1995

A New Pinworm, *Didelphoxyuris thylamisis* n. gen., n. sp. (Nematoda: Oxyurida) from *Thylamys elegans* (Waterhouse, 1839) (Marsupialia: Didelphidae) in Bolivia

Scott Lyell Gardner
University of Nebraska - Lincoln, slg@unl.edu

Jean-Pierre Hugot
Museum National d'Histoire Naturelle de Paris, hugot@cimrs1.mnhn.fr

Research and Reviews in Parasitology, 55 (3): 139-147 (1995)

Published by A.P.E.
Printed in Barcelona, Spain

A NEW PINWORM, *DIDELPHOXYURIS THYLAMISIS* N. GEN., N. SP. (NEMATODA: OXYURIDA) FROM *THYLAMYS ELEGANS* (WATERHOUSE, 1839) (MARSUPIALIA: DIDELPHIDAE) IN BOLIVIA

S.L. GARDNER[1] & J.P. HUGOT[2]

[1]*H.W. Manter Laboratory of Parasitology, University of Nebraska State Museum, W529 Nebraska Hall, 68588-0514 Lincoln, Nebraska, USA*

[2]*Muséum National d'Histoire Naturelle de Paris, Laboratoire de Biologie Parasitaire-Protistologie-Helminthologie, URA No. 114, 61 rue Buffon, 75231 Paris Cedex 05, France*

Received 31 March 1995; accepted 7 May 1995

REFERENCE: GARDNER (S.L.) & HUGOT (J.P.), 1995.– A new pinworm, *Didelphoxyuris thylamisis* n. gen., n. sp. (Nematoda: Oxyurida) from *Thylamys* elegans (Waterhouse, 1839) (Marsupialia: Didelphidae) in Bolivia. *Research and Reviews in Parasitology*, 55 (3): 139-147.

ABSTRACT: *Didelphoxyuris thylamisis* n. gen., n. sp. is described from the caecum of *Thylamys elegans* (Waterhouse, 1839) (Marsupialia: Didelphidae) collected in the eastern region of the Andes of Bolivia. *Didelphoxyuris thylamisis* n. sp. differs from the only pinworm described from marsupials in the Neotropics (*Neohilgertia venusti* Navone, Suriano et Pujol, 1990) in having only three oesophageal teeth, non-operculated eggs, females that are didelphic, and males that possess no preanal papillae. Several other species of pinworms have been described from marsupials in Australia, but all are characterised by possessing a buccal capsule that is strongly cuticularized with inter-radial lamellae. These structures are lacking in *D. thylamisis*. *Didelphoxyuris* n. gen. is characterised by a mouth opening into a depression and lateral alae composed of two lengthwise crests. All males possess an area rugosa composed of a ventral sagittal crest, a caudal extremity truncated at the level of the cloaca, and four pairs of genital papillae (two pairs lateral adanal and sessile, one pair just posterior to spicule aperture, and last pair at posterior extremity and pedunculated). All females possess an opisthodelphic uterus, a reflexed ovary and a thick and laterally enlarged cephalic vesicle containing a complex reticulated network of rounded confluent vesicles.

KEY WORDS: Nematoda, Oxyuridae, *Didelphoxyuris thylamisis* n. gen., n. sp., Marsupialia, Didelphidae, *Thylamys elegans*, Bolivia, biodiversity.

INTRODUCTION

From 1984 approximately 10000 individual mammals were collected and examined for parasites from throughout Bolivia. During this general survey several species of marsupials representing more than 8 genera were examined for parasites. Of these, several were found to be infected with nematodes of the Order Oxyurida. Recent collections of parasites (1990-1993) from marsupials obtained from the eastern foothills of the Andes contained sufficient numbers of pinworms to enable us to describe a new genus from mouse opossums of the genus *Thylamys* (Waterhouse, 1839). In the Neotropical region, marsupials of the family Didelphidae have a fossil record extending from deposits of middle to late Palaeocene age (Riochican) [about 55-60 million years old] (MARSHALL, 1982). Members of the genus *Marmosa sensu lato* (Gray, 1821) first appear in deposits of Friasian age [approx. 16 mya] (MARSHALL, 1982). Mouse opossums of the genus *Thylamys*, formerly subsumed in the genus *Marmosa*, have a strictly southern Neotropical distribution occurring in suitable habitats throughout the southern cone of the continent of South America, including southern Bolivia and Brazil south through Paraguay to the tip of the continent in Chile and Argentina (REDFORD & EISENBERG, 1992; STREILEIN, 1982; GARDNER & CAMPBELL, 1993).

Herein we provide the description of a new genus and species of nematode of the family Oxyuridae, recovered from the caecum of individuals of the mouse opossum, *Thylamys elegans* (Waterhouse, 1839) (Marsupialia: Didelphidae) collected from the south-eastern foothills of the Andes of Bolivia.

MATERIAL AND METHODS

Mammals were collected in live-traps, killed in chloroform and examined for helminths within a few minutes of death. Pinworms were collected from the large intestine and caecum and either placed directly in 10% formalin or plunged into glacial acetic acid for a few seconds prior to fixation in 10% formalin. Some specimens were saved in both 95% ethanol (ETOH) and liquid nitrogen for future analyses of genetic material. Specimens were studied with the light microscope as temporary wet mounts, first in water and later in lactophenol. We studied cross-sections made «free-hand» using small pieces of razor blade and a small brush. Drawings were made with the aid of a drawing tube.

RESULTS

Didelphoxyuris thylamisis n. gen., n. sp.

Symbiotype: Thylamys elegans (Waterhouse, 1839) (Marsupialia: Didelphidae), Museum of Southwestern Biology (MSB), Division of Biological Materials, New Mexico Kryovoucher No. NK22814 and Museum of Southwestern Biology (MSB), Division of Biological Materials, New Mexico Kryovoucher No. NK22815.

Date of collection: both host specimens collected 27 May, 1991.

Location in the host: caecum and colon.

Type locality: 5 km NE Quiñe, 1900 m, Department of

Santa Cruz, Bolivia, South America (18° 03' S; 64° 19' W).

Specimens deposited: A) *Holotype male*: Harold W. Manter Laboratory of Parasitology Collection HWML 39072, Museum of Southwestern Biology Division of Biological Materials (MSB) New Mexico Kryovoucher No. NK22814A. B) *Allotype female*: HWML 39073, Museum of Southwestern Biology Division of Biological Materials (MSB) New Mexico Kryovoucher No. NK22814A. C) *Paratypes*: 5 males and 5 females, Muséum National d'Histoire Naturelle de Paris, numbers 70KJ (NK22814) and 71 KJ (NK22815).

Description

Holotype male: Small worms; width gradually increasing posterior to cephalic vesicle, reaching maximum at level of midbody. Body terminating in short truncated tail (Fig. 1A). Mouth opening in a depression surrounded by three distinct lips, four submedian labial papillae, two amphids (Fig. 1B, C), and three small oesophageal teeth (Fig. 1D). Lateral alae well developed, composed of two lengthwise crests, beginning near oesophageal bulb, ending before cloaca (Fig. 1A, E, F). Monorchic with testis bending just posterior to level of oesophageal bulb (Fig. 1A). Area rugosa composed of a ventral medial crest triangular in cross section, which begins posterior to excretory pore, and ends just before cloaca (Fig. 1A, E, G, H, I). Four pairs of genital papillae; two pairs lateral adanal and sessile, one pair just posterior to spicule aperture, last pair posterior and pedunculated. Phasmids situated laterally and posterior to last pair of caudal papillae (Fig. 2A, C). Orifice of spicule pouch protruding from opening of cloaca (Fig. 2A, B). Spicule weakly curved ventrally and relatively well-sclerotized, with rounded tip (Fig. 2B, D, E, F). Gubernaculum present and well developed (Fig. 2B, G, H, I, J, K, L). Posterior to cloaca, cuticle bearing ornamentation resembling cobblestones (Fig. 2A, C).

Allotype female: Small worms with inflated cephalic vesicle; body narrowing just posterior to vulva and terminating in short tail (Fig. 3A); cephalic vesicle thick, enlarged laterally, with a complex reticulated network of rounded confluent vesicles, some of them protruding through surface of cuticle (Fig. 4A, B, C, D). Head showing the same disposition described in males, but amphids and cephalic papillae are present in depression (Fig. 4A, C, D). Lateral alae as in males, beginning posterior to bulb of oesophagus, ending posterior to anus (Fig. 3B, C). Excretory pore and vulva closely adjacent situated in the first third of body. Genital tract didelphic and symmetrical, excluding the blind ends of the ovaries: left ovary situated in posterior half of body, right ovary near vulva (Fig. 3A). Oviducts S-shaped, situated at level of junction of muscular vagina and vagina uterina (Fig. 4F). Uteri emptying into vagina uterina in posterior half of body, just anterior to anus (Fig. 3A). Vagina with thick muscular wall (Fig. 3E, F). Eggs oval non-operculated and unembryonated (Fig. 4E).

Measurements: See Table 1 (males) and Table 2 (females).

Didelphoxyuris n. gen.

Diagnosis

General: Mouth opening apically into a depression surrounded by three distinct lips, four submedian labial papillae and two amphids; lateral alae present composed of two longitudinal crests.

Male: Area rugosa composed of a ventral sagittal crest; caudal extremity truncated at level of cloaca; genital papillae in four pairs, two pairs lateral adanal and sessile, one pair just posterior to spicule aperture, last pair posterior and pedunculated; phasmids situated laterally and dorsal to last pair of caudal papillae; spicule well keratinized; gubernaculum present and well developed.

Female: Cephalic vesicle thick and enlarged laterally, with a complex reticulated network of rounded confluent vesicles; excretory pore and vulva in close proximity, situated in the first third of body; genital tract prodelphic; oviducts S-shaped, situated at level of junction of muscular vagina and vagina uterina; vagina with thick muscular wall; eggs oval non-operculated and unembryonated.

Etymology: This genus is named after the family of host from which individuals of the type species were recovered.

DISCUSSION

Didelphoxyuris thylamisis n. sp. differs from the only pinworm described from marsupials in the Neotropics (*Neohilgertia venusti* Navone, Suriano et Pujol, 1990) in having only three oesophageal teeth, non-operculated eggs, females that are didelphic, and males that possess no preanal papillae. Several other species of pinworms have been described from Australian marsupials (JOHNSTON & MAWSON, 1938, 1939; MAWSON, 1963, 1978; HUGOT & BOUGNOUX, 1988), but all are characterised by the presence of a strongly cuticularized buccal capsule with inter-radial lamellae (PETTER & QUENTIN, 1976); these structures are completely lacking in our specimens. In all males of the family Oxyuridae thus far described from Australian marsupials, the fourth pair of genital papillae is supported by very long and flexible peduncles, the tail has a well-defined caudal point, and the phasmids are posterior to the last pair of genital pallae. Our specimens differ from all other oxyurids described up to the present in the absence of these traits. Therefore, a new genus is proposed: *Didelphoxyuris* n. gen.

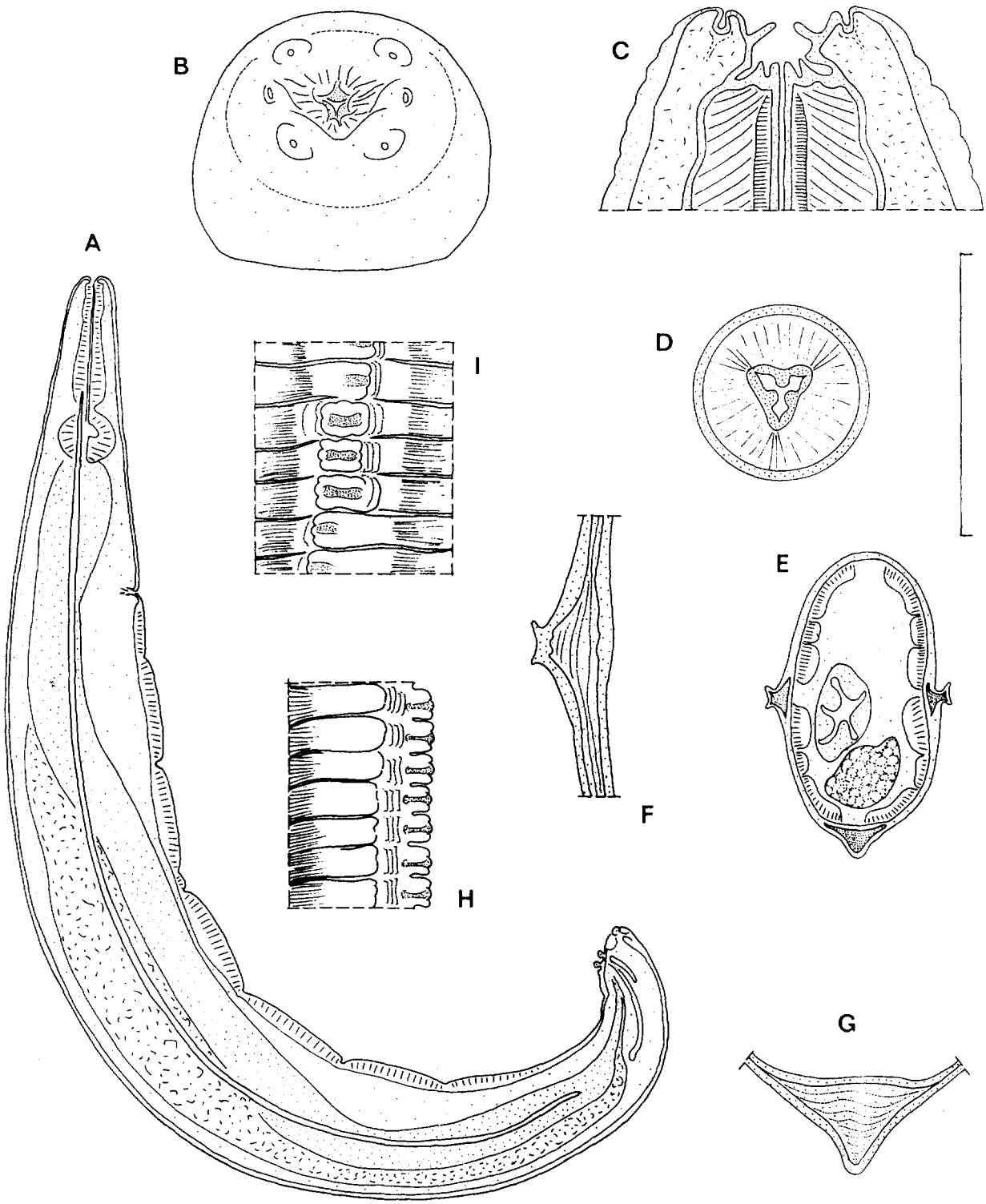

Fig. 1.– *Didelphoxyuris thylamisis* n. gen., n. sp., holotype male: A) entire worm, right lateral view; B) head, apical view; C) cephalic extremity, ventral view, optical section through amphids; D) cross section through base of oesophagal teeth; E) cross section at level of mid-body; F) *idem*, detail of left lateral wing; G) *idem*, detail of median ventral crest; H) right lateral view of median ventral crest; I) *idem*, ventral view. Scale bars: A: 500 µm; B, C, D: 50 µm; E: 250 µm; F, H, I: 75 µm; G: 100 µm.

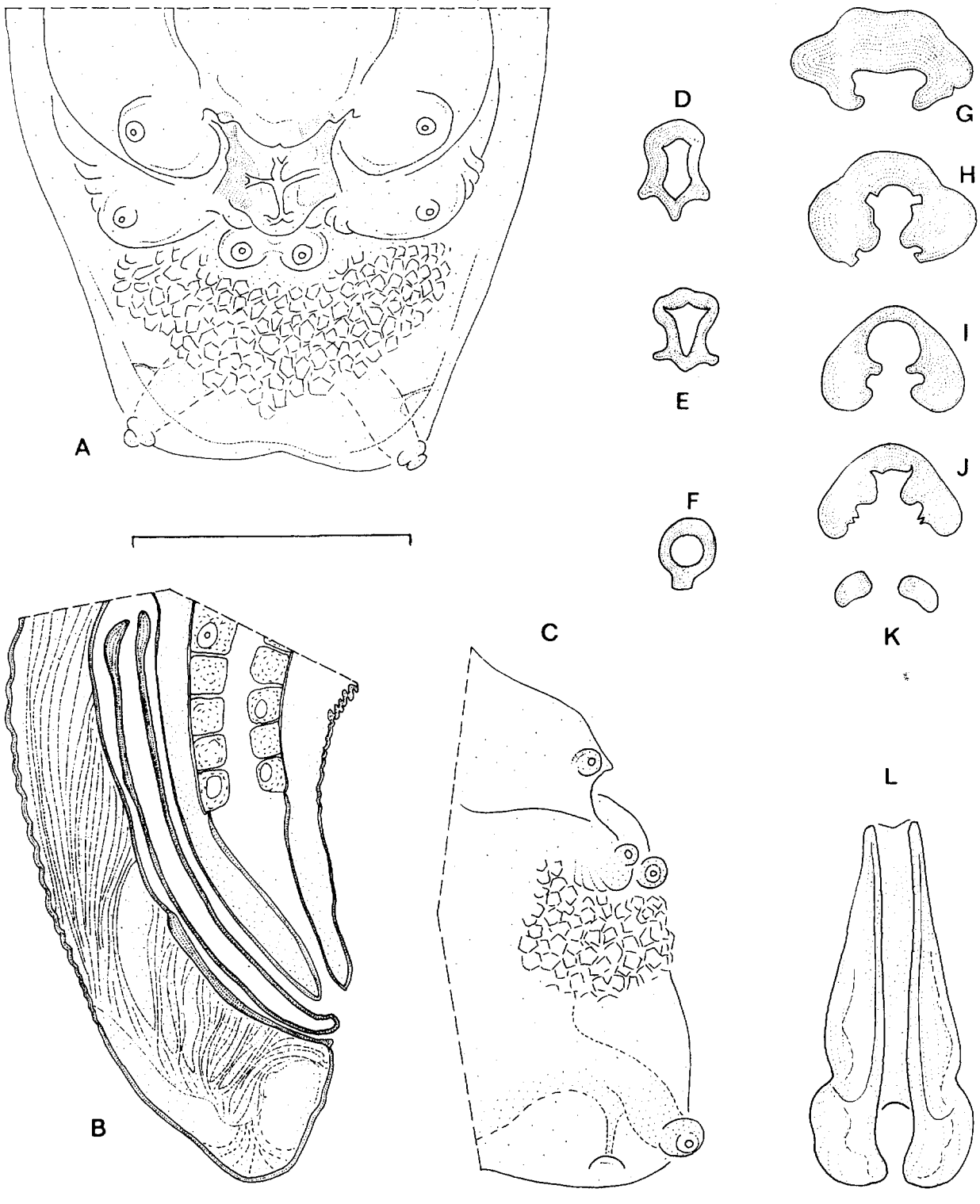

Fig. 2.– *Didelphoxyuris thylamisis* n. gen., n. sp., holotype male: A) caudal bursa, ventral view; B) *idem*, lateral view, sagittal optical section; C) lateral view of cloaca and genital papillae; D, E, F) three transverse sections of spicule; G, H, I, J, K) five transverse sections of gubernaculum; L) gubernaculum after dissection, ventral view. Scale bars: A, C, D, E, F, G, H, I, J, K: 50 µm; B: 100 µm; L: 65 µm.

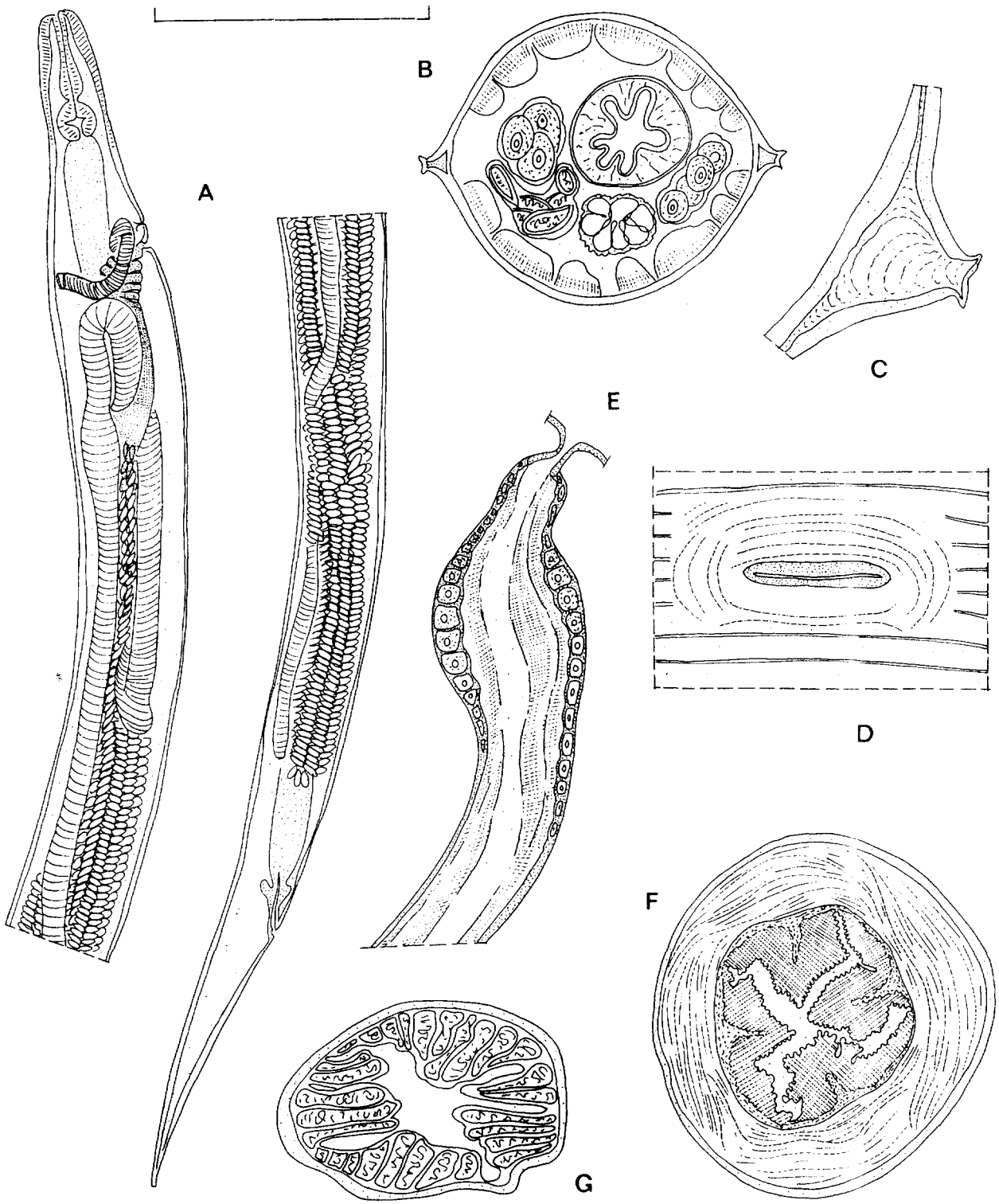

Fig. 3.– *Didelphoxyuris thylamisis* n. gen., n. sp., allotype female: A) entire worm, right lateral view; B) cross section at level of mid-body; C) *idem*, detail of right lateral wing; D) vulva, ventral view; E) vulva, muscular vagina and beginning of vagina uterina, optical section in right lateral view after dissection; F) cross section of muscular vagina; G) cross section of vagina uterina. Scale bars: A: 800 µm; B, E: 250 µm; C, D: 125 µm; F, G: 100 µm.

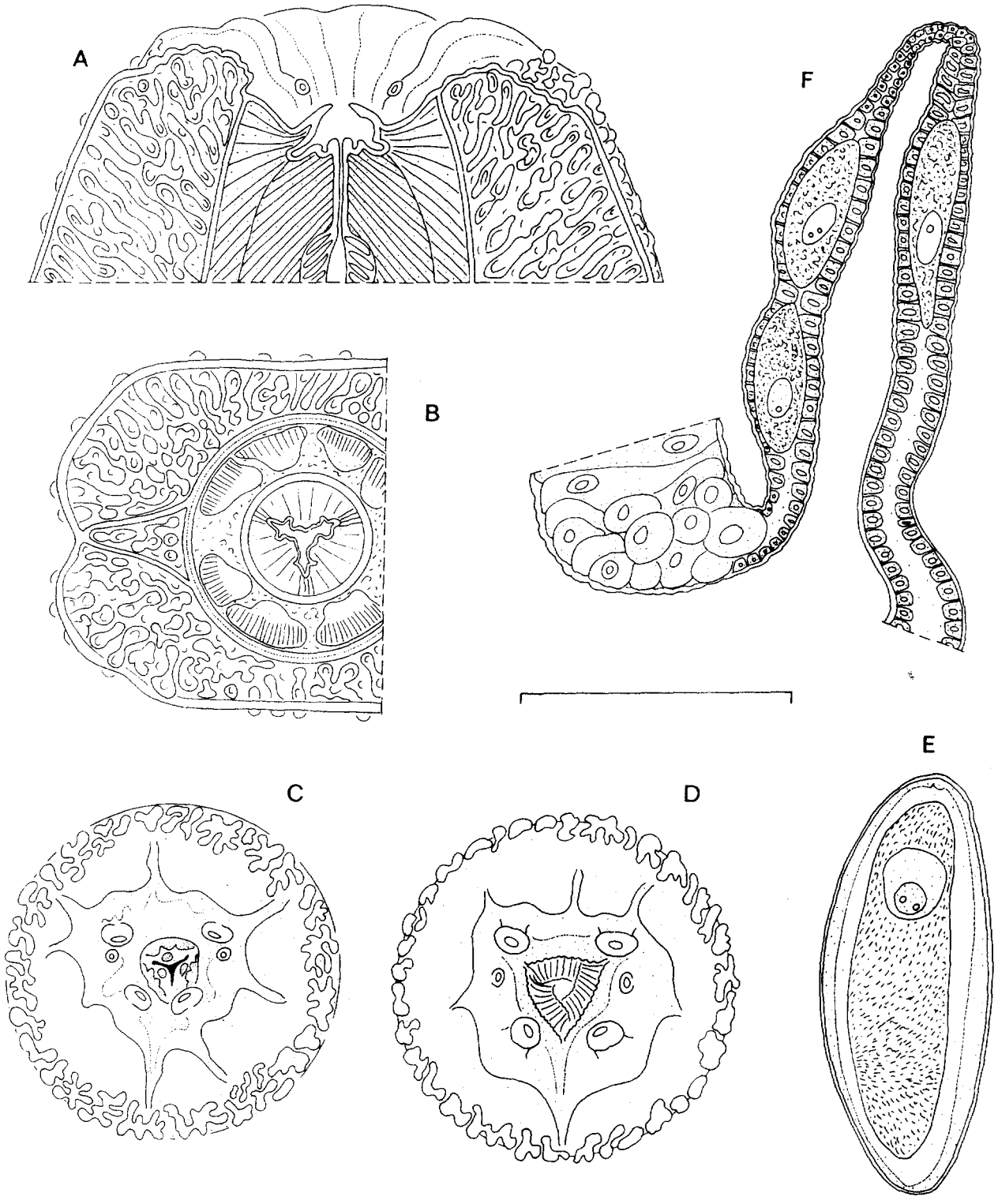

Fig. 4.– *Didelphoxyuris thylamisis* n. gen., n. sp., allotype female: A) cephalic extremity, ventral view after frontal section; B) *idem*, cross section through oesophagus and cephalic vesicle; C) *idem*, apical view; D) *idem*, other view; E) egg; F) end of ovary and beginning of oviduct after dissection. Scale bars: A, B, C, D: 50 µm; E, F: 125 µm.

	holotype	22815E	22815A	22814B	22814A	22814F	22814C	22814J	22814D	22814G	22814E	22814I	*mean*	*max.*	*min.*	*CV*
amph (gap)	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
body L	2578	1309	1383	1497	1565	1651	1665	1729	1763	1794	1830	1850	1718	2578	1309	19
W (head)	40	35	67	37	34	43	36	37	39	37	26	37	39	67	26	25
W (max)	165	285	239	247	266	326	291	271	292	338	205	263	266	338	165	18
W (nv)	97	104	128	106	75	85	85	98	84	86	65	75	91	128	65	19
W (blb)	140	169	190	148	133	145	123	133	123	162	102	115	140	190	102	18
W (ex)	190	204	210	210	208	198	191	199	196	242	151	191	199	242	151	10
W (as)	90	78	84	88	77	99	81	93	85	85	76	108	87	108	76	11
cvc L	110	33	37	22	24	38	23	23	24	26	33	21	35	110	21	71
cvc W	85	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ospg L	330	235	252	261	261	342	194	260	245	282	264	284	268	342	194	15
blb W	105	84	90	81	87	100	89	90	88	92	78	93	90	105	78	8
blb L	100	72	93	70	72	95	62	79	61	89	74	84	78	100	61	66
apex to:																
–nv	100	71	73	86	95	109	87	86	62	101	101	94	89	109	62	16
–lw	210	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–ex	590	330	338	400	461	565	416	440	422	523	475	504	455	590	330	18
–test (bent)	515	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–arug	600	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T	42	51	65	63	63	54	53	54	57	49	47	63	55	65	42	13
spcL	187	10	133	138	128	164	188	175	183	206	174	197	157	206	10	34
gubL	82	68	68	60	60	95	62	69	59	66	71	70	69	95	59	15

Table 1.– Measurements of males of *Didelphoxyuris thylamisis* n. gen., n. sp. Twelve individuals measured by host field-collection number. Paratypes are sorted by increasing body size. Measurements in micrometers. Missing data are denoted by a «-». For each line: *mean* is the mean; *max.* is the maximum and *min.* the minimum; «*CV*» is the coefficient of variation. Abbreviations: *amph (gap)*=amphidial gap; *body L*=body length; *W(max), W(head), W(blb), W(ex)*, or *W(as)*=maximum body width, body width measured at level of head, oesophageal bulb, at excretory pore, or anus, respectively; *cvc L*=cephalic vesicle length; *cvc W*=cephalic vesicle width; *ospg L*=length of oesophagus; *blb L*=length of oesophageal bulb; *blb W*=width of oesophageal bulb; *apex to: nv, lw, ex, test (bent)*, or *arug*=distance from anterior end to nerve ring, beginning of lateral wing, excretory pore, testicle bent or beginning of area rugosa, respectively; *T*=tail length; *spc L*=length of spicule; *gub L*=length of gubernaculum.

	allotype	22814C	22814F	22814J	22814E	22814A	22814D	22814I	22814H	22814B	22814G	*mean*	*max.*	*min.*	*CV*
amph (gap)	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–
body L	5669	–	3177	3214	4021	4587	4750	4831	5351	5726	5915	4724	5915	3177	21
W (head)	61	55	42	43	43	61	52	50	45	84	62	54	84	42	23
W (max)	360	378	291	338	311	379	413	374	361	326	298	348	413	291	11
W (nv)	177	125	108	92	96	118	138	151	117	190	156	133	190	92	24
W (blb)	189	251	174	192	191	206	255	283	242	234	196	219	283	174	16
W (ex)	320	315	252	275	270	290	328	332	303	283	233	291	332	233	11
W (as)	166	–	135	121	130	143	195	173	90	149	109	141	195	90	22
cvc L	417	–	–	–	–	–	–	–	–	–	–	–	–	–	–
cvc W	171	–	–	–	–	–	–	–	–	–	–	–	–	–	–
ospg L	390	381	338	350	356	365	372	358	376	373	387	368	390	338	4
blb W	120	122	124	122	127	146	138	131	140	140	135	131	146	120	7
blb L	130	125	103	116	114	113	116	115	124	118	126	118	130	103	6
apex to:															
–nv	140	83	124	91	111	105	105	109	105	144	145	115	145	83	18
–lw	370	–	–	–	–	–	–	–	–	–	–	–	–	–	–
–ex	680	532	530	559	622	565	579	509	556	685	640	587	685	509	10
–vlv	760	570	629	640	678	683	705	636	648	815	752	683	815	570	10
T	830	–	582	714	632	768	426	732	652	773	612	672	830	426	17
egg L	98	94	–	–	–	90	94	92	93	86	92	92	98	86	4
egg W	40	31	–	–	–	30	35	35	36	32	35	34	40	30	9

Table 2.– Measurements of females of *Didelphoxyuris thylamisis* n. gen., n. sp. Eleven individuals measured by host field-collection number. Paratypes are sorted by increasing body size. Measurements in micrometers. Missing data are denoted by a «-». For each line: *mean* is the mean; *max.* is the maximum and *min.* the minimum; «*CV*» is the coefficient of variation. Abbreviations: *amph (gap)*=amphidial gap; *body L*=body length; *W(max), W(head), W(blb), W(ex), W(vlv)* or *W(as)*=maximum body width, body width measured at level of head, oesophageal bulb, at excretory pore, at vulva or anus, respectively; *cvc L*=cephalic vesicle length; *cvc W*=cephalic vesicle width; *ospg L*=length of oesophagus; *blb L*=length of oesophageal bulb; *blb W*=width of oesophageal bulb; *apex to: nv, lw, ex or vlv*=distance from anterior end to nerve ring, beginning of lateral wing, excretory pore or vulva, respectively; *T*=tail length; *egg L*=length of egg; *egg W*=width of egg.

Genus *Didelphoxyuris* n. gen. includes only the type species: *Didelphoxyuris thylamisis* n. sp. parasite of *Thylamys* sp. in Bolivia.

Although the helminths of marsupials from the Neotropics have a long history of study, starting most notably with the works of VON LINSTOW (1899) and VON JANICKI (1906), it has been only recently that pinworms have been discovered in these mammals (NAVONE, SURIANO & PUJOL, 1990; present paper). This lack of knowledge of the biological characteristics of a relatively well-known and widespread group of hosts is an indication of how little information is available to researchers interested in biodiversity and Parasitology of wild populations of vertebrates.

Data from surveys of parasites of mammals of Bolivia are still being assembled. However, from preliminary analyses of these data, it appears that species of most genera of small marsupials from the southern Neotropics may serve as hosts of oxyurid nematodes in addition to a taxonomically and ecologically diverse fauna of other parasites. Based on the presence of relict populations of similar taxa of cestodes (*Linstowia*) in both Neotropical and Australian marsupials, GARDNER & CAMPBELL (1992a, b) advanced the hypothesis of the existence of an ancient (65-70 mya) and perhaps structurally intact arthropod-mammal ecosystem spanning both time and distance. The present data on distribution and host-range show that the oxyurid fauna of the marsupials may mirror the pattern seen in the cestodes. Robust tests of the hypothesis of GARDNER & CAMPBELL (1992a) will result only from continued collecting and analysis of data on diversity of the fauna and flora of the southern continents.

ACKNOWLEDGEMENTS

For assistance in collection of specimens and in reading drafts of this paper, we thank Luma Al Banna, Sara V. Brant, Mariel Campbell, Jorge Salazar Bravo, Otto Carlos Jordan Camacho, Joseph A. Cook, Emma Luna Pizarro, and Terry L. Yates. For support in the field we thank the National Museum of Natural History in La Paz, Bolivia and the Zoo Santa Cruz, Fauna Sudamericana, Santa Cruz, Bolivia. This work was supported in part by NATO Grant No. CRG 920612 and National Science Foundation Grant (NSF Grant) Nos. BSR-8612329 and BSR-9024816.

REFERENCES

GARDNER (S.L.), 1993.– Checklist of mammal species of the world, Order Didelphimorphia. In: *Mammal species of the world: a taxonomic and geographic reference*, 2nd Edition (D. Wilson & D.M. Reeder edit.), Smithsonian Institution Press, Washington: 15-23.

GARDNER (S.L.) & CAMPBELL (M.L.), 1992a.– Parasites as probes for biodiversity. *Journal of Parasitology*, 78: 596-600.

GARDNER (S.L.) & CAMPBELL (M.L.), 1992b.– A new species of *Linstowia* Zschokke, 1899 (Cestoda: Anoplocephalidae) from marsupials in Bolivia. *Journal of Parasitology*, 78: 795-799.

HUGOT (J.P.) & BOUGNOUX (M.B.), 1988.– Etude morphologique de *Austroxyuris finlaysoni* (Oxyuridae, Nematoda), parasite de *Petauroides volans* (Petauridae, Marsupialia). *Systematic Parasitology*, 11: 113-122.

JANICKI (C. VON), 1906.– Studien an Säugetiercestoden. *Zeitschrift für Wissenschaftliche Zoologie*, 81: 505-597.

JOHNSTON (T.H.) & MAWSON (P.M.), 1938.– Some nematodes from Australian marsupials. *Records of the South Australian Museum*, 6: 187-198.

JOHNSTON (T.H.) & MAWSON (P.M.), 1939.– Some nematodes from Victorian and Western Australian marsupials. *Transactions of the Royal Society of South Australia*, 63: 307-310.

LINSTOW (O.F.B. VON), 1899.– Nematoden aus der Berliner Zoologischen Sammlung. *Mitteilungen des Zoologischen Museums Berlin*, 1 (2): 1-28.

MARSHALL (L.G.), 1982.– Evolution of the South American Marsupialia. In: *Mammalian Biology in South America* (M.A. Mares & H.H. Genoways edit.), *The Pymatuning Symposia in Ecology, Special Publication Series of the Pymatuning Laboratory of Ecology*, 6: 251-272.

MAWSON (P.M.), 1964.– Some nematoda (Strongylina and Oxyurina), from Kangaroos (*Macropus* spp.), from Eastern Australia. *Parasitology*, 54: 237-262.

MAWSON (P.M.), 1978.– A new genus *Adelonema* (Nematoda:Oxyuridae) from Australian Phalangerid Marsupials. *Transactions of the Royal Society of South Australia*, 102: 223-226.

NAVONA (G.T.), SURIANO (D.M.) & PUJOL (C.A.), 1990.– *Neohilgertia venusti* gen. n. sp. n. (Nematoda: Oxyuridae) from *Thylamys venustus cinderellus* (Thomas) Reig, Kirsch & Marshall, 1985 (Marsupialia: Didelphidae) in Burruyacu, Tucuman, Argentina - Systematic position and possible evolution. *Memórias do Instituto Oswaldo Cruz*, 85: 185-189.

QUENTIN (J.C.) & PETTER (A.), 1976.– Keys to genera of the Oxyuroidea. In: *CIH Keys to the Nematode Parasites of Vertebrates* (R.C. Anderson, A.G. Chabaud & S. Willmott edit.), Commonwealth Agricultural Bureaux, Farnham Royal, Bucks, No. 4: 1-30.

REDFORD (K.H.) & EISENBERG (J.F.), 1992.– *Mammals of the Neotropics, The Southern Cone, Volume 2, Chile, Argentina, Uruguay, Paraguay*. The University of Chicago Press, Chicago, 430 pp.

STREILEIN (K.E.), 1982.– Behaviour, ecology, and evolution of the South American marsupials. In: *Mammalian Biology in South America* (M.A. Mares & H.H. Genoways edit.), *The Pymatuning Symposia in Ecology, Special Publication Series of the Pymatuning Laboratory of Ecology*, 6: 231-250.

ZSCHOKKE (F.), 1899.– Neue Studien an Cestoden aplancentaler Säugetiere. *Zeitschrift für Wissenschaftliche Zoologie*, 65: 404-445.