of this genus, it has been intensively studied (Lamothe-Argumedo, 2003).

The first taxonomic revision of this genus was conducted by Baylis and Lane (1920); these authors established *Gnathostoma* as type genus of the family Gnathostomatidae; almost all species described at that time, were considered synonyms of *G. spinigerum*, except for *G. hispidum* and *Gnathostoma turgidum* Stossich, 1902. Miyazaki (1960) analyzed the validity of the 19 described species of *Gnathostoma*, confirming the independence of only 7 of them. In a further revision, Daengsvang (1980) recognized the validity of 12 species. Finally, Miyazaki (1991) reduced this number to 10, not validating *Gnathostoma brasiliensis*

Ruiz, 1952 nor *Gnathostoma didelphis* Chandler, 1932. Since then, 2 more species have been described: *G. binucleatum* and *Gnathostoma lamothei* Bertoni-Ruiz, García-Prieto, Osorio-Sarabia and León-Règagnon, 2005 (Almeyda-Artigas, 1991; Bertoni-Ruiz et al., 2005) (Table 1).

The taxonomic status of several American species of *Gnathostoma* has been questioned (Table 1); authors as Miyazaki (1960), Anderson (1964) and Daengsvang (1980) pointed out the necessity of re-studying material of *Gnathostoma socialis* (Leidy, 1858), *G. brasiliensis*, and *G. didelphis*. On the other hand, original descriptions of valid species as *Gnathostoma americanum* Travassos, 1925, *Gnathostoma miyazakii* Anderson, 1964, *Gnathostoma procyonis* Chandler, 1942 and *G. turgidum* are incomplete in different morphological aspects. For these reasons, the main goal of this work is to clarify the status of the American species, based on specimens deposited in scientific collections. In addition, we present new morphological data which complete the original descriptions.

Materials and methods

Between 2002-2005, specimens pertaining to all species recorded for the genus *Gnathostoma* in the Americas, were obtained through loans from the following institutions: Canadian Museum of Nature Invertebrate Collections-Parasites (CMNPA), Ottawa, Canada; Colección Nacional de Helminthos (CNHE), Instituto de Biología, UNAM, Mexico City; Harold W. Manter Laboratory of Parasitology (HWML), University of Nebraska-Lincoln, Nebraska, USA.; Coleção Helminológica do Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil; Coleção de Parasitos do Museu de Zoologia, Universidade de São Paulo (MZUSP), São Paulo, Brazil, and the United States National Parasite Collection (USNPC), Beltsville, Maryland, USA. Specimens were cleared using Amman's lactophenol and temporary mounted for morphological study. Measurements are presented as the range, with means, standard deviation and sample size in parentheses and expressed in millimeters, unless otherwise stated. Some voucher specimens deposited in several collections were studied under scanning electron microscopy (SEM), with the respective Curators permission. These specimens were dehydrated using gradual ethanol series, and dried to critical point with carbon dioxide. Dry specimens were mounted on metal specimen stubs, coated with gold-palladium mixture, and examined with a SEM Hitachi S2460N.

Results

Based on the present study, the genus *Gnathostoma* in the Americas is composed by 7 species: 2 parasites of Felidae (*G. binucleatum* and *G. americanum*), 2 of Procyonidae (*G. lamothei* and *G. procyonis*), *G. miyazakii* and *G. socialis* that have been recorded in Mustelidae, and finally, *G. turgidum*, a common parasite of Didelphidae. The last 4 species' original descriptions are poor, so we present a detailed re-description of them. The original descriptions or re-descriptions of *G. binucleatum* and *G. lamothei* are more detailed, reason being why we only transcribe their diagnostic characteristics as were referred to by the original authors. In the case of *G. americanum*, its original description is incomplete and type specimens are in poor condition; for these reasons, we only present a very small diagnosis based on the original description. In some cases, we add some morphological observations not mentioned previously. Additionally, the validity of each species is briefly discussed.

Gnathostoma americanum Travassos, 1925

Diagnosis: based on Travassos (1925). Small size worms; cephalic bulb armed with uncinata hooks in 8 transverse, complete rows. One pair of lips. Cervical papilla located at first quarter of body. Body covered with cuticular spines in $\frac{3}{4}$ of their length. Spines varying in shape and size according to body region of worms: body spines immediately behind the cephalic bulb to cervical papillae level, short and broad, with 5-7 points; posterior to this region, spines gradually diminishing in size and points number (in accordance with Travassos' drawings, number of points vary from 3-4 in anterior region to 1 in the caudal region). Unequal and thin spicules, thickening from the base toward the apex; left spicule longer than right (0.97 and 0.31, respectively). Vulva opening post-equatorially. Bipolar eggs (0.63 X 0.28), with thickened shell at pole.

Taxonomic summary

Type host: *Leopardus tigrina* (Linnaeus, 1758)

Site of infection: stomach.

Type locality: Angra do Reis, Rio de Janeiro, Brazil.

Distribution: Brazil (Travassos, 1925).

Specimens examined: type CHIOC (5066).

Remarks

This species has not been recorded since its original description; re-examination of type specimens reveals its poor condition, precluding an adequate re-description. Type hosts of *G. americanum* and *G. binucleatum* pertain to the genus *Leopardus* Gray, 1842; however, both species are clearly differentiated by the morphology of eggs (with 2 polar caps in *G. americanum* and 1 polar cap in *G. binucleatum*) and by the characteristics of body spines immediately behind the cephalic bulb (with 5-7 points in the Brazilian species and 1-3 in the Mexican species).

Gnathostoma binucleatum Almeyda-Artigas, 1991

Diagnosis: based on Almeyda-Artigas (1991) and Koga et al. (1999): Medium size worms; cephalic bulb armed with uncinata hooks in 8-10 transverse, complete rows. One pair of lips. Cervical papilla located at first quarter of body (16-20 rows of body spines). Body totally covered with cuticular spines. Spines varying in shape and size according to body region of worms: body spines immediately behind the cephalic bulb to cervical papillae level, short and broad, with 1-3 points (this later, with central point larger than

laterals); spines in mid-esophageal region long and slender, with 1-2 points. From this region, number of points of spines decrease until 1 single point. Size and density of these spines gradually diminish posteriorly along the body, but not disappear. Unequal spicules, blunt apices; left spicule longer than right (1.4 and 0.31, respectively). Vulva opening slightly post-equatorially. Unipolar eggs with smooth surface and thickened shell at pole.

Additional morphological data (based on direct observations of specimens: CNHE 4026; USNPC 88152): lips trilobed, central lobe smaller than laterals. Cephalic hooks with a thick and conical base; point acute and small. Shape of cuticular spines isometric-convergent along the body. Caudal pedunculated papillae size gradient descendent (with the proximal papillae larger than the subsequent one).

Taxonomic summary

Type host: *Leopardus pardalis* Linnaeus, 1758

Site of infection: stomach.

Type locality: presa Presidente Miguel Alemán, Temascal, Oaxaca, Mexico.

Distribution: Mexico (Almeyda-Artigas, 1991); Ecuador (Almeyda-Artigas et al., 2000).

Type material: Colección Helmintológica de la Universidad Autónoma Metropolitana Unidad Xochimilco (CHUAMX), Mexico City; Holotype: 010-01; Allotype 010-02; Paratypes 010-03.

Remarks

Some previous records of *G. binucleatum* in the Americas were originally ascribed to *G. spinigerum* (e.g., Ollague et al., 1988) because both species exhibit several similar characteristics: number of rows and shape of cephalic hooks, body surface totally covered with spines, unipolar eggs, and hosts (canids and felids); however, *G. binucleatum* differs from *G. spinigerum* by the number of points in cuticular spines (a maximum of 3 points in the Mexican species and 4-5 in *G. spinigerum*) (Ratanarapee, 1982; Scholz and Ditrich, 1990; Almeyda-Artigas, 1991; Koga et al., 1999); moreover, in *G. binucleatum* most of the spines at esophagus-intestine junction level possess only 1 point, while in *G. spinigerum* spines at same region all have 3 points. In addition, the eggshell in Asiatic species has numerous pits on the surface, while the eggshell in *G. binucleatum* shows a smooth surface (Koga et al., 1999). The independence of *G. binucleatum* from *G. spinigerum*

was confirmed by Almeyda-Artigas et al. (2000), based on ITS2 sequences of both species. Up to now, *G. binucleatum* is the only species reported to be responsible of human infections in Mexico (Almeyda-Artigas et al., 2000, León-Régagnon et al., 2002) and Ecuador (Almeyda-Artigas et al., 2000).

Gnathostoma miyazakii Anderson, 1964 (Plate I, Column A) *Redescription* (based on direct observations of specimens USNPC 74372, 84150). *General:* medium size worms, with the narrowest body between the species of the genus. Cephalic bulb armed with uncinate hooks in 10 transverse, complete rows + 1 or 2 incomplete rows; cephalic hooks with a thick and ovate base; point acute and short. One pair of unilobed lips, with internal edge smooth; wider than large, protrude in the anterior end of cephalic bulb. Two simple papillae on each lip. One small amphid located between each pair of papillae. Ballonets 4 in number. All body covered with cuticular spines (spines in anterior region well defined; in posterior region spines scale-like in shape), varying in shape and size according to region and sex of worms. Cervical papilla located at the first quarter of body. Cervical sacs extend from ballonets to near nervous ring. Esophagus divided in anterior muscular (small) and posterior glandular sections.

Male (based on 2 adult): Body 42-47.6 (44.8 ± 3.95 , $n=2$) long, $0.69-0.83$ (0.76 ± 0.098 , $n=2$) maximum wide. Cephalic bulb $0.115-0.228$ (0.169 ± 0.17 , $n=2$) long, $0.113-0.130$ (0.121 ± 0.012 , $n=2$) wide; lips $0.048-0.043$ (0.045 ± 0.0035 , $n=2$) long, $0.176-0.178$ (0.177 ± 0.007 , $n=2$) wide. Cephalic hooks $0.014-0.017$ (0.016 ± 0.015 , $n=4$) long, $0.004-0.006$ (0.005 ± 0.0009 , $n=4$) wide at base. Body spines of first few rows posterior to neck are short and broad ($0.015-0.022$ [0.019 ± 0.0024 , $n=10$] long by $0.007-0.010$ [0.009 ± 0.001 , $n=10$] wide), with 2-4 points similar in size; spines at cervical papilla level similar in shape but larger than the anterior ones, $0.020-0.024$ [0.022 ± 0.0014 , $n=10$] long and $0.009-0.011$ [0.010 ± 0.0006 , $n=10$] wide at distal region; with 4-5 points, laterals larger than medial. Spines in mid-esophageal region increase their size ($0.030-0.035$ [0.033 ± 0.002 , $n=10$ long] by $0.013-0.018$ [0.016 ± 0.001 , $n=10$ wide]), with 5-7 points, laterals slightly larger than medial. Spines at esophagus-intestinal junction diminishing in size, $0.021-0.025$ [0.022 ± 0.0014 , $n=10$] long, and $0.015-0.018$ [0.017 ± 0.001 , $n=10$] wide, with 3-6 small and broad points. Lateral edges curved, resembling serrated scales. From this region, size of points and spines diminishes, turning into spines simple and rounded, lacking points. Nerve ring, cervical papillae, and excretory pore located between 12-13, 18-22, and 27-29 rows of body spines, respectively. Cervical sacs $1.2-1.6$ (1.4 ± 0.3 , $n=2$) long. Esophagus $6.7-8.6\%$ (7.63 ± 1.3 , $n=2$) of body length; long

3.2-3.6 (3.4 ± 0.28 , $n=2$). Muscular region 0.47-0.49 (0.48 ± 0.14 , $n=2$) long; glandular region 2.73-3.11 (2.92 ± 0.26 , $n=2$) long. Spicules unequal with blunt apices. Left spicule 0.32-0.40 (0.36 ± 0.056 , $n=4$) long; right spicule 0.4-0.5 (0.48 ± 0.11 , $n=2$) long, representing 12.5-15.5% (14%) of total body length. Caudal extremity lobated, tail end thin and narrow; 0.36-0.46 (0.41 ± 0.07 , $n=2$) wide; surface totally covered with rounded and minute spines, exception made of area around cloacal opening. Alae with 4 pairs of lateral, pedunculate papillae (2 precloacal, 2 postcloacal). Caudal pedunculated papillae size gradient ascendant (pairs 1-3) and descendent in pair 4. Four pairs of umbilicated ventral papillae, delicate and sessile (1 precloacal, 3 postcloacal).

Female (based on 2 complete specimens): body 37.5-41 (39.25 ± 2.47 , $n=2$) long, 0.73-0.89 (0.81 ± 0.113 , $n=2$) of maximum wide. Cephalic bulb 0.15-0.20 (0.17 ± 0.035 , $n=2$) long, 0.22-0.26 (0.24 ± 0.28 , $n=2$) wide; cephalic hooks 0.017-0.019 (0.018 ± 0.0009 , $n=4$) long, 0.0048-0.005 (0.0049 ± 0.0003 , $n=4$) wide at base. Shape of body spines similar to those described for the males. Posterior half of body with spines simple and rounded, lacking points. Nerve ring and excretory pore not observed. Cervical papillae located at the 12th-13th rows of body spines. Vulva opening at 36.06-40.05 (38.78 ± 2.82 , $n=2$) from anterior extremity. Unipolar eggs 0.067-0.075 (0.07 ± 0.003 , $n=4$) long, 0.030-0.044 (0.036 ± 0.006 , $n=4$) wide. Numerous irregularly distributed granulations on surface of eggshell. Anus 0.30-0.35 (0.32 ± 0.035 , $n=2$) from posterior end. Caudal extremity with 1 digitiform appendage.

Taxonomic summary

Type host: *Lontra canadensis canadensis* (Schreber)

Site of infection: fibrous tissue of kidneys.

Type locality: Black trout lake, Township 30, Range 22, Ontario, Canada.

Type material: holotype and allotype: USNPC 60163; paratypes Nematode Collection, Ontario Research Foundation (NCORF) 631. *Distribution*: Canada (Anderson, 1964); United States of America (Fleming et al., 1977; Whelan et al., 1983).

Remarks

The validity of this species has remained without question since its establishment by Anderson (1964); this is due to the presence of several diagnostic characteristics: very thin body, presence of roundish bosses in the posterior

part of male body, bursa ending in a digitiform appendage, vulva located in the caudal region, as well as the adult forms inhabiting kidneys. In addition, its geographic distribution is restricted to Canada and USA (Flemming et al., 1977; Whelan et al., 1983).

Gnathostoma procyonis Chandler, 1942 (Plate I, Column B)

Redescription (based on direct observations of specimens HWML 23656, 23916, 23917, 23925, 23931, 23943, 23963, 23970, 23983, 23984, 24012, 24019, 24029, 24033, 24038, 24049, 24052, 24056, 24063, 24074, 24213, 24224, 24238, 24250, 24272, 24294, 24306, 24312, 24467, 24502, 24524, 24676; USNPC 31106, 31234, 31248, 56641, 56832).

General: medium size worms, with the posterior half slightly wide. Cephalic bulb armed with uncinuate hooks in 9 transverse, complete rows + 1 incomplete row; cephalic hooks with a thick and ovate base; point acute and large. One pair of trilobed lips, central larger than laterals; wider than large, protrude in the anterior end of cephalic bulb. Two simple papillae on each lip. One small amphid located between each pair of papillae. Ballonets 4 in number. Anterior half of body covered with cuticular spines, well defined; spines in posterior region have their points reduced to short terminal prongs, then become shortened, and fused into continuous serrated ridges at the base. Spines varying in shape and size according to region and sex of worms. Cervical papilla located at the first quarter of body. Cervical sacs extend from ballonets to nervous ring, overpassing it. Esophagus divided in anterior muscular (small) and posterior glandular sections.

Male (based on 4 adults): body 17-19.2 (18.22 ± 1.01 , $n=4$) long, 1.2-1.32 (1.26 ± 0.05 , $n=4$) maximum wide. Cephalic bulb 0.26-0.28 (0.27 ± 0.14 , $n=2$) long, 0.64-0.66 (0.65 ± 0.014 , $n=2$) wide; lips 0.088-0.095 (0.091 ± 0.005 , $n=2$) long, 0.176-0.178 (0.176 ± 0.0007 , $n=2$) wide. Cephalic hooks 0.019-0.024 (0.022 ± 0.0015 , $n=8$) long, 0.0045-0.0067 (0.0055 ± 0.0006 , $n=4$) wide at base. Body spines of first few rows posterior to neck are short and broad ($0.024-0.031$ [0.028 ± 0.002 , $n=10$] long by $0.013-0.019$ [0.016 ± 0.0016 , $n=10$] wide), with 3-5 points similar in size; spines at cervical papilla level slightly larger than the anterior ones, $0.030-0.039$ [0.035 ± 0.002 , $n=10$] long and $0.028-0.034$ [0.030 ± 0.002 , $n=10$] wide at distal region; with 3-4 points, central larger 3-4 times than medial; central point ending bifurcated or with 1-2 small accessory points. Spines in mid-esophageal region increase their size ($0.043-0.047$ [0.045 ± 0.014 , $n=10$] long] by $0.017-0.020$ [0.019 ± 0.0086 , $n=10$] wide], with 3 points, medial 3-4 times larger than laterals and with 1 or 2 accessory points. Spines at esophagus-intestinal junction diminishing in size, $0.042-0.044$ [0.042 ± 0.0008 , $n=10$] long, and $0.015-0.018$ [0.016 ± 0.001 , $n=10$] wide, with 3 points, central larger than laterals. From

this region, size of points and spines diminishes; spines in posterior region have their points reduced to short terminal prongs, then become shortened, and fused into continuous serrated ridges at the base. Cervical papillae, nerve ring, and excretory pore located between 12-13, 19-23, and 26-27 rows of body spines, respectively. Cervical sacs 1.1-1.8 (1.37 ± 0.3 , $n=4$) long. Esophagus 18-21.2% (19.65 ± 1.3 , $n=4$) of body length; long 3.4-3.8 (3.6 ± 0.17 , $n=4$). Muscular region 0.44-0.49 (0.46 ± 0.02 , $n=4$) long; glandular region 2.96-3.33 (3.1 ± 0.16 , $n=4$) long. Spicules unequal with blunt apices. Left spicule 0.40-0.45 (0.42 ± 0.02 , $n=4$) long; right spicule 1.35-1.41 (1.40 ± 0.06 , $n=4$) long, representing 7.4-7.9% (7.74%) of total body length. Caudal extremity lobulated; 0.68-0.92 (0.8 ± 0.11 , $n=4$) wide; surface totally covered with small and simple spines, exception made of area around cloacal opening. Alae with 4 pairs of lateral, pedunculate papillae (2 precloacal, 1 adcloacal, and 1 postcloacal). Caudal pedunculated papillae size gradient ascendant (pairs 1-3) and descendent in pair 4. Four pairs of umbilicated ventral papillae, delicate and sessile (1 precloacal, 3 postcloacal).

Female (based on 2 complete specimens): body 20.9-23.1 (21.5 ± 1.05 , $n=2$) long, 1.35-1.45 (1.39 ± 0.04 , $n=2$) of maximum wide. Cephalic bulb 0.28-0.29 (0.28 ± 0.07 , $n=2$) long, 0.18-0.19 (0.18 ± 0.007 , $n=2$) wide; cephalic hooks 0.021-0.024 (0.022 ± 0.008 , $n=8$) long, 0.0049-0.0051 (0.005 ± 0.0003 , $n=5$) wide at base. Shape of body spines similar to those described for the males. Spines in posterior region have their points reduced to short terminal prongs, then become shortened, and fused into continuous serrated ridges at the base. Cervical papillae located at the 12-13 rows of body spines. Vulva opening at 19.89-21.98 (20.93 ± 1.47 , $n=2$) from anterior extremity. Unipolar eggs 0.058-0.064 (0.060 ± 0.002 , $n=6$) long, 0.033-0.035 (0.034 ± 0.003 , $n=5$) wide. Numerous irregularly distributed pits on surface of eggshell. Anus 0.26-0.30 (0.28 ± 0.02 , $n=2$) from anterior end..

Taxonomic summary

Type host: *Procyon lotor lotor* Linnaeus, 1758

Site of infection: stomach

Type locality: Angelina County, Texas, USA. *Distribution:* United States of America (Lockhart, 2007).

Type material: holotype, deposition not specified (see Chandler, 1942); paratypes: USNPC: 44931.

Remarks

Gnathostoma procyonis most closely resembles *G. lamothei* (for morphological differentiation see remarks on *G. lamothei*). For this reason, previous records of *G. lamothei* in Mexico (Almeyda-Artigas et al., 1994; Almeyda-Artigas et al., 2000) were erroneously assigned to Chandler's species (see Bertoni-Ruiz et al., 2005). Currently, the distribution of *G. procyonis* is restricted to USA (Lockhart, 2007). Moreover, specimens recorded in *Procyon lotor* from several localities of USA, originally identified as *Gnathostoma* sp., and deposited at HWML and USNPC, were re-identified in this study as *G. procyonis*: HWML (24074, 24156, 24213, 24224, 24238, 24250, 24272, 24294, 24306, 24312, 24467, 24676), and USNPC (31234, 31238); likewise, specimens assigned to *G. spinigerum* in HWML (23916-17, 23925, 23931, 23943, 23963, 23970, 23983-84, 24012, 24019, 24029, 24033, 24038, 24049, 24052, 24056, 24524), actually pertain to *G. procyonis*.

Gnathostoma turgidum Stossich, 1902 (Plate I, Column C) *Redescription* (based on direct observations of specimens (CNHE 4261, 4519, 4736, 4737, 4739, 4740; USNPC 8552, 44710, 88148). *General:* large size worms. Cephalic bulb armed with uncinate hooks in 8 transverse, complete rows + 2 incomplete rows; cephalic hooks with a thick and conical base; point acute and short. One pair of unilobed lips, with internal edge trilobed; wider than large, protrude in the anterior end of cephalic bulb. Two simple papillae on each lip. One small amphid located between each pair of papillae. Ballonets 4 in number. Anterior half of body covered with cuticular isometric-divergent spines. Spines varying in shape and size according to region and sex of worms. Cervical papilla located at the first quarter of body. Cervical sacs extend from ballonets to near nervous ring. Esophagus divided in anterior muscular (small) and posterior glandular sections.

Male (based on 2 adult): Body 39.8-41.5 (40.06 ± 0.12 , $n=2$) long, 1.61-1.74 (1.67 ± 0.09 , $n=2$) maximum wide. Cephalic bulb 0.60-0.64 (0.62 ± 0.3 , $n=2$) long, 0.83-0.85 (0.84 ± 0.01 , $n=2$) wide; lips 0.09-0.12 (0.10 ± 0.02 , $n=4$) long, 0.27-0.28 (0.27 ± 0.007 , $n=4$) wide. Cephalic hooks 0.015-0.020 (0.018 ± 0.001 , $n=10$) long, 0.006-0.009 (0.008 ± 0.0006 , $n=10$) wide at base. Body spines of first few rows posterior to neck are short and narrow ($0.049-0.057$ [0.053 ± 0.003 , $n=10$ long] by $0.018-0.026$ [0.022 ± 0.003 , $n=10$] wide), with 3-9 points similar in size; spines at cervical papilla level similar in shape but larger than the anterior ones, $0.051-0.059$ [0.056 ± 0.003 , $n=10$] long and $0.028-0.034$ [0.030 ± 0.002 , $n=10$] wide at distal region; with 5-10 points. Spines in mid-esophageal region increase their size

(0.079-0.095 [0.089 ± 0.005 , $n=10$ long] by $0.051-0.061$ [0.055 ± 0.003 , $n=10$ wide]), with 5-8 points similar in size. Spines at esophagus-intestinal junction 0.079-0.1 [0.088 ± 0.006 , $n=10$] long, and 0.053-0.063 [0.057 ± 0.002 , $n=10$] wide, with 5-10 points located anterior and laterally. From this region, number of points and size of spines are constant to mid body region; from this region, gradually diminish posteriorly, turning into spines of 3-2-1 points, and finally disappearing at equatorial region of body. Posterior half of body lacking spines. Nerve ring and cervical papillae located between 9-10, and 24-26, rows of body spines, respectively. Excretory pore not observed. Cervical sacs 2.8-4 (3.4 ± 0.84 , $n=2$) long. Esophagus 21.5-23.5% (22.5 ± 1.4 , $n=2$) of body length; long 7.85-9.64 (8.74 ± 1.26 , $n=2$). Muscular region 1.3-2 (1.8 ± 0.28 , $n=2$) long; glandular region 6.94-7.64 (6.94 ± 0.98 , $n=2$) long. Spicules unequal, blunt apices. Left spicule 0.88-1 (0.94 ± 0.08 , $n=2$) long; right spicule 1.97-2.2 (2.08 ± 0.16 , $n=2$) long, representing 4.82-5.3% (5.06%) of total body length. Caudal extremity lobated, 1.92-1.96 (1.94 ± 0.028 , $n=2$) wide; surface totally covered with minute and simple spines, exception made of area around cloacal opening. Alae with 4 pairs of lateral, pedunculate papillae (2 precloacal, 2 postcloacal). Caudal pedunculated papillae size gradient ascendant (pairs 1-3) and descendent in pair 4. Four pairs of umbilicated ventral papillae, delicate and sessile (1 precloacal, the second pair adcloacal and 2 more postcloacal pairs).

Female (based on 2 complete specimens): body 66.8-71.9 (66.68 ± 0.71 , $n=2$) long, 2.05-2.18 (2.11 ± 0.09 , $n=2$) of maximum wide. Cephalic bulb 0.7-0.8 (0.75 ± 0.07 , $n=2$) long, 0.88-0.91 (0.89 ± 0.02 , $n=2$) wide; cephalic hooks 0.017-0.029 (0.023 ± 0.008 , $n=5$) long, 0.007-0.01 (0.008 ± 0.002 , $n=5$) wide at base. Shape of body spines similar to those described for the males. Posterior half of body lacking spines. Nerve ring, and excretory pore not observed. Cervical papillae located at the 10th row of body spines. Vulva opening at 64.2-68.86 (63.53 ± 0.18 , $n=2$) from anterior extremity. Bipolar eggs 0.048-0.055 (0.51 ± 0.005 , $n=6$) long, 0.031-0.039 (0.035 ± 0.05 , $n=6$) wide. Numerous irregularly distributed pits on surface of eggshell. Anus 0.33-0.42 (0.37 ± 0.06 , $n=2$) from posterior end. Caudal extremity tapering to rounded apex.

Taxonomic summary

Type host: *Didelphis aurita* Wied-Neuwied, 1826 (= *Didelphis azarae*)

Site of infection: stomach wall tunnels.

Type locality: Buenos Aires, Argentine (Stossich, 1902).

Type material: Collezione Elmintogica del Prof. Dott.

Corrado Parona, Geneve, Italy.

Distribution: Argentine (Stossich, 1902); Brazil (Travassos, 1925); Mexico (Caballero, 1958, see Lamothe-Argumedo et al., 1998; Akahane et al., 1999); Peru (Miyazaki et al., 1978); Panama (Miyazaki, 1991); United States of America (Chandler, 1932).

Remarks

The presence of several points on the posterior end of cuticular spines at esophagus-intestine junction level, the body size (*G. turgidum* is the largest species of the genus in accordance with Akahane et al., 1999), and the lack of spines in the posterior region of body, constitutes the diagnostic traits of this species and establish it as a valid member of the genus. This species is the most widely distributed in the Americas, with various opossum species as definitive hosts (see Miyazaki, 1991); for this reason, *G. turgidum* has been described under several denominations, i. e., *G. brasiliense* and *G. didelphis* (see Chandler, 1932; Ruiz, 1952). For comparative purposes we analyzed specimens of *G. didelphis* (USNPC 8552, 44710, 58600, 77171), *G. brasiliense* (MZUSP 598), and *G. turgidum* (CNHE 4739; USNPC 26821, 30794). Based on this comparison, we confirm the conspecific identity of all 3 species, since they exhibit an identical shape and distribution of body spines, and lack spines at the posterior half of body; likewise, the morphology and the row number of cephalic hooks are similar in all the specimens studied. However, because specimens of *G. brasiliense* and *G. didelphis* analyzed were collected infecting the liver, represent immature stages of the parasites and therefore have smaller body size. After a detailed examination of the specimens labeled as *Gnathostoma oligomucronatum*, a parasite of the pyloric region of *Philander opossum pallidum* from El Jobo Lagoon, Tlacotalpan, Veracruz, Mexico, deposited at USNPC under accession numbers: 88148, and 58535.02 by Javier Almeyda Artigas, we concluded that they in fact correspond with *G. turgidum*. For this reason, *G. oligomucronatum* is relegated to the status of *nomen nudum*.

Finally, the record of *G. didelphis* (actually *G. turgidum*) deposited at USNPC (077171) infecting the liver of *Ursus americanus* from Florida, USA, increases the number of host species parasitized by this nematode species.

Gnathostoma lamothei Bertoni-Ruiz, García-Prieto, Osorio-Sarabia and León-Règagnon, 2005 (Plate I, column D)

Diagnosis: based on Bertoni-Ruiz et al. (2005): Medium size worms; cephalic bulb armed with uncinat hooks in 8-9 transverse, complete rows + 2 incomplete rows. One pair

of trilobated lips, central lobe larger than laterals. Cervical papilla located at the first quarter of body (7-11 rows of body spines). Anterior half of body covered with cuticular spines. Spines varying in shape and size according to body region of worms: body spines of first few rows posterior to neck are short and broad, with 3-6 points; spines at cervical papilla level short, and wide at distal region with 4-6 points; central points slightly longer than lateral points. Spines in mid-esophageal region longer than wide, with 3 main points (middle longer than laterals) and 1-3 secondary points. Spines at esophagus-intestinal junction, long and slender, with 3 points; middle point typically longer. From this region, number of points and size of spines gradually diminish posteriorly finally disappearing at equatorial region of body. Posterior half of body covered with rows of roundish bosses located between cuticular transverse striations. Spicules unequal, blunt apices. Left spicule 0.39-0.41 long; right spicule 1.32-1.41 long. Vulva opening slightly post-equatorially. Unipolar eggs with numerous irregularly distributed pits on surface of eggshell.

Additional morphological data (based on direct observations of specimens: CNHE 4421, 4735, 5232; USNPC 88151): lips trilobed, central lobe smaller than laterals. Cephalic hooks with a thick and conical base; point acute and large. Shape of cuticular spines isometric-divergent along the body. Caudal pedunculated papillae size gradient descendent (with the proximal papillae larger than the subsequent one).

Taxonomic summary

Type host: *Procyon lotor hernandezii* Wagler 1831.

Site of infection: stomach, partially embedded in the gastric wall.

Type locality: Laguna Herrera, Tlacotalpan, Veracruz, Mexico.

Type material: holotype CNHE 4735 (male); allotype CNHE 4421; paratypes CNHE 5232; USNPC 095893.0.

Distribution: Mexico: Río Sapo, San José Independencia, Oaxaca (Bertoni-Ruiz et al., 2005); La Laguneta, Tlacotalpan, Veracruz, Mexico (Almeyda-Artigas et al., 1994).

Remarks

Records of *G. procyonis* (Almeyda-Artigas et al., 1994) and *Gnathostoma* sp. I (Almeyda-Artigas et al., 2000) parasitizing *P. lotor hernandezii* in Tlacotalpan, Veracruz, actually correspond to *G. lamothei* (see Bertoni-Ruiz et al.,

2005). The main differences among these 2 species are: (1) the right spicule is smaller in *G. lamothei* than in *G. procyonis* (1.32-1.41 vs. 1.8-2.95, respectively), representing 8.9 and 13.1% of body length, respectively; (2) the density of spines posterior to neck and at cervical papilla level is minor in *G. lamothei* than in *G. procyonis*; and (3) in the posterior half of the body of *G. procyonis*, spines points are reduced to short terminal prongs, then become shortened, and fused into continuous serrated ridges at the base. In *G. lamothei*, the posterior half of body is covered with rows of roundish bosses located between cuticular transversal striations, i.e., lacking spines (Bertoni-Ruiz et al., 2005).

Gnathostoma socialis (Leidy, 1858) (Plate I, Column E)

Redescription (based on direct observations of specimens USNPC 44714, 47048, 47717, 49112).

General: medium size worms. Cephalic bulb armed with uncinata hooks in 9-10 transverse, complete rows + 1 incomplete row; cephalic hooks with a thick and conical base; point acute and large. One pair of unilobed lips, with internal edge smooth; wider than large, protrude in the anterior end of cephalic bulb. Two simple papillae on each lip. One small amphid located between each pair of papillae. Ballonets 4 in number. Anterior half of body covered with cuticular isometric-divergent spines. Spines varying in shape and size according to region and sex of worms. Cervical papilla located at the first quarter of body. Cervical sacs extend from ballonets to near nervous ring. Esophagus divided in anterior muscular (small) and posterior glandular sections.

Male (based on 2 adults): body 19.81-24 (21.9 ± 2.9 , $n=2$) (14.8) long, 1.2-1.4 (1.3 ± 0.14 , $n=2$) maximum wide. Cephalic bulb 0.25-0.29 (0.27 ± 0.03 , $n=2$) long, 0.38-0.41 (0.39 ± 0.02 , $n=2$) wide; lips 0.128-0.132 (0.130 ± 0.035 , $n=2$) long, 0.175-0.177 (0.176 ± 0.007 , $n=2$) wide. Cephalic hooks 0.016-0.019 (0.017 ± 0.0016 , $n=6$) long, 0.005-0.008 (0.005 ± 0.0006 , $n=9$) wide at base. Body spines of first few rows posterior to neck are long (0.026-0.031 [0.027 ± 0.002 , $n=8$ long] by 0.010-0.014 [0.011 ± 0.0013 , $n=7$] wide), with 3-4 points (central points slightly longer than lateral points); spines at cervical papilla level similar in shape to the anterior ones, 0.031-0.04 [0.030 ± 0.003 , $n=6$] long and 0.009-0.015 [0.012 ± 0.001 , $n=6$] wide at distal region; with 3-5 points. Spines in mid-esophageal region increase their size (0.054-0.068 [0.061 ± 0.004 , $n=6$ long] by 0.014-0.020 [0.017 ± 0.002 , $n=6$ wide]), with 3-5 points (middle longer 3 times than laterals). Spines at esophagus-intestinal junction 0.054-0.065 [0.058 ± 0.004 , $n=6$] long, and 0.015-0.022 [0.017 ± 0.001 , $n=6$] wide, with 3-4 small points; middle point more than 3 times longer than laterals. From this region, number of points and size of spines gradually diminish posteriorly, turning into spines of 1 single point; finally disappearing

at equatorial region of body. Posterior half of body lacking spines. Nerve ring, cervical papillae, and excretory pore located between 9-10, 18-23, and 28-32 rows of body spines, respectively. Cervical sacs $0.93-1$ (0.96 ± 0.05 , $n=4$) long. Esophagus $16.25-16.6\%$ (16.4 ± 0.2 , $n=2$) of body length; long $3.3-3.9$ (3.5 ± 0.43 , $n=2$). Muscular region $0.5-0.52$ (0.51 ± 0.014 , $n=2$) long; glandular region $2.8-3.4$ (3.1 ± 0.41 , $n=2$) long. Spicules unequal, blunt apices. Left spicule $0.31-0.42$ (0.36 ± 0.08 , $n=2$) long; right spicule $0.6-0.67$ (0.63 ± 0.05 , $n=2$) long, representing $3.2-4.04\%$ (3.5%) of total body length. Caudal extremity lobated, $0.59-0.68$ (0.63 ± 0.063 , $n=2$) wide, totally covered with minute and simple spines, excepting the area surrounding cloacal opening. Alae with 4 pairs of lateral, pedunculate papillae (2 precloacal, 2 postcloacal). Caudal pedunculated papillae size gradient ascendant (pairs 1-3) and descendent in pair 4. Four pairs of umbilicated ventral papillae, delicate and sessile (1 precloacal, 3 postcloacal, with the second pair adcloacal).

Female (based on 2 complete specimens): body $30-32$ (31 ± 1.4 , $n=2$) long, $2.04-2.1$ (2.07 ± 0.04 , $n=2$) of maximum wide. Cephalic bulb $0.18-0.21$ (0.19 ± 0.032 , $n=2$) long, $0.32-0.35$ (0.33 ± 0.025 , $n=2$) wide; cephalic hooks $0.018-0.021$ (0.019 ± 0.0017 , $n=6$) long, $0.005-0.008$ (0.005 ± 0.0016 , $n=6$) wide at base. Shape of body spines similar to those described for the males. Posterior half of body lacking spines. Nerve ring and excretory pore not observed. Cervical papillae located between 10-11 rows of body spines. Vulva opening at $13.8-14.2$ (14 ± 0.05 , $n=2$) from anterior extremity. Unipolar eggs $0.067-0.075$ (0.07 ± 0.003 , $n=4$) long, $0.030-0.044$ (0.036 ± 0.006 , $n=4$) wide. Numerous irregularly distributed pits on surface of eggshell. Anus $0.30-0.35$ (0.32 ± 0.035 , $n=2$) from posterior end. Caudal extremity tapering to rounded apex.

Taxonomic summary

Type host: *Mustela vison* Schreber, 1777.

Site of infection: stomach wall deeply penetrated.

Type locality: presumably Pennsylvania, USA (see Anderson, 1964).

Distribution: United States of America: Pasquottank County, New Carolina (USNPC 40574); Chautauqua County, New York (USNPC 47048); Tioga, New York (USNPC 47717); Jamestown, New York (USNPC 49112).

Type material: not specified (Leidy, 1858). Material identified by Leidy as *Cheiracanthus socialis*, deposited in the USNPC (000056), was designated as voucher specimen.

Remarks

This species was described as *Cheiracanthus socialis* Leidy, 1858 by Leidy (1858) parasitizing *Mustela vison* presumably from Pennsylvania, USA (Anderson, 1964); Baylis and Lane (1920) considered it as a probable synonym of *G. spinigerum*, based on the scarce information contained by the original description. Miyazaki (1960) also considered *C. socialis* as synonym of *G. spinigerum*; however, based on its host species and distribution in North America, pointed out that this material could represent an independent species. Anderson (1964) re-described this species with specimens deposited at the USNPC, including some individuals identified by Leidy; notwithstanding, due to the poor conditions of preserved specimens, Anderson left the status of *G. socialis* in doubt. In this study, we re-established the validity of *G. socialis*. This species can be differentiated from all American congeners by the shape of cuticular spines at first few rows posterior to neck: isometric-divergents, with 3-4 points (central points slightly longer than lateral ones). In addition, Leidy's species differs from *G. binucleatum*, *G. miyazakii*, *G. procyonis*, and *G. americanum*, as well as *G. spinigerum*, by lacking spines in the posterior region of body surface (which are present in all these 5 species). As in *G. socialis*, 2 other American species lack spines in the posterior part of body: *G. lamothei* and *G. turgidum*; the presence of roundish bosses in the posterior part of the body is a diagnostic trait of *G. lamothei* which allows differentiates it from Leidy's species. *Gnathostoma turgidum* differs from *G. socialis* because in the former species the number of points in body spines overpasses 5 and the eggs are bipolar, while in the later this number does not exceed 5 and the eggs are unipolar.

Discussion

The current composition of the genus *Gnathostoma* in the Americas is conformed by 7 species: 2 of them with Pan American distribution: *G. turgidum* (= *G. brasiliensis*, and *G. didelphis*), and *G. binucleatum* (Stossich, 1902; Travassos, 1925; Miyazaki, 1991; Almeyda-Arigas et al., 2000); 3 species with punctual distribution in North America: *G. miyazakii*, *G. lamothei*, and *G. socialis*, which adult forms have been only recorded once (Anderson, 1964; Bertoni-Ruiz et al., 2005; Leidy, 1858); one more species with punctual distribution in South America: *G. americanum* (Travassos, 1925), and finally 1 species widely distributed in USA: *G. procyonis* (Lockhart, 2007).

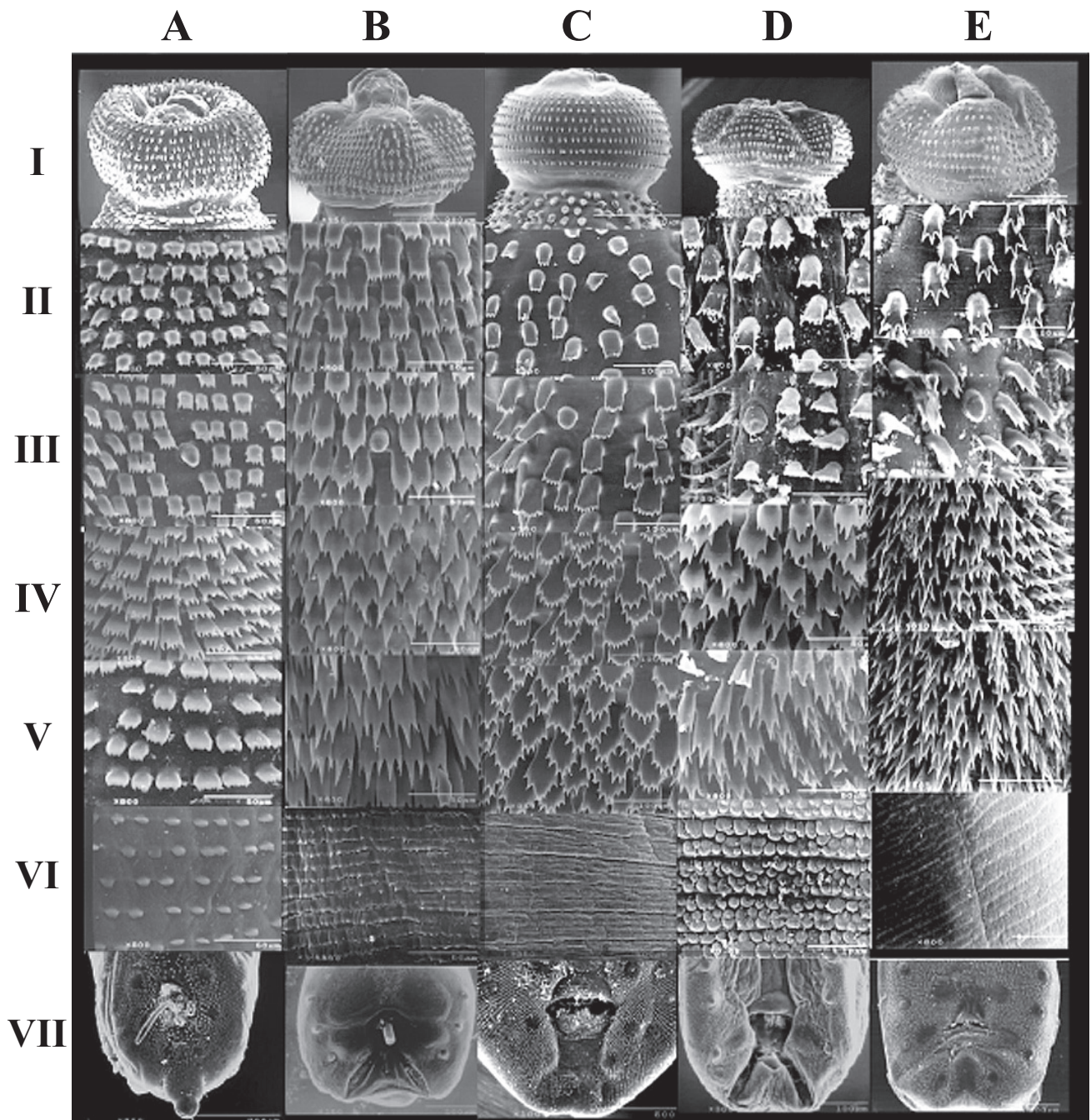


Plate I. Scanning electronic micrographs of some American species of the genus *Gnathostoma*. A) *Gnathostoma miyazaki*; B) *Gnathostoma procyonis*; C) *Gnathostoma turgidum*; D) *Gnathostoma lamothei*; E) *Gnathostoma socialis*. I) Cephalic bulb; Escale bars: 200 μ m. II) Body spines of first few rows posterior to neck; Escale bars: 50 μ m, excepting column C: 100 μ m. III) Body spines at cervical papillae level; Escale bars: 50 μ m, excepting column C: 100 μ m. IV) Body spines at mid-esophagical level; Escale bars: 50 μ m, excepting columns C and E: 100 μ m. V) Body spines at esophagus-intestinal junction; Escale bars: 50 μ m, excepting columns C and E: 100 μ m. VI) Posterior half of body; Escale bars: 100 μ m, excepting columns A and B: 50 μ m. VII) Male, caudal extremity (ventral view); Escale bars: 200 μ m, excepting columns C: 500 μ m, and D: 100 μ m.

On the other hand, specimens recorded as *G. spinigerum* in USA and deposited at HWML, were re-identified by us as *G. procyonis*. *Gnathostoma socialis*, considered synonym of *G. spinigerum* by several authors (e.g., Chandler, 1941; Miyazaki, 1960), has been re-established as a valid species in this study; Mexican and Ecuadorian records of *G. spinigerum* (Caballero, 1958; Ollague et al., 1988) have been re-assigned to *G. turgidum* (Lamothe-Argumedo et al., 1998) and *G. binucleatum* (Almeyda-Artigas et al., 2000). Based on the anterior considerations, we can affirm that *G. spinigerum* is not naturally distributed in the Americas.

This study represents the first step to deepen in the knowledge of the systematics and evolution of the group in the Americas; phylogenetic studies based on morphological and molecular traits are needed to establish the relationships among the species of the genus worldwide. This phylogenetic framework will allow the prediction of the infective potential of each one of the species to man, based on the knowledge of the zoonotic species that have been well studied to date.

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