Article

An endemic *Taenia* from South America: validation of *T. talicei* Dollfus, 1960 (Cestoda: Taeniidae) with characterization of metacestodes and adults

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Abstract

Taenia talicei is redescribed based on new data from polycephalic, fimbriocercus and cysticercus metacestodes found in *Ctenomys* spp. (Rodentia: Ctenomyidae) from Argentina. Strobilate adult specimens, derived from experimental infections in domestic dogs, are described for the first time. Identity of the adult and metacestodes stages is based on the number of rostellar hooks (44–50 hooks in 2 rows), their dimensions (large hooks= 232–242; small= 150–187) and shape. *Taenia talicei* is distinguished from those species that occur naturally in Neotropical Felidae and from those cosmopolitan species that circulate in synanthropic cycles with rodents (or lagomorphs) and domestic hosts such as cats and dogs in South America based on the structure of the metacestode, dimensions and numbers of rostellar hooks and a suite of specific characters of the genital system in strobilate adults. This species is the first that can be considered endemic to South America. Origins of an endemic *Taenia* species or taeniid assemblages in South America would have relationships to either North American or Eurasian placental carnivores. In these instances, the expansion of *Taenia* may have resulted from geographic colonization of South America, radiation in both felids (and canids), and host switching by tapeworms to caviomorphs, prior to the emergence of the Panamanian Isthmus. *Taenia talicei* is capable of development in domestic dogs, and metacestodes in species of *Ctenomys* were found in urban or semi-urban environments. These factors may establish a role for synanthropic cycles linked to definitive hosts including dogs and cats as a route for exposure of humans to infection by this taeniid.

Key words: South American rodent, *Ctenomys,* cestodes, larval forms, taeniid tapeworms

Introduction

Taeniids (Cestoda: Cyclophyllidea) are characteristic parasites of carnivores, and are unique among the tapeworms in having 2 obligate mammalian hosts linked in a predator-prey association involved in transmission. Species of the genus *Taenia* Linnaeus, 1758 are geographically widespread, and inhabit all continents except Australia and Antarctica (Hoberg 2002). The genus is relatively large, and most of the approximately 42 species (Loos-Frank 2000; Hoberg 2006) have been described based on both strobilate adults and metacestodes; 7 species are based only on adults and 3, *T. talicei* Dollfus, 1960, *Taenia saigoni* Le-Van-Hoa, 1964, *Taenia kotlani* Murai, Gubanyi & Sugar, 1993 are based only on metacestodes. *T. talicei* was described based on two metacestodes from the peritoneal cavity of *Ctenomys torquatus* Lichtenstein (Rodentia, Ctenomyidae) from Uruguay (Dollfus1960). This species, which is the focus of the current study, remained undetected following its original description and was omitted from major revisions of genus (e.g., Abuladze 1964; Verster 1969; Loss-Frank 2000).

Ctenomyids, commonly named tuco-tucos, are the most speciose of the subterranean rodents of South America (approximately 60 species) and are widely distributed in a wide variety of habitats (Reig *et al*. 1990). At present, only three records of infection by taeniid metacestodes have been documented for these fossorial rodents; one corresponding to an unidentified species in *Ctenomys peruanus* Sanborn et Pearson from Peru

(Voge 1954), the second to *T. talicei* Dollfus, 1960 and a third to *Taenia taeniaeformis* Batsch, 1786 in *Ctenomys talarum* Thomas, from urban areas of Mar de Cobo, Argentina (Rossin *et al.* 2004). Metacestodes of the later species were initially characterized as strobilocerci and the identification was based on adult tapeworms obtained from experimental infections of domestic dogs (*Canis lupus familiaris* L.) (Rossin *et al.* 2004).

Subsequently, during an extensive parasitological survey of 4 additional species of *Ctenomys* Blainville**,** metacestodes including cysticerci, unique fimbriocerci and polycephalic forms (see Hoberg *et al.* 2000) referable to a species of *Taenia* were found in the abdominal cavity of *Ctenomys australis* Rusconi. These metacestodes were compared with those previously described by Dollfus (1960) and Rossin *et al.* (2004). As the strobilate form of *T. talicei* remains unknown in natural definitive hosts, we re-examined adult worms obtained by Rossin *et al.* (2004) from experimentally exposed domestic dogs to metacestodes from naturally infected *Ctenomys talarum*. We provide the first complete description of this apparently endemic Neotropical species of *Taenia* and reassessed a previous report of *Taenia taeniaformis* in *C. talarum* by Rossin *et al.* (2004).

Material and methods

Five species of *Ctenomys* (tuco-tuco) from Argentina were studied, including 45 specimens of *C. australis* from Necochea (Paraje Las Grutas), Buenos Aires Province (3833´S, 5845´W), 15 *Ctenomys porteusi* from west-central Buenos Aires Province (3640´S, 6209´W), 3 *Ctenomys sociabilis* and 2 *Ctenomys heagui* from Rio Negro Province (4108´S, 7117´O). Live traps were placed in active burrow systems, easily distinguished by the conspicuous mounds of fresh earth brought to the surface during burrowing activities, and checked every hour throughout the day during each trapping session. Captured rodents were killed by ether inhalation in the laboratory. Rodents were dissected and gastrointestinal tracts, liver, lungs, kidneys, gonads, body cavity and subcutaneous tissues were examined for metacestodes using a Wild M3B stereomicroscope. Host taxonomy is consistent with Wilson and Reeder (2005).

Metacestodes were collected from abdominal cavity of ctenomyids, fixed in 10% formalin and stained with chlorhydric carmine for study. The new specimens were compared with previously collected metacestodes from *C. talarum* at Mar de Cobo, Buenos Aires Province (37º58´S, 57º34´W) and with the adult forms obtained by experimental infection of dogs with these metacestodes in a previous study (Rossin *et al.* 2004). Serial sections of proglottids were made according to standard histological techniques. Strobilate specimens included in this description were represented by 10 tapeworms; metacestodes were represented by 20 specimens.

Taxonomic identification was based on comparisons with data for strobilate adults and metacestodes summarized in Dollfus (1960), Verster (1969) and Loos-Frank (2000). Type specimens of *T. talicei* designated by Dollfus (1960) could not be located for examination. All measurements are given in micrometers unless otherwise indicated; mean values, ranges and standard deviations are provided for a series of meristic characters. Parasite prevalence, mean intensity of infection, and mean abundance were calculated according to Bush *et al.* (1997).

Representative voucher specimens (metacestodes and adults) were deposited in the Helminthological Collection of the Museo de La Plata (CHMLP), La Plata Argentina, under CHMLP Nos. 6192–6196. Additional specimens of strobilate adults and metacestodes were deposited in the US National Parasite Collection (USNPC), US Department of Agriculture, Agricultural Research Service, Beltsville, MD, USA, under USNPC Nos. 103211–103215.

Results

Metacestodes were found in the peritoneal cavity of naturally infected *C. talarum* and *C. australis*; *C. porteusi*, *C. sociabilis* and *C. heagui* examined were not infected. Prevalence of infection was variable

between *C. talarum* (64 %) and *C. australis* (11%); mean intensity, respectively, in these hosts was 15 (range 1–95) and 10 (8–15).

Cyclophyllidea van Beneden in Braun, 1900

Taeniidae Ludwig, 1886

Taenia talicei Dollfus, 1960
(Figs. 1–14)

Type host: *Ctenomys torquatus* Lichtenstein, as established by the original description of the metacestode by Dollfus (1960).

Other hosts: *C. talarum* Thomas and *C. australis* Rusconi.

Microhabitat: Abdominal cavity.

Definitive host: *Canis lupus familiaris* Linnaeus (experimental infection); natural definitive host unknown.

Type locality: Uruguay.

Other localities: Mar de Cobo (Mar Chiquita, 37º58´S, 57º34´W) and Las Grutas (Necochea, 3833´S, 5845´W), Buenos Aires Province, Argentina.

Description: *Adult forms* (Figs. 1–8): Strobila 26.71 1.91 (22.80–30.50; N=10) cm in total length, with 120–150 proglottids each with single set of reproductive organs. Scolex 631 123 (450–860) long and 1.017 176 (710–1.210) wide bearing four rounded muscular suckers 273 31 (220–330) in diameter (Figs. 1–2). Rostellum armed with two rows of hooks; small hooks 168 26 (150–187), large hooks 237.50 7 (232–242). Total number of hooks 46 (44–50) (Figs. 1–4).

Male genitalia (meristic data and morphological description of male genitalia based on serial sections and whole specimens, measurements of male genital system corresponding to 5 proglottids from 3 worms): Testes oval, 124–138 in number, 65 (42–77) long, 54 (35–67) wide. Testicular field not extending laterally beyond osmoregulatory canals. In mature proglottid, cirrus pouch elongated and curved, reaching poral osmoregulatory canals, 157 18 (132–175) long and 121 6 (112–125) wide; coiled cirrus inside (Figs. 5–6). Vas deferens highly coiled; coiled region extends well into the medulla (Fig. 5). Male and female genital ducts pass between the ventral and dorsal longitudinal excretory canals (Fig. 7).

Female genitalia (meristic data and morphological description of female genitalia based on serial sections and whole specimens, measurements of female genital system corresponding to 5 proglotids from 3 worms): In mature segments, ovary bilobed; poral lobe 450 61 (360–480) by 350 28 (304–360) smaller than antiporal lobe 590 23 (48–60) by 580 76 (56–60). Vitelline gland postovarian. Vagina, thick-walled running parallel to cirrus sac, descending posteriorly forming a seminal receptacle at level of ootype region (Fig. 5). Vaginal sphincter absent. In gravid segments, number of uterine branches (unilateral) 10 to 12 which then subdivide (Fig. 8). Embryophore subspherical, 30 (29–30) by 25 (25– 27).

Metacestodes (Figs. 9–11, 12–14, Tables 1, 2): Both monocephalic and polycephalic metacestodes were found free in abdominal cavity. Cysticercus, small, transparent and globular with invaginated scolex. Fimbriocercus, elongated, milky-white form with invaginated scolex; polycephalic forms representing multiple fimbriocerci were also common (Figs. 11–12). Comparative morphometry of metacestodes is given in Table 1, number and measurements of rostellar hooks were similar among metacestodes. Comparative morphometry of monocephalic metacestodes from three *Ctenomys* species is given in Table 2.

Differential diagnosis: Based on our redescription, morphological characters of metacestodes observed in material from *C. talarum* and *C. australis* agree with the diagnostic characteristics of *T. talicei* described originally from *C. torquatus* by Dollfus (1960) (Table 2). The number and size of rostellar hooks of both larvae and adults, and the particular morphology of polycephalic and fimbriocercus metacestodes (see Hoberg *et al*. 2000) further agree with the original description of *T. talicei*. The structure, dimensions, and numbers of

rostellar hooks serve to establish identity for adults and metacestodes, and are an additional basis for differentiating *T. talicei* from other related species in the genus.

TABLE 1. Comparative morphometry of *Taenia talicei* metacestodes.

Larval types of *Taenia talicei*	Cysticercus (n=5)			Fimbriocercus (n=5)			Polycephalic fimbriocercus (n=2)		
	Mean	Range	SD	Mean	Range	SD	Mean	Range	SD
Total length (mm)	4.77	3.27–6.08	1.27	24.70	9.36–35.8	12.9	29.01	18.20–39.80	15.22
Number of hooks	46.4	44–48	0.75	46	40–50	2.12	44	44–46	0.70
Length of large hooks	237	225–244	7.21	242	241–244	1.14	242.3	241–243	1.94
Length of small hooks	157	150–161	4.16	161	158–162	1.54	156	155–156	0.77

TABLE 2. Comparative morphometry of *Taenia talicei* monocephalic metacestodes from *Ctenomys talarum*, *C. australis* and *C. torcuatus*.

Taenia talicei	*C. talarum* (Present paper, n= 10)			*C. australis* (Present paper, n= 10)			*C. torquatus* (Dollfus 1960, n=2)
	Mean	Range	SD	Mean	Range	SD	
Total length (cm)	1.05	0.50–2.00	0.54	2.04	0.90–3.50	0.80	0.60
Number of hooks	46	40–52	6.00	46	40–50	2.50	48 and 52
Diameter of rostellum	407	390–420	11.65	424	370–500	47.42	
Diameter of suckers	258	200–320	40.21	291	260–320	22.32	
Length of large hooks (n=50)	243	240–248	2.46	236	230–243	2.18	245–247
Length of small hooks (n=50)	161	158–168	2.78	154	150–160	3.70	154–160

Taenia talicei can be considered in the context of the phylogeny established for species of the genus (Hoberg *et al.* 2000; Hoberg 2006). Fimbriated metacestodes are limited to a few species of *Taenia,* and are most evident among those species that parasitize Mustelidae as definitive hosts (Korniushin & Sharpilo 1986) and have rodents as intermediate hosts (e.g. *Taenia martis* Zeder, 1803). Some polycephalic metacestodes are also limited to this group of host species (e.g. *Taenia twitchelli* Schwartz, 1924) although such metacestodes are also characteristic of *Taenia endothoracicus* Kirschenblatt, 1948, a parasite of Canidae.
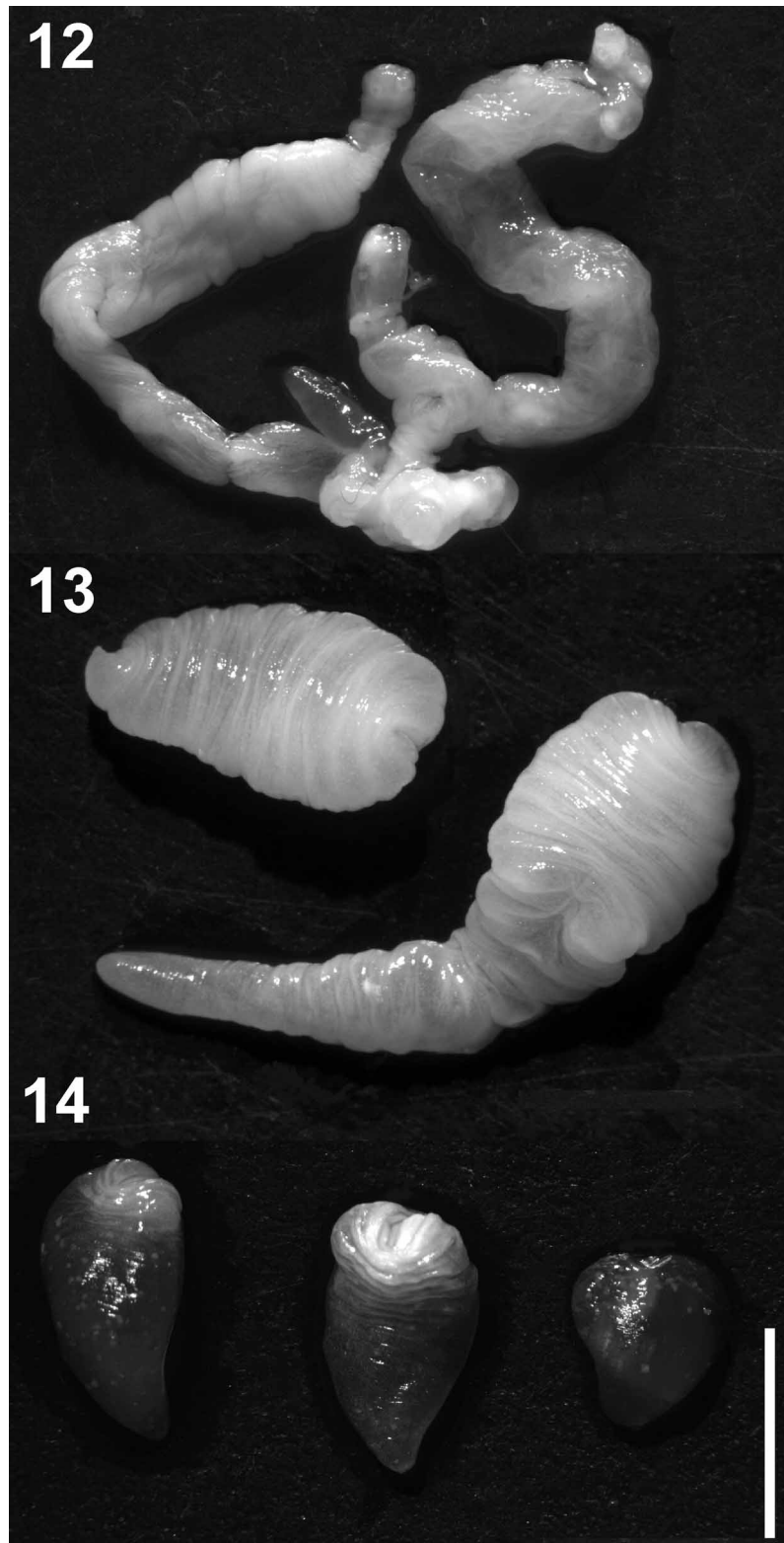
Fimbriocercus and polycephalic metacestodes that develop by exogenous budding are proliferating metacestodes that usually occur in the pleural or pertitoneal cavity of a rodent intermediate host. Polycephalic metacestodes of *T. talicei* appear to develop by exogenous budding from a central bladder; in this case, fimbriated protoscolices eventually are arranged on elongate stalks following regression of the bladder. Fimbriocerci may subsequently break off of the original larval mass and thus can appear free in the peritoneal cavity. This ontogenetic pattern appears to be most similar to that described for *Taenia twitchelli* in porcupines (*Erethizon dorsatum* (L.)) (Rausch 1977). It is not clear, however, that the simple cysticerci of *T. talicei* that co-occur with polycephalic and fimbriocercus metacestodes in *Ctenomys* develop through a similar pattern, or represent an endpoint in ontogeny. Polymorphism in larval development is known among other species such as *Taenia mustelae* Gmelin, 1790 (e.g. Freeman 1956). Also in this regard, metacestodes of *Taenia polyacantha arctica* Rausch & Fay, 1988 are represented by cysticerci when mature, but ontogeny involves proliferation by exogenous budding (Rausch & Fay 1988).

Taenia talicei is clearly differentiated from those species with proliferating larvae (which develop through exogenous budding) based on structure, size and number of rostellar hooks (Verster 1969; Loos-Frank 2000). Proliferating metacestodes reported by Voge (1954) in *C. peruanus*, and the sigmodontids *Phyllotis osilae* Allen and *Chinchilla sahamae* Thomas from Peru, could be conspecific with *T. talicei*; these metacestodes were reported as having a 40–44 rostellar hooks with lengths of 120–140μm for small and 190–220 for large.
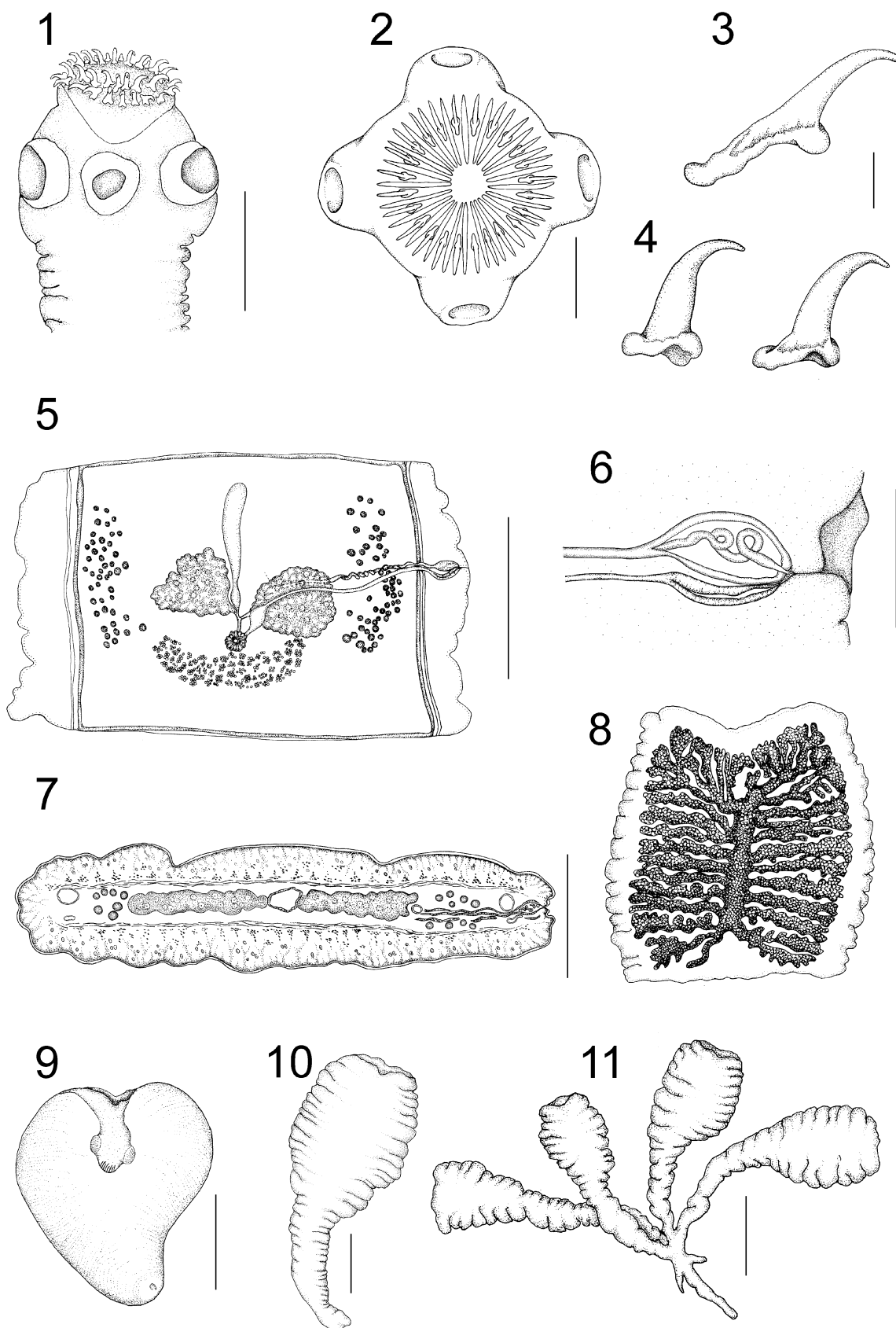
FIGURES 1–11. *Taenia talicei* Dollfus, 1960. **1–8.** Adult form. **1**. Scolex (ventral view). **2.** Scolex (apical view). **3–4.** Rostellar hooks. **3.** Large hooks. **4.** Small hooks. **5.** Mature segment. **6.** Cirrus pouch and vagina. **7.** Transverse section of mature segment. **8**. Gravid proglottid. **9–11.** Metacetodes. **9.** Cysticercus. **10.** Fimbriocercus. **11.** Polycephalic forms. Scale bars in mm: **1**, 0.5; **2**, 0.3; **3–4**, 0.05; **6**, 0.25; **7,** 1; **5** and **8–11**, 2.

FIGURES 12–14. *Taenia talicei* Dollfus, 1960. Metacestodes. **12.** Polycephalic fimbriocercus. **13.** Fimbriocercus. **14.** Cysticercus. Scale bar: 0.5 cm.

Strobilate adults of *T. talicei* can be differentiated from other species in the global fauna. Serial sections of proglotids showed that the genital ducts pass between the longitudinal excretory canals when crossing from the medulla into the cortex. From a diagnostic standpoint (but not a phylogenetic one; see Hoberg *et al.* 2000),

this feature is characteristic of Group 1 defined by Verster (1969); in Group 2 species such as *T. taeniaeformis* genital ducts pass ventrally to the longitudinal excretory canals.

Taenia talicei is distinguished from those species that occur naturally in Felidae from South America; no species are known in endemic Canidae. *Taenia talicei* is distinct from the following species based on the structure of the metacestode, dimensions and numbers of rostellar hooks and a suite of specific characters of the genital system in strobilate adults: (1) *Taenia macrocystis* Diesing, 1850 (in small felids and lagomorphs) by smaller and fewer rostellar hooks; in *T. macrocystis*- large hooks= 300–480 µm, small hooks= 180–250, number = 52–74. (2) *Taenia omissa* Lühe, 1910 (large felids and deer) by smaller and a greater number of rostellar hooks; in *T. omissa*- large hooks= 230–300, small hooks= 160–225, number= 38–44. (3) *Taenia pseudolaticollis* Verster 1969 (small felids) by substantially smaller hooks of a different structure; in *T. pseudolaticollis*- large hooks= 350–420, small hooks= 220–240, number= 38–42. Non-proliferating cysticerci are typical metacestodes for *T. omissa*; a strobilocercus is described for *T. macrocystis*; the complete life cycle is unknown for *T. pseudolaticollis* (Loos-Frank 2000).

Taenia talicei is differentiated from those cosmopolitan species that circulate in synanthropic cycles with rodents (or lagomorphs) and domestic hosts such as cats and dogs in South America including *Taenia pisiformis* Bloch, 1780, *Taenia serialis serialis* Gervais, 1847, and *T. taeniaeformis* based on structure and number of the rostellar hooks and form of the metacestode. A simple cysticercus is typical for *T. pisiformis*, a coernurus is typical in *T. serialis*, whereas a strobilocercus is characteristic for *T. taeniaeformis*. Furthermore, *T. taeniaeformis* could be readily distinguished from *T. talicei* by having larger and a different number of rostellar hooks (number of rostellar hooks 34–36, large hooks 370–402, and small hooks 210–261).

Discussion

The present study constitutes the first complete morphological description of strobilate specimens of *T. talicei* in a carnivore definitive host. Unequivocal identity for adults and metacestodes is established, along with the first data documenting morphometric variability. *Taenia talicei* is, therefore considered as a valid species.

Verster (1969) published a valuable revision of *Taenia,* in which she assessed the relative importance of diagnostic characters used for species identification and reviewed the status of the known species. Owing to the similarity and overlap of diagnostic characters, Verster (1969) did not provide a key to species for the genus, but stated that the differences in number and size of the rostellar hooks were among the most reliable diagnostic criteria. In contrast, the shape and size of strobila, scolex, rostellum and suckers were considered to be dependant on the method of fixation. Loos-Frank (2000) summarized the work by Verster (1969) and included species subsequently described along with an extensive treatment of diagnostic characters, host associations and life history. Despite an extensive literature dealing with comparative morphology on this group, species of *Taenia* are not easily identified based on morphology because many characters commonly used are subject to some intraspecific variation; additionally there is homoplasy in most characters assessed in phylogenetic studies (Hoberg *et al*. 2000). Thus reliance on a single character (such as rostellar hooks) as the sole criterion for specific diagnosis can occasionally lead to erroneous identifications. For example, substantial variation in meristic data is commonly reported for several species (e.g. *T. taeniaeformis*; see Verster 1969; Rossin *et al*. 2004). Re-evaluation during the current study of the specimens reported as *T. taeniaeformis* by Rossin *et al*. 2004, indicates that these tapeworms are referable to *T. talicei*. Confusion over identity of the metacestodes in *Ctenomys* was in part attributable to the obscurity of the original description for metacestodes of *T. talicei* which was published in a local journal (Archivos de la Sociedad de Biología de Montevideo) (Dollfus 1960) now out of print for over 50 years.

The natural definitive host of *T. talicei* is unknown. The potential definitive hosts would be expected to be wild carnivores inhabiting the area where metacestodes infect ctemomyids. For example, the wild felid *Oncifelis geoffroyi* d´Órbigny & Gervais, or the fox *Lycalopex gymnocercus* Fischer are both known to prey on *C. talarum* and *C. australis* and occur in the general area where metacestodes of *T. talicei* have been collected (Canepuccia 1999; 2006; Farias 2000; B *et al*. 2002). In Argentina, *O. geoffroyi* is parasitized by an

undescribed species of *Taenia*, which resembles *Taenia hydatigena* Pallas, 1766 based on the number and shape of rostellar hooks (Beldomenico *et al*. 2005). Unfortunately, the authors could not to identify this species, but provided morphometric data that distinguish it from *T. talicei* in having smaller rostellar hooks (large hooks 165–170, small hooks 130–140) (Beldomenico *et al*. 2005). This suggests that multiple species of *Taenia* are circulating in an assemblage of small felids and canids from southern South America.

Numerous species of *Taenia* have been reported across the Americas with *T. hydatigena*, *Taenia multiceps* Leske, 1780, *Taenia ovis* (Cobbold, 1896), *T. pisiformis* (Bloch, 1780), *Taenia saginata* Goeze, 1782, *T. serialis* (Gervais, 1847), *Taenia solium* Linnaeus, 1758 and *T. taeniaeformis* (Batsch, 1786) being cosmopolitan (Loos-Frank 2000). These species largely have synanthropic associations involving ungulates, lagomorphs or rodents as intermediate hosts and distributions globally and in South America that were determined by anthropogenic translocation since the 1500's. Few species, namely *T. macrocystis*, *T. omissa* and *Taenia pseudolaticollis* are shared among Felidae from North America and South America. These latter species circulate in sylvatic cycles among felids and rodents, or cervids and large cats including *Puma concolor* (L.) with distributions determined by natural expansion from the Nearctic. Associations for introduced and endemic species demonstrate the importance of invasive processes across disparate temporal and spatial scales which result in a mosaic structure for *Taenia* faunas in South America (see. Hoberg 2010).

Taenia talicei is the first described species that can be considered endemic from South America. Origins of an endemic *Taenia* or an assemblage of *Taenia*-species in South America would have relationships to either North American or Eurasian placental carnivores. *Taenia* is not associated with marsupials, and thus would not have become established in South America prior to the Miocene, coincidental with the dispersal and radiation of felids and canids on the continent. The temporal limits for geographic colonization by *Taenia* in the Neotropical region are constrained by the timing of expansion events for a Felidae and Canidae. The presence of a susceptible rodent fauna, including the endemic caviomorphs such as sigmodontids and ctenomyids with species of *Ctenomys*, may have facilitated colonization by cestodes of carnivores. For example, small felids are known to have entered and radiated in South America prior to 8 million years before present (MYBP), substantially earlier than the emergence of the Panamanian Isthmus and the faunal interchange at the Pliocene-Pleistocene boundary (Webb & Marshall 1981; Marshall *et al*. 1982; Johnson *et al*. 2006). Canids, however did not arrive until the emergence of the isthmus, and thus represented a component of the faunal interchange after 3MYBP (Marshall *et al*. 1982). Such a putative history for *Taenia*, would parallel that demonstrated for *Trichinella*- nematodes in the Neotropical region where episodes of geographic and host colonization from Eurasia through North America have structured the fauna (Zarlenga *et al*. 2006; Pozio *et al*. 2009; Hoberg & Brooks 2010). In these instances both the expansion of *Taenia* and *Trichinella* may have resulted from geographic colonization of South America, radiation of both felids (and canids), and host switching by tapeworms to caviomorphs, prior to the emergence of the Panamanian Isthmus (Johnson *et al*. 2006). Such a history suggests that additional endemic species of *Taenia* remain to be discovered through survey and inventory of the Neotropical fauna.

A further consideration is warranted given the observation that some species of *Taenia* may infect humans and thus are the cause of zoonotic disease in many regions of the world (e.g. Hoberg 2002; 2006). *Taenia talicei* is capable of development in domestic dogs, and metacestodes in species of *Ctenomys* were found in urban or semi-urban environments. These factors establish the role for synanthropic cycles linked to definitive hosts including dogs and cats as a route for exposure of humans to infection by this taeniid.

Acknowledgments

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