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ORIGINAL PAPER

New species of *Eimeria* (Apicomplexa: Eimeriidae) from *Thrichomys fosteri* and *Clyomys laticeps* (Rodentia: Echimyidae) of the Brazilian Pantanal

Wanessa Teixeira Gomes Barreto[1] · Lúcio André Viana[2] · Filipe Martins Santos[1] · Grasiela Edith de Oliveira Porfírio[1] · Alessandra Cabral Perdomo[3] · Alanderson Rodrigues da Silva[4] · Keyla Carstens Marques de Sousa[5] · Michel Angelo Constantino de Oliveira[1] · Heitor Miraglia Herrera[1] · Gisele Braziliano de Andrade[1]

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Abstract The echimyid rodents *Thrichomys fosteri* and *Clyomys laticeps* are among the most commonly recorded small mammals in the Pantanal wetland of Brazil. These species play important ecological roles since they are the basis of the food chain of some predators and are parasitized by some pathogens. Knowledge of the eimerians that parasitize echimyid rodents in Brazil is absent, and only one report is available for South America. We therefore investigated parasitism by coccidians in the echimyids *T. fosteri* and *C. laticeps* in the Pantanal. Using morphological and morphometric features and associated statistical analyses, we describe five new eimerian species parasitizing *T. fosteri* (*Eimeria nhecolandensis* n. sp., *Eimeria jansenae* n. sp., and *Eimeria fosteri* n. sp.) and *C. laticeps* (*E. nhecolandensis* n. sp., *Eimeria corumbaensis* n. sp., and *Eimeria laticeps* n. sp.) in different types of infection associations. We document the developmental forms in the tissues, and describe lesions in the enteric tract of some infected animals. We also discuss some approaches regarding epidemiological and ecological data. Our results demonstrate that echimyid rodents in the Brazilian Pantanal are important hosts for the maintenance of enteric coccidia. Moreover, in some circumstances, this parasitism may threaten the health of the hosts.

Keywords Small mammals · *Thrichomys fosteri* · *Clyomys laticeps* · Coccidia · Histopathology · Pantanal

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✉ Heitor Miraglia Herrera
herrera@ucdb.br

[1] Programa de Pós-Graduação em Ciências Ambientais e Sustentabilidade Agropecuária, Universidade Católica Dom Bosco, Campo Grande, MS, Brazil

[2] Departamento de Ciências Biológicas e da Saúde, Universidade Federal do Amapá, UNIFAP, Macapá, Amapá, Brazil

[3] Curso de Medicina Veterinária, Universidade Católica Dom Bosco, Campo Grande, MS, Brazil

[4] Programa de Pós-Graduação em Biotecnologia, UCDB, Campo Grande, MS, Brazil

[5] Faculdade de Ciências Agrárias e Veterinárias, Universidade Federal Paulista, UNESP, Jaboticabal, SP, Brazil

Introduction

The superfamily Octodontoidea is the most diverse superfamily of caviomorph rodents (Rodentia), comprising six families, 38 genera, and 193 living species (Upham and Patterson 2012). Its distribution extends from arid deserts to tropical forests and alpine steppes (Mares and Ojeda 1982; Redford and Eisenberg 1992). The octodontoidean family Echimyidae comprises about 80 species. It is a diverse family and also the one that presents the greatest diversity of ecomorphological adaptations within the infraorder Hystricognathi (Emmons and Feer 1997; Eisenberg and Redford 1999). Studies have demonstrated that the echimyid rodents *Thrichomys fosteri* Thomas, 1903, and *Clyomys laticeps* (Thomas, 1909) are among the most commonly recorded small mammals in the Pantanal wetland (Herrera et al. 2007; Andreazzi et al. 2011).

The genus *Thrichomys* comprises four recognized species: *Thrichomys apereoides* (Lund, 1839), *T. inermis* (Pictet, 1843), *T. fosteri* (syn. *pachyurus*), and *T. laurentius* Thomas,

1904 (Pessôa et al. 2015). *Thrichomys fosteri* is a medium-sized small mammal distributed across open tropical regions in central and eastern South America, including the Chaco and Pantanal ecoregions of Brazil, Bolivia, and Paraguay (Bonvicino et al. 2008; D'Elía and Myers 2014; Lacher 2016). This species is nocturnal and primarily terrestrial, although it may climb the lower strata of trees and shrubs, and males occupy slightly larger home ranges than females (Oliveira and Bonvicino 2011; Pessôa et al. 2015; Porfirio et al. 2016). Its diet is composed mainly of fruits, shoots, leaves, and arthropods (Camilo-Alves and Mourão 2009; Oliveira and Bonvicino 2011; Antunes et al. 2016).

The broad-headed spiny rat *C. laticeps* is another medium-sized rodent that inhabits the tropical savannas and grasslands of central Brazil and the open vegetation areas of the Paraguayan Chaco and the Brazilian Pantanal (Bishop 1974; Avila-Pires and Wutke 1981; Lacher and Alho 1989; Vieira 1997). This species is the only representative of its genus, as recently revised by Bezerra et al. (2016). *Clyomys laticeps* exhibits fossorial to semi-fossorial habits and lives in excavated burrows (Lacher and Alho 1989; Bezerra and De Oliveira 2010). Studies carried out in São Paulo state and in the Pantanal of Mato Grosso do Sul state revealed a positive association between *C. laticeps* populations and the presence of palm trees (*Attalea geraensis*, *A. phalerata*, and *Syagrus petraea*) (Almeida and Galetti 2007; Antunes et al. 2016), areas of cultivation of corn and manioc (Alho et al. 1987), areas of *Pinus* monoculture (Carvalho and Bueno 1975), and areas with monocot plants (Vieira 2003). The diet of the species is composed of the seeds of palms and monocot plants (Vieira 2003; Almeida and Galetti 2007).

Although *T. fosteri* and *C. laticeps* overlap in geographic distribution, competition is avoided since one is scansorial while the other is fossorial (Lacher and Alho 1989). Moreover, due to their abundance, these species play important ecological roles as seed dispersers and are the basis of the food chains of some predators (Lessa and Costa 2009; Bianchi et al. 2014; Bezerra et al. 2016). These two rodents have been found to be parasitized in the Pantanal region by some species of protozoans, helminths, bacteria, and ticks (Herrera et al. 2007; Simões et al. 2010; Vieira et al. 2013; Wolf et al. 2016). To our knowledge, however, no previous information regarding enteric coccidian infections has been reported in these two species.

The genus *Eimeria* Schneider, 1875, comprises more than 1200 species and is considered the largest genus in the family Eimeriidae (Tenter et al. 2002). Traditionally, enteric coccidians are identified based on the morphometry and morphology of the oocysts, as well as the identity of the host species (Tenter et al. 2002; Berto et al. 2014). Duszynski and Wilber (1997) prepared a guideline for description and species differentiation in order to better evaluate and propose new species of Eimeriidae. These authors recommended that new coccidian species should be compared in detail with similar coccidian species found in the same host genus and, in particular, that comparisons should be made between the candidate new species and all described species found in the host family in order to avoid naming new species based only on the host. Moreover, sporulated oocysts in the Eimeriidae may exhibit polymorphism, and this should be an important element to be considered in the identification of new eimerian species (Gardner and Duszynski 1990; Berto et al. 2011).

Knowledge of eimerians parasitizing echimyid rodents in Brazil is lacking, and only one report is available for South America (Arcay-de-Peraza 1964). Our objective was therefore to investigate parasitism by coccidians in the echimyid rodents *T. fosteri* and *C. laticeps* sampled in the Brazilian Pantanal. We also collected epidemiological and ecological data from these species.

Material and methods

Study area and sampling procedures

Our study was carried out at the research station of the Brazilian Agricultural Research Corporation (Embrapa), located in the Nhecolândia sub-region of the Pantanal wetland, Corumbá municipality, Mato Grosso do Sul state, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W). The climate is tropical sub-humid (Aw), with a characteristic dry season from May to October and a rainy season from November to April. The annual precipitation is ~ 1180 mm, the minimum average temperature is 19 °C, while the maximum can reach 38 °C (Cadavid 1984; Soriano and Alves 2005). The main economic activity in the area is cattle ranching (Zucco and Mourão 2009), which increases the likelihood of contact between domestic and wild species. The study area is characterized by sandy soil with a mosaic vegetation of semi-deciduous forest, dispersed shrub vegetation, and seasonally flooded fields. Permanent and temporary freshwater ponds and alkaline ponds occur throughout the area. The understory is dominated by patches of caraguatá bromeliad (*Bromelia balansae*), and stands of acuri palm (*Attalea phalerata*) and bamboo (*Guadua paniculata*) (Abdon et al. 1998; Antunes et al. 2016).

Study animals were captured with Tomahawk (45 × 17.5 × 15 cm) and Sherman (31 × 0.8 × 0.9 cm) live traps baited with a mix of banana, peanut candy, sardine, and rolled oats in March 2015. The traps were placed on the ground at 10-m intervals along five linear transects in forested areas, with 15 Tomahawk and 15 Sherman traps alternating in each transect. Traps were rebaited daily and remained open for seven consecutive nights, for a total sampling effort of 2100 trap-nights, equally distributed among the linear transects. Captured animals were sedated by intramuscular injection of ketamine and acepromazine (5–10 mg/kg) and were euthanized by

intracardiac injection of 0.2–2 mL/individual of T61® (Intervet; Unterschleissheim, Germany) (mebezonium iodide 5 g + embutramide 20 g + tetracaine hydrochloride 0.5 g).

Small mammals were trapped and collected by authorization of the Sistema de Autorização e Informação em Biodiversidade (SISBIO) under licenses 38145 and 38787-1, and according to the Ethical Guidelines for Animal Research established by the Brazilian Society of Laboratory Animal Science (SBCAL); the work was approved by the university's Animal Research Ethics Committee (protocol number UCDB 013/2016). Photosyntypes of the parasites have been deposited in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro (UFRRJ), located in Seropedica, Rio de Janeiro, Brazil.

Coprological analysis

Conventional methods for concentration, preservation, and description of oocysts followed Duszynski and Wilber (1997). At necropsy, fecal material was removed from the lower bowel of each animal, preserved in Falcon™ 50-mL tubes containing 2.5% aqueous (*w*/*v*) potassium dichromate ($K_2Cr_2O_7$) solution, and maintained at room temperature. Sporulated oocysts were concentrated by flotation in Sheather's sugar solution and examined from 329 to 522 days after the specimens were collected using a Zeiss Axio Scope.A1 microscope equipped with a camera. The oocysts were measured and photographed with the software Zen lite Blue edition 2011 using 100× objective lenses. All measurements were recorded in micrometers (μm). The ratio of length by width (shape-index, L × W) was used to demonstrate the shape of the oocysts and sporocysts. The morphology of the Stieda body was described according the recommendations of Berto et al. (2014). Morphometrical and morphological features were primarily compared with those *Eimeria* species previously reported from members of the Echimyidae family. Moreover, due to the scarcity of studies in echimyid rodents and to their phylogenetic proximity, we used in our comparisons rodent species belonging to the Ctenomyidae family, within the superfamily Octodontoidea (Blanga-Kanfi et al. 2009; Upham and Patterson 2015).

Histological analysis

For histopathological examination, tissue samples of the intestine of each rodent were prepared by the Swiss roll technique (Moolenbeek and Ruitenberg 1981) to increase the surface area for analysis, and by conventional transverse cuts. The samples were fixed in neutral-buffered 10% formaldehyde for preparation of histological slides, and stained with hematoxylin-eosin (HE). Inflammatory infiltrates were characterized as described by Solano-Gallego et al. (2004): (a) discrete and focal, with small isolated foci of inflammatory cells; (b) moderate and multifocal, with coalescent foci; and (c) severe and diffuse, with large diffuse areas. To quantify parasite load, endogenous stages (meronts, immature gametocytes, macrogamonts, microgametocytes, and oocysts) were counted on slides stained by HE under a light microscope. Ten microscopic fields of 145.649 μm^2 (20× objective) were selected from among those showing endogenous stages of coccidian parasites, for a final total evaluation area of 1456.49 μm^2, following Verçosa et al. (2012) with adaptations, such as the number of fields that were counted and the magnification used.

Data analysis

Statistical analyses were performed on morphotypes of coccidian oocysts identified in each host species sampled (*T. fosteri* and *C. laticeps*). We tested for differences in morphometrical measurements of oocysts, in addition to considering host species identity, in order to distinguish eimerian species, following the recommendations of Duszynski and Wilber (1997). Measurements of six characters of each oocyst (oocyst length, oocyst width, oocyst index, sporocyst length, sporocyst width, and sporocyst index) were used in the analysis. Data were log10 transformed before analysis due to slight deviations from normality.

To test for possible differences in morphotypes with respect to the six measurements taken, we performed a MANOVA (multiple analysis of variance). Wilk's lambda was selected as the MANOVA test criterion. If the MANOVA was significant ($p \leq 0.05$), a Hotelling test was performed for each morphotype in order to determine the pairwise significance. Canonical variable analysis (CVA) yielded a scatter plot of morphotypes on the first two canonical axes through discriminant analysis. The axes are linear combinations of the original variables, and the eigenvalues show the amount of variation that was explained in the axes. Levels of statistical significance were set a priori at $p \leq 0.05$. This approach was carried out initially with oocyst measurements taken from one host species, and then the analyses were performed with measurements taken from both studied species.

Linear regression was performed to assess polymorphism, which occurs when variations in width and length of oocysts are observed (Norton and Joyner 1981; Berto et al. 2011). When R^2 is higher than 0.5, it means that there is little variation in the length and width of the species, demonstrating that the oocysts have uniform characteristics. On the other hand, when the R^2 is lower than 0.5, variation in the length and width of the species is confirmed, thereby confirming polymorphism.

Results

Fecal samples from 38 specimens of *T. fosteri* and two specimens of *C. laticeps* were obtained. Coprological prevalence of oocysts morphologically compatible with *Eimeria* spp. was 40% (14 *T. fosteri* and two *C. laticeps*). We found three morphotypes of *Eimeria* spp. in *T. fosteri* (M1, M2, and M3) and three morphotypes of *Eimeria* spp. in *C. laticeps* (M4, M5, and M6). Measurements of all eimerian morphotypes from both the rodent species sampled and from other Octodontoidea described in the literature are shown in Table 1. Note that in the case of *Eimeria opimi*, the oocysts recovered from different species of *Ctenomys* presented different measurements.

Thrichomys fosteri

We observed statistical differences in morphometrical data among the three *Eimeria* morphotypes found in *T. fosteri* ($F = 37.6$, $p < 0.01$). Moreover, the Hotelling test showed significant differences between the measurements of all the morphotypes (Online Resource 1).

Differences among the three *Eimeria* morphotypes in *T. fosteri* were also observed in the CVA test. Online Resource 2 displays a scatter plot of the morphotypes that includes 100% of the variation in the data in the first two canonical axes.

Clyomys laticeps

We observed statistical differences in morphometrical data among the three *Eimeria* morphotypes found in *C. laticeps* ($F = 26.3$, $p < 0.01$). The Hotelling test also showed significant differences between all the morphotypes (Online Resource 3).

The CVA test produced a scatter plot of the morphotypes that includes 100% of the variation in the data in the first two canonical axes (Online Resource 4).

The measurements of the six morphotypes observed in *T. fosteri* and *C. laticeps* showed statistical differences ($F = 31.4$, $p < 0.0001$). Also, the Hotelling test revealed significant interspecific variation among the morphometrical data of all six morphotypes (Online Resource 5). However, we found an overlap between the measurements of M1 and M4 in the CVA test, with 92.7% of the variation in the data in the first two canonical axes (Online Resource 6).

We found polymorphism, demonstrated by linear regression, in two *Eimeria* morphotypes from *T. fosteri*: M1 ($R^2 = 0.46$, $p = 6.372e{-}08$) and M2 ($R^2 = 0.21$, $p = 0.001238$). M3 was the only morphotype that presented uniform characteristics ($R^2 = 0.75$, $p = 5.139e{-}12$) (Online Resource 7). We also observed polymorphism in three *Eimeria* morphotypes from *C. laticeps*: M4 ($R^2 = 0.25$, $p = 5.139e{-}12$), M5 ($R^2 = 0.28$, $p = 9.15e{-}05$), and M6 ($R^2 = 0.36$, $p = 1.995e{-}06$) (Online Resource 8).

Species descriptions

We considered M1 found in *T. fosteri* and M4 found in *C. laticeps* to be the same species due to their similarity in morphometrical and morphological data, as demonstrated by statistical and morphological analyses.

Eimeria nhecolandensis n. sp.

Sporulated oocysts ovoidal, L × W ($n = 105$) 27.6 μm (23.3–31.6) × 22.2 μm (19.0–25.1), shape-index (L/W) 1.2 (1.1–1.4). Oocyst wall ~ 1.8 μm (1.4–2.5) in total thickness, bilayered, inner layer smooth and outer layer slightly rough. Micropyle absent. Polar granule present with shape ranging from spherical to elongate, highly refractile. Oocyst residuum composed of spheroidal structures that vary in number and shape from a single large sphere to various small spheres, L × W ($n = 31$) 6.5 μm (3.7–10.2) × 5.6 μm (3.2–9.1). Sporocysts ($n = 100$) ovoidal to ellipsoidal, 11.0 μm (8.6–12.9) × 8.2 μm (6.7–9.8), with a shape-index of 1.4 (1.1–1.7). Stieda body present, nipple-shaped. Sub-stieda and parastieda bodies absent. A diffuse sporocyst residuum composed of small granules of different sizes is present, sometimes forming a line along the sporocyst wall and/or dispersed in the sporocyst. Sporozoites not measured (Fig. 1).

Taxonomic summary *Type-host: Thrichomys fosteri* (Thomas, 1903) (Rodentia, Echimyidae).

Type-locality: Nhumirim Farm, Nhecolândia Pantanal subregion, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W).

Other hosts: Clyomys laticeps (Thomas, 1909).

Type-material: Phototypes are deposited and available (http://r1.ufrrj.br/labicoc/colecao. html) in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro, located in Seropédica, Rio de Janeiro, Brazil. Photographs of the type-host specimen (symbiotype) are deposited in the same collection. The repository number is P-71/2017.

Sporulation time: Unknown.

Site of infection: Small intestine.

Prevalence: Found in 35% (14/40) of the animals examined (13 *T. fosteri* and one *C. laticeps*).

Etymology: The specific epithet is derived from the name of the study area.

Remarks: The slight roughness of the oocyst wall of *E. nhecolandensis* differs from the other eimerian oocysts examined in our study, which were rough (*E. jansenae*), strongly rough (*E. fosteri*), and smooth (*E. laticeps*). Moreover, the ovoidal oocysts of *E. nhecolandensis* differ from the

Table 1 Measurements of oocyst characters of *Eimeria* spp. from rodents of the Brazilian Pantanal (present study) and data available in rodents from superfamily Octodontoidea

Host species		Oocyst					Sporocysts			References
	Morphotype/ *Eimeria* spp.	Length (μm)	Width (μm)	Length/width ratio (μm)	Shape[a]	Wall width (μm)	Length (μm)	Width (μm)	Length/width ratio (μm)	
Thrichomys fosteri	*E. nhecolandensis*	27.9 (23.3–31.6) ± 1.7	22.7 (20.4–25.1) ± 1.1	1.2 (1.1–1.3) ± 0.1	OV	1.8 (1.4–2.5) ± 0.3	11.0 (8.6–12.9) ± 0.9	7.9 (6.7–9.8) ± 0.8	1.4 (1.1–1.7) ± 0.1	Present study
	E. jansenae	31.4 (27.1–37. 7) ± 1.9	22.6 (19.6–24.9) ± 1.2	1.4 (1.3–1.6) ± 0.1	EL	1.9 (1.4–2.7) ± 0.3	11.9 (9.5–15.6) ± 1.1	8.3 (7.1–10.2) ± 0.7	1.4 (1.2–1.8) ± 0.1	
	E. fosteri	25.1 (20.9–37.3) ± 4.6	20.1 (16.7–30.1) ± 3.4	1.2 (1.2–1.3) ± 0.1	OV	1.8 (1.0–3.4) ± 0.5	10.0 (7.6–16.0) ± 2.2	7.2 (5.1–11.1) ± 1.5	1.4 (1.2–1.7) ± 0.1	
Clyomys laticeps	*E. nhecolandensis*	27.3 (24.8–29.6) ± 1.2	21.8 (18.5–24.0) ± 1.1	1.3 (1.1–1.4) ± 0.1	OV	1.8 (1.4–2.1) ± 0.2	11.4 (9.6–12.6) ± 0.7	8.5 (7.4–9.4) ± 0.5	1.3 (1.1–1.4) ± 0.1	Present study
	E. corumbaensis	28.9 (20.7–33.4) ± 2.5	20.2 (15.03–22.8) ± 1.6	1.4 (1.1–1.7) ± 0.1	EL	1.7 (1.1–2.2) ± 0.3	11.3 (9.0–12.9) ± 0.8	8.4 (7.9–9.4) ± 0.5	1.3 (1.2–1.5) ± 0.1	
	E. laticeps	23.8 (19.2–27.3) ± 1.7	21.6 (17.1–26.7) ± 1.5	1.1 (0.9–1.2) ± 0.1	SP/SS	1.7 (1.1–2.2) ± 0.2	10.7 (8.7–12.3) ± 0.9	8.1 (6.4–9.2) ± 0.6	1.3 (1.0–1.5) ± 0.1	
Myocastor coypus[b]	*E. seideli*	(38.4–44.8)			SP		(25.6–28.2)	12.8		Pellérdy (1957)
	E. nutriae	20.0 (19.5–22.5) ± 1.9	16.1 (15.0–18.0) ± 1.4	1.3 (1.2–1.5) ± NR	OV/SS	NR	11.2 (10.5–12.0) ± 0.3	5.2 (4.5–6.0) ± 0.3	NR	Prasad (1960)
	E. myocastori	14.2 (13.5–15.0) ± 0.3	12.2 (11.5–13.0) ± 0.3	1.1 (1.4–1.5) ± NR	OV	NR	9.6 (9.0–10.5) ± 0.2	3.7 (3.0–4.5) ± 0.3	NR	
Proechimys guayanensis	*E. proechimyi*	22.9 ± NR	17.1 ± NR	NR	EL	NR	6.7 ± NR	6.7 ± NR		Arcay-de-Peraza (1964)
	E. caripensis	20.0 ± NR	20.0 ± NR	NR	SP	NR	8.7 ± NR	5.5 ± NR	NR	
Ctenomys opimus	*E. granifera*	21.1 (15.0–26.0) ± NR	17.2 (11.0–20.0) ± NR	1.2 ± NR	SS/EL	2.0 ± NR	11.3 (8.0–14.0) ± NR	7.1 (5.0–9.0) ± NR	1.6 ± NR	Lambert et al. (1988)
	E. montuosi	24.2 (21.0–28.0) ± NR	22.0 (18.0–25.0) ± NR	1.1 ± NR	SP	3.0 ± NR	10.5 (8.0–14.0) ± NR	7.3 (6.0–9.0) ± NR	1.4 ± NR	
	E. opimi	24.3 (18.0–29.0) ± NR	21.8 (15.0–26.0) ± NR	1.1 ± NR	SP/SS	1.5 ± NR	11.6 (10.0–13.0) ± NR	7.6 (6.0–9.0) ± NR	1.6 ± NR	
	E. oruroensis	27.3 (23.0–32.0) ± NR	23.6 (20.0–28.0) ± NR	1.2 ± NR	SP/SS	2.3–3.0 ± NR	13.2 (10.0–16.0) ± NR	8.6 (8.0–11.0) ± NR	1.5 ± NR	
Ctenomys boliviensis	*E. opimi*	21.7 (19.0–25.0) ± NR	19.4 (15.0–22.0) ± NR	1.1 ± NR	SP	NR	9.5 (7.0–11.0) ± NR	6.8 (6.0–8.0) ± NR	1.4 ± NR	Gardner and Duszynski (1990)
Ctenomys conoveri		20.9 (19.0–23.0) ± NR	19.2 (17.0–21.0) ± NR	1.1 ± NR		NR	10.3 (8.0–11.0) ± NR	7.0 (5.0–8.0) ± NR	1.3 ± NR	
Ctenomys frater		21.7 (19.0–26.0) ± NR	19.9 (16.0–25.0) ± NR	1.1 ± NR		NR	10.5 (9.0–13.0) ± NR	7.0 (5.0–8.0) ± NR	1.5 ± NR	
Ctenomys lewisi		23.7 (18.0–26.0) ± NR	21.2 (17.0–25.0) ± NR	1.1 ± NR		NR	10.5 (8.0–13.0) ± NR	7.5 (5.0–8.0) ± NR	1.5 ± NR	

Data provided in the following form: mean, range (in parentheses), and standard deviation

M1 morphotype 1, *M2* morphotype 2, *M3* morphotype 3, *M4* morphotype 4, *M5* morphotype 5, *M6* morphotype 6, *NR* not reported

[a] Oocyst shape as described—EL: ellipsoidal; OV: ovoidal; SP: spheroidal; SS: sub-spheroidal

[b] *E. myopotami*, *E. pellucida*, and *E. coypi* described by Yakimoff (1933) and Obitz and Wadowski (1937) in *Myocastor coypus* are not detailed due to controversial and inconsistencies in their descriptions

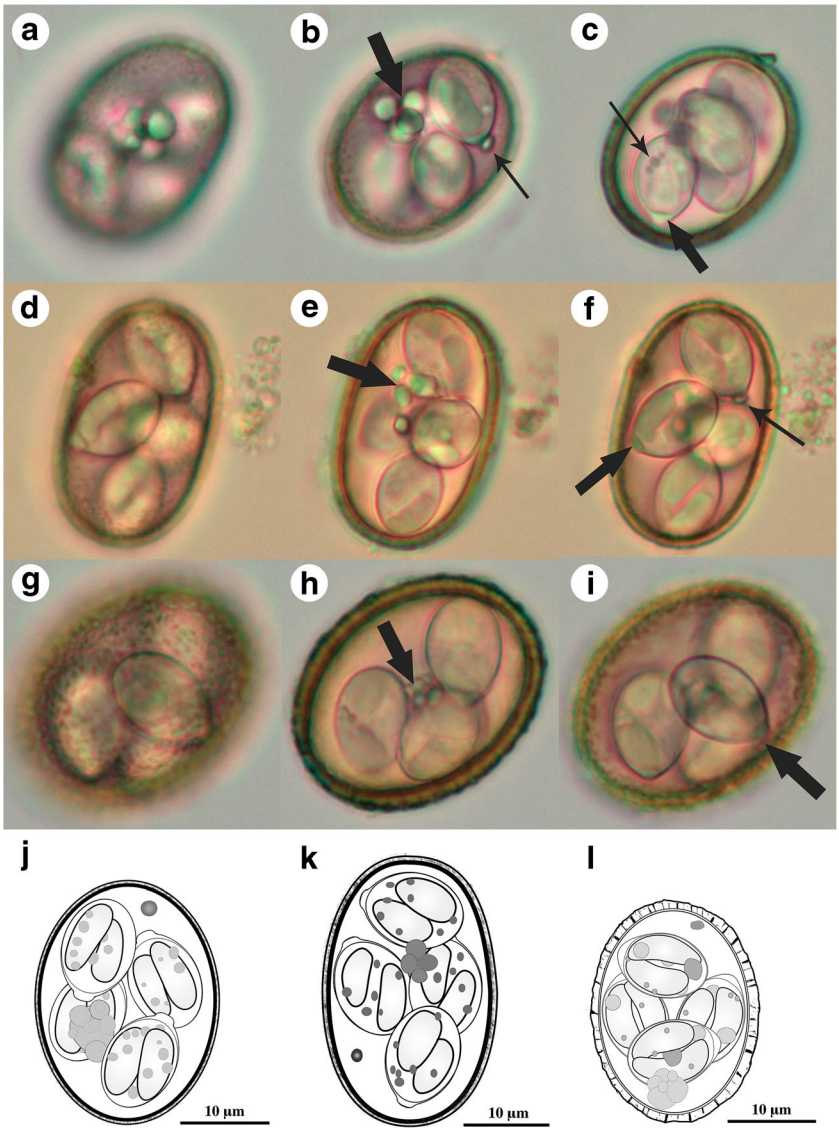

Fig. 1 Photomicrographs and line drawing of *Eimeria nhecolandensis* recovered from *Thrichomys fosteri* and *Clyomys laticeps* (**a**–**c**, **j**), and *E. jansenae* (**d**–**f**, **k**) and *E. fosteri* (**g**–**i**, **l**) recovered from *T. fosteri* in Brazilian Pantanal. **a** Note the slight roughness of the oocyst wall. **b** Spheroidal polar granule (thin arrow), compact oocyst residuum composed of numerous slightly uniform granules (arrow). **c** Nipple-like Stieda body (arrow) and sporocyst residuum (thin arrow). **d** Note the roughness of the oocyst wall. **e** Oocyst residuum composed by spheroidal structures (arrow). **f** Stieda body (arrow) and polar granule (thin arrow). **g** Note the strongly rough oocyst wall with plenty of granulation (arrows). **h** Oocyst residuum composed by some spheroidal structures (arrow). **i** Stieda body. (Obj. ×63. **j** Line drawing of a sporulated oocyst of *E. nhecolandensis*. **k** Line drawing of a sporulated oocyst of *E. jansenae*. **l** Line drawing of a sporulated oocyst of *E. fosteri*

ellipsoidal oocysts of *E. jansenae* and *E. corumbaensis* and the spheroidal oocysts of *E. laticeps*. Morphometrically, when comparing *E. nhecolandensis* with *E. caripensis* and *E. proechimyi* described by Arcay-de-Peraza (1964) in *Proechimys guyanensis* E. Geoffroy, 1803 (Rodentia: Echimyidae), from Venezuela, *E. nhecolandensis* is larger (27.9 × 22.6 µm) than *E. proechimyi* (22.9 × 17.1 µm) and *E. caripensis* (20.0 µm). Morphologically, these two species differed in having ellipsoidal and spherical oocysts, respectively, in contrast to the ovoidal oocysts of *E. nhecolandensis*. Furthermore, the oocyst residuum found in *E. nhecolandensis* was not observed in both species. Additionally, *E. nhecolandensis* has ellipsoidal sporocysts, in contrast to the spherical sporocysts reported in *E. proechimyi*. Finally, the Stieda body found in *E. nhecolandensis* and *E. caripensis* is absent in *E. proechimyi*. The four *Eimeria* spp. recovered from *Ctenomys* spp. Blainville, 1826 (Rodentia: Ctenomyidae) (*E. granifera*, *E. montuosi*, *E. opimi*, and *E. oruroensis*) (Lambert et al. 1988), all differ from *E. nhecolandensis*. Morphometrically, only *E. oruroensis* had the oocysts close to *E. nhecolandensis*, while the other species are smaller, as shown in Table 1. Regarding oocyst shape, *E. nhecolandensis* is ovoidal whereas *E. granifera* is sub-spheroidal to

ellipsoidal; *E. opimi* and *E. oruroensis* are sub-spheroidal to spheroidal, and *E. montuosi* is spheroidal. The ovoidal shape and size of sporocysts recovered from *E. nhecolandensis* are similar to those of *E. granifera*, *E. montuosi*, *E. opimi*, and *E. oruroensis* as demonstrated in Table 1. In spite of the abovementioned morphological and morphometrical differences, we also found some structural features that differentiate *E. nhecolandensis* from the other species. The lack of an oocyst residuum, a button-like Stieda body, and compact sporocyst residuum differentiates *E. granifera* from *E. nhecolandensis*. The slight roughness of the wall and a polar granule observed in *E. nhecolandensis* differ from *E. montuosi* due to the oocyst wall composed of two or three layers with large protruding bumps on the surface, and the lack of a polar granule. While *E. nhecolandensis* presents a diffuse sporocyst residuum composed of small granules of different sizes, *E. opimi* differs in the uniformity and number of granules in the oocyst (8–10 uniform granules) and sporocyst residuum (2–3 granules). The same difference regarding the sporocyst residuum was observed in *E. oruroensis*, which presents a sporocyst residuum composed of two to three granules. Six species of *Eimeria* (*E. myopotami* and *E. pellucida* Yakimoff 1933; *E. coypi* Obitz and Wadowski 1937; *E. seideli* Pellerdy, 1957; *E. nutriae*; and *E. myocastor* Prasad 1960) were described from the rodent *Myocastor coypus* (Molina, 1782) (Rodentia: Echimyidae). In spite of some controversy and discussion about *E. myopotami*, *E. pellucida*, and *E. coypi* in subsequent works (Levine and Ivens 1965), none of the six eimerians mentioned are similar to the new species reported in our study, since all of them differ in structural details: absence of an oocyst residuum in all six *Eimeria* spp. recovered from *M. coypus*; presence of micropyle in *E. myocastori* and *E. pellucida*; lack of a polar granule in *E. myocastori*, *E. seideli*, and *E. myopotami*; and lack of a Stieda body in *E. myocastori*, *E. nutriae*, *E. coypi*, and *E. myopotami*. These four morphological characters differ from those of the new species described in this study, besides the size and shape of oocysts of some species, as shown in Table 1.

Eimeria jansenae n. sp.

Sporulated oocysts ($n = 45$) ellipsoidal, L × W 31.4 μm (27.1–37.7) × 22.6 μm (19.6–24.9), shape-index (L/W) 1.4 (1.3–1.6). Oocyst wall composed of at least two layers, 1.9 μm (1.4–2.7) thick, inner layer smooth and outer layer rough. Micropyle absent. Polar granule present, usually spherical, highly refractile. Oocyst residuum composed of spheroidal structures that vary in number, form, and size, L × W ($n = 31$) 8.7 μm (6.7–13.8) × 7.6 μm (5.6–9.9). Sporocysts ($n = 45$) ovoidal, 11.9 μm (9.5–15.6) × 8.3 μm (7.1–10.2), with a shape-index of 1.4. Stieda body present, nipple-shaped. Sub-stieda and parastieda bodies absent. Sporocyst residuum composed of small granules distributed in the sporocysts. Sporozoites not measured.

Taxonomic summary *Type-host: Thrichomys fosteri* (Thomas, 1903) (Rodentia, Echimyidae).

Type-locality: Nhumirim Farm, Nhecolândia Pantanal subregion, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W).

Type-material: Phototypes are deposited and available (http://r1.ufrrj.br/labicoc/colecao.html) in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro, located in Seropédica, Rio de Janeiro, Brazil. Photographs of the type-host specimen (symbiotype) are deposited in the same collection. The repository number is P-72/2017.

Sporulation time: Unknown.

Site of infection: Small intestine.

Prevalence: Found in 20% (8/40) of the animals examined.

Etymology: The specific epithet is derived from the name of the great parasitologist Ana Maria Jansen (1945), researcher of Fundação Oswaldo Cruz, Rio de Janeiro, Brazil.

Remarks: Eimeria jansenae is the largest of the *Eimeria* spp. described in this study. It differs from the other species that parasitize *T. fosteri* in having ellipsoidal oocysts. Among the eimerian oocysts recovered from *C. laticeps*, the morphological characteristics of *E. jansenae* are similar to *E. corumbaensis*. The oocyst wall is somewhat rougher in *E. jansenae* than in *E. corumbaensis*. In addition, *E. jansenae* is larger than *E. corumbaensis*. In comparison to *E. proechimyi* described in *P. guyanensis*, *E. jansenae* is larger (31.4 × 22.6 μm) than *E. caripensis* (20.0 μm) and *E. proechimyi* (22.9 × 17.1 μm). Morphologically, it differs in having an oocyst residuum, ellipsoidal sporocysts (as opposed to spherical sporocysts), and a Stieda body. The ellipsoidal oocyst and the oocyst residuum in *E. jansenae* differs from the spherical oocyst and lack of oocyst residuum in *E. caripensis.* Oocysts of *E. jansenae* are also larger than the other four species of *Eimeria* recovered from *Ctenomys opimus* Wagner, 1848 (Rodentia: Ctenomyidae) (Lambert et al. 1988), as shown in Table 1. Morphologically, *E. jansenae* differs in having ellipsoidal oocysts, while in *E. montuosi* they are spheroidal, in *E. granifera* oocysts are sub-spheroidal to ellipsoidal, and in *E. opimi* and *E. oruroensis* oocysts are spheroidal to sub-spheroidal. In addition to morphometry and shape, other morphological characteristics differentiate *E. jansenae* from *Eimeria* spp. recovered from *C. opimus*. While *E. jansenae* presents a variable oocyst residuum, a nipple-like Stieda body, and sporocyst residuum composed by small granules, *E. granifera* lacks an oocyst residuum, a button-like Stieda body, and compact sporocyst residuum. When comparing to *E. montuosi*, an oocyst wall with large protruding bumps on the surface and the lack of polar granules differentiate this species from *E. jansenae*.

While *E. jansenae* presents a variable oocyst residuum with one or more spheroidal structures that vary in size, number, and shape, *E. opimi* presents a compact oocyst residuum with 8–10 uniform granules. The species of *Eimeria* recorded from *M. coypus* differ from *E. jansenae* in the same structural details of oocysts as *E. nhecolandensis*, as pointed out in our previous remarks.

Eimeria fosteri n. sp.

Sporulated oocysts (n = 41) ovoidal, L × W 25.1 μm (20.9–37.3) × 20.1 μm (16.7–30.1), shape-index (L/W) 1.2 (1.2–1.3). Oocyst wall strongly rough, bi-layered, 1.8 μm (1.0–3.4) in total thickness. Micropyle absent. Polar granule present, varying from sub-spherical to elongate in shape. Oocyst residuum composed of spheroidal structures that vary from a single large sphere to two to eight spheroidal structures of different sizes, L × W (n = 24) 6.8 μm (4.9–8.3) × 5.9 μm (4.0–7.1). Sporocysts (n = 41) ovoidal, 10.0 μm (7.6–16.0) × 7.2 μm (5.1–11.1), with a shape-index of 1.4 (1.2–1.7). Stieda body present, nipple-shaped. Sub-stieda and parastieda bodies absent. Sporocyst residuum composed of small granules distributed along the sporozoites, sometimes forming a line. Sporozoites not measured.

Taxonomic summary *Type-host: Thrichomys fosteri* (Thomas, 1903) (Rodentia, Echimyidae).

Type-locality: Nhumirim Farm, Nhecolândia Pantanal subregion, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W).

Type-material: Phototypes are deposited and available (http://r1.ufrrj.br/labicoc/colecao.html) in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro, located in Seropédica, Rio de Janeiro, Brazil. Photographs of the type-host specimen (symbiotype) are deposited in the same collection. The repository number is P-73/2017.

Sporulation time: Unknown.

Site of infection: Small intestine.

Prevalence: Found in 10% (4/40) of the animals examined.

Etymology: The specific epithet is derived from the specific name of the host.

Remarks: Eimeria fosteri differs from the other species found in *T. fosteri* and *C. laticeps* in having a strongly rough oocyst wall with deep grooves. In addition, the ranges of the oocyst length and width and of the wall thickness were higher than in other species (Table 1). The only two species previously described in echimyid rodents (*E. proechimyi* and *E. caripensis*) (Arcay-de-Peraza 1964) differ from *E. fosteri*. When compared to *E. fosteri*, *E. proechimyi* differs in having an ellipsoidal oocyst shape (as opposed to ovoidal), in lacking an oocyst residuum, in having spherical sporocysts (as opposed to ellipsoidal), and in lacking a Stieda body. *Eimeria caripensis* differs from *E. fosteri* in having spherical oocysts and in lacking an oocyst residuum. Unlike the *Eimeria* spp. recovered from *C. opimus*, *E. fosteri* has ovoidal oocysts. Differences between *E. fosteri* and *E. granifera*: ovoidal vs. spheroidal/ellipsoidal oocysts, strongly rough oocyst walls vs. smooth, presence of oocyst residuum and polar granule vs. lack of both structures, and nipple-like vs. button-like Stieda body. Differences between *E. fosteri* and *E. montuosi*: ovoidal oocysts vs. spheroidal, strongly rough oocyst wall vs. large protruding bumps on the surface, and polar granule sub-spherical to elongate vs. lack of a polar granule. Differences between *E. fosteri* and *E. opimi*: oocysts ovoidal vs. spheroidal to sub-spheroidal, strongly rough walls vs. finely sculptured walls. Differences between *E. fosteri* and *E. oruroensis*: oocysts ovoidal vs. spheroidal to sub-spheroidal. The species of *Eimeria* recorded from *M. coypus* differ from the *E. fosteri* in the same structural details of oocysts as *E. nhecolandensis*, as pointed out in our previous remarks.

Eimeria corumbaensis n. sp.

Sporulated oocysts ellipsoidal, L × W (n = 49) 28.9 μm (20.7–33.4) × 20.2 μm (15.0–22.8), shape-index (L/W) 1.4 (1.1–1.7). Oocyst wall 1.67 μm (1.1–2.2) thick, bi-layered, slightly rough. Micropyle absent. Polar granule present, ranging from sub-spherical to ovoidal. Oocyst residuum composed in most cases of a large sphere, but sometimes 1–10 small spheres, L × W (n = 8) 5.3 μm (4.4–6.5) × 4.8 μm (2.8–6.5). Sporocysts (n = 49) ovoidal to ellipsoidal, 11.3 μm (9.0–12.9) × 8.4 μm (7.2–9.4), with a shape-index of 1.3. Stieda body present, nipple-shaped. Sub-stieda and parastieda bodies absent. Sporocyst residuum composed of small granules sometimes forming a line along the sporocyst wall. Sporozoites not measured (Fig. 2).

Taxonomic summary *Type-host:* Broad-headed spiny rat *Clyomys laticeps* (Thomas, 1909) (Rodentia, Echimyidae).

Type-locality: Nhumirim Farm, Nhecolândia Pantanal subregion, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W).

Type-material: Phototypes are deposited and available (http://r1.ufrrj.br/labicoc/colecao.html) in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro, located in Seropédica, Rio de Janeiro, Brazil. Photographs of the type-host specimen (symbiotype) are deposited in the same collection. The repository number is P-74/2017.

Sporulation time: Unknown.

Site of infection: Small intestine.

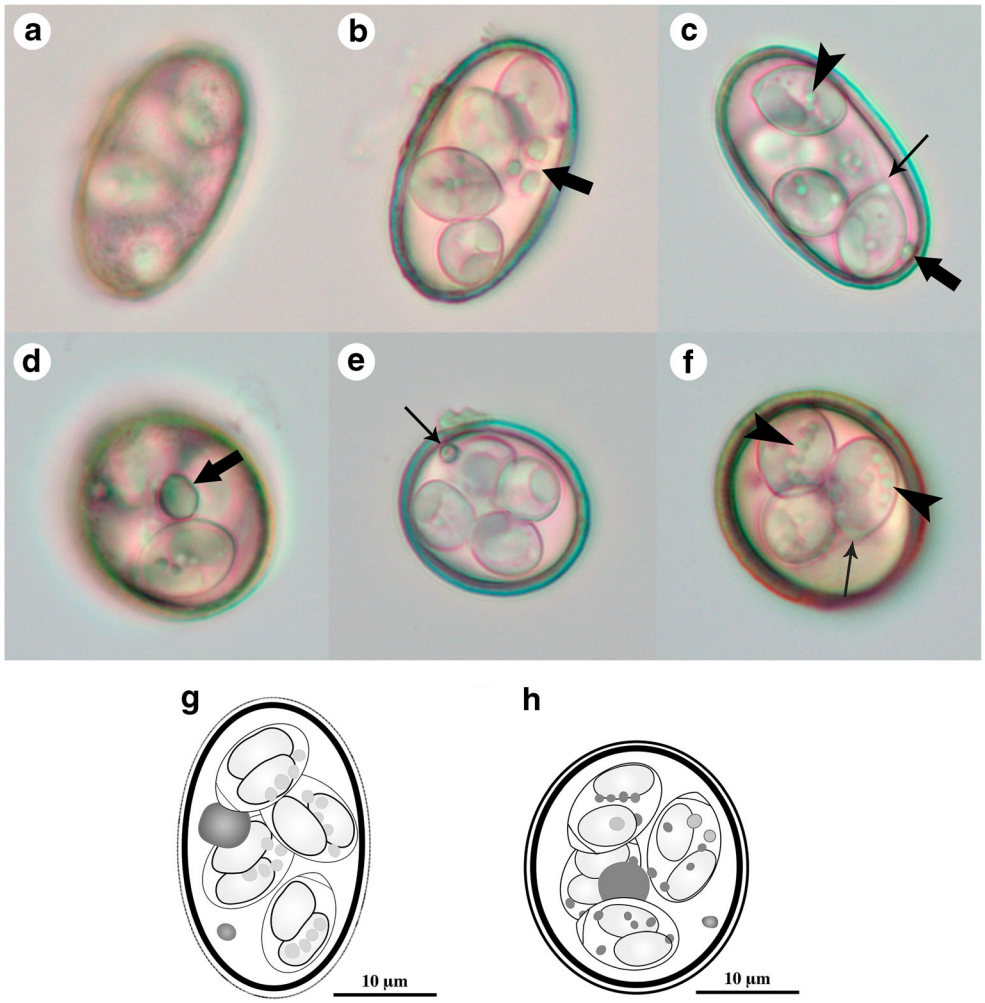

Fig. 2 Photomicrographs and line drawing of *Eimeria corumbaensis* (**a**–**c**, **g**) and *Eimeria laticeps* (**d**–**f**, **h**) recovered from *Clyomys laticeps* in Brazilian Pantanal. **a** Note the slightly rough wall with a discrete granulation. **b** Oocyst residuum composed by three spheroidal structures (arrow). **c** Note the by layered oocyst wall. Nipple-like Stieda body (thin arrow), spheroidal polar granule (arrow), and sporocyst residuum composed by small granules diffusely distributed (arrowhead). **d**, **e** Note the smooth oocyst wall without granulation, the oocyst residuum composed by a single spheroidal structure (arrow), and the spheroidal polar granule (thin arrow). **f** Sporocyst residuum composed by small granules forming a line along the sporozoites (head arrow). Obj. 63×. **g** Line drawing of a sporulated oocyst of *E. corumbaensis*. **h** Line drawing of a sporulated oocyst of *E. laticeps*

Prevalence: Found in 1/40 (2.5%) of the animals examined.

Etymology: The specific epithet is derived from the name of the municipality where the study area is located.

Remarks: Eimeria corumbaensis differs from the other *Eimeria* spp. described in this study mainly regarding the shape of oocysts, except *E. jansenae* which is also ellipsoidal. Nevertheless, *E. corumbaensis* is smaller than *E. jansenae*, and has a slightly rough oocyst wall, while *E. jansenae* has a rough oocyst wall. Among the species described for the superfamily Octodontoidea, the one that most resembles *E. corumbaensis* is *E. proechimyi* recovered from *P. guyanensis* due to its ellipsoidal shape. Moreover, *E. corumbaensis* is larger than *E. proechimyi* (28.9 × 20.2 vs. 22.9 × 17.1, respectively). Yet, sporulated oocysts of *E. proechimyi* differ from those of *E. corumbaensis* by having spherical sporocysts without Stieda body and oocyst residuum. Sporulated oocysts of *E. caripensis* differ from those of *E. corumbaensis* in shape (spherical vs. ellipsoidal), lack of oocyst residuum, and size (20.0 vs. 28.9 × 20.2). All the species of *Eimeria* found in *Ctenomys* spp. are different in shape, besides the lack of oocyst residuum and shape of Stieda body (button-like Stieda body) in *E. granifera*. In addition, the oocyst wall of *E. corumbaensis* is slightly rough, while in *E. granifera* the wall is smooth. In *E. montuosi*, the oocyst wall has large protruding bumps on the surface, and lacking polar granule, whereas in *E. oruroensis* the oocyst wall is rough. The species of *Eimeria* recorded from *M. coypus* differ from the *E. corumbaensis* in the same structural details of oocysts of *E. nhecolandensis*, as previously pointed out.

Eimeria laticeps n. sp.

Sporulated oocysts spherical to sub-spherical, L × W (n = 52) 23.9 μm (19.2–27.3) × 21.6 μm (17.1–26.7), shape-index (L/W) 1.1 (0.9–1.2). Oocyst wall 1.7 μm (1.1–2.2) thick, bi-layered and smooth. Micropyle absent. Polar granule present, spherical to sub-spherical, located close to the wall. Oocyst residuum compact, in most cases composed of a large sphere, L × W (n = 6) 5.1 μm (4.4–6.0) × 4.2 μm (3.9–4.4). Sporocysts (n = 52) ovoidal to ellipsoidal, 10.7 μm (8.7–12.3) × 8.1 μm (6.4–9.2), with a shape-index of 1.3. Stieda body present, nipple-shaped. Sub-stieda and parastieda bodies absent. Sporocyst residuum composed of small granules. Sporozoites ovoidal but not measured.

Taxonomic summary *Type-host:* Broad-headed spiny rat *Clyomys laticeps* (Thomas, 1909) (Rodentia, Echimyidae).

Type-locality: Nhumirim farm, Nhecolândia Pantanal sub-region, municipality of Corumbá, State of Mato Grosso do Sul, Brazil (19° 08′ 28″ S, 56° 49′ 23″ W).

Type-material: Phototypes are deposited and available (http://r1.ufrrj.br/labicoc/colecao.html) in the Parasitology Collection of the Laboratório de Biologia de Coccídios at Universidade Federal Rural do Rio de Janeiro, located in Seropédica, Rio de Janeiro, Brazil. Photographs of the type-host specimen (symbiotype) are deposited in the same collection. The repository number is P-75/2017.

Sporulation time: Unknown.

Site of infection: Small intestine.

Prevalence: Found in 5% (2/40) of the animals examined.

Etymology: The specific epithet is derived from the specific name of the host species.

Remarks: Eimeria laticeps is the only *Eimeria* species that possessed spherical oocysts and smooth walls in this study. The morphological characteristics of *E. proechimys*, with its ovoidal oocysts, absence of oocyst residuum, and spherical sporocysts, differ from *E. laticeps*. The lack of an oocyst residuum and Stieda body differentiate *E. caripensis* from *E. laticeps*. The lack of an oocyst residuum and a polar granule and the button-like Stieda body of *E. granifera* differentiate it from *E. laticeps*. The oocyst wall composed of large protruding bumps on the surface and the absence of a polar granule of *E. montuosi* differentiate this species from *E. laticeps*. Regarding *E. oruroensis*, the rough wall composed of three layers and the size of the oocysts (27.3 × 23.6 vs. 23.9 × 21.7) differentiate this species from *E. laticeps*. The species that is closest morphologically and morphometrically to *E. laticeps* is *E. opimi*, but the more pronounced roughness of the wall of *E. opimi* and the oocyst residuum composed by a compact mass of 8–10 uniform granules differentiate this species from *E. laticeps*. The species of *Eimeria* recorded from *M. coypus* differ from the *E. laticeps* in the same structural details of oocysts as *E. nhecolandensis*, as detailed above.

Epidemiological data

Eimerian oocysts were found in 40% of sampled rodents (n = 40): 14 *T. fosteri* and two *C. laticeps*. In *T. fosteri*, the prevalence found in males was 45% (13/29), and in females we recorded a prevalence of 13% (1/8). It was not possible to identify the sex of one specimen of *T. fosteri.* Five new *Eimeria* spp. were described in our study. We found three species parasitizing *T. fosteri* (*E. nhecolandensis*, *E. jansenae*, and *E. fosteri*) and three species parasitizing *C. laticeps* (*E. nhecolandensis*, *E. corumbaensis*, and *E. laticeps*). *Eimeria nhecolandensis* was the most prevalent species in *T. fosteri* (12/38, 32%), followed by *E. jansenae* (8/38, 21%) and *E. fosteri* (4/38, 11%). In *C. laticeps*, *E. nhecolandensis* and *E. laticeps* were observed in both individuals and *E. corumbaensis* was found in only one.

We found a single infection by *E. nhecolandensis* and *E. fosteri* in five individuals and one individual of *T. fosteri*, respectively. Furthermore, we recorded co-infections in *T. fosteri* by *E. nhecolandensis* and *E. jansenae* (n = 5), *E. jansenae* and *E. fosteri* (n = 1), and *E. nhecolandensis* + *E. jansenae* + *E. fosteri* (n = 2). In *C. laticeps*, we found co-infection by *E. nhecolandensis* and *E. laticeps* in one individual, and by *E. nhecolandensis* + *E. corumbaensis* + *E. laticeps* in another single individual.

Histopathological analysis

Endogenous stages (meront, immature gametocyte, macrogamont, microgametocyte, and oocyst) were observed in the small intestines of 69% (11/16) of the coprologically positive animals. Two *T. fosteri* (8.3%) that were negative for the coprological test presented endogenous stages in the tissue sections (meront and immature gametocyte). All monoinfections were observed only in *T. fosteri*, and among them endogenous stages (n = 13) were detected in only one specimen. Conversely, in all co-infected animals we recorded developmental forms ranging from 1 to 596. Moreover, in the two *C. laticeps* specimens, we observed endogenous stages.

Host: Thrichomys fosteri

Single infections Just one individual from among the five that were eliminating oocysts of *E. nhecolandensis* possessed endogenous stages (n = 13) of coccidians in the enterocyte villi of the small intestine, including macrogamonts and immature gametocytes. In general, in the lamina propria of the small intestine of this animal, a mild to intense inflammatory reaction was also observed, multifocal to diffuse, composed predominantly of macrophages, a few eosinophils, lymphocytes, plasmocytes, and basophils. The most prominent lesions

were hyperplasia of the epithelium, incipient necrosis of the apical portion, and merger of the villi.

Endogenous stages of coccidia were not observed in the individual that was eliminating oocysts of *E. fosteri*. However, we observed an intense and diffuse inflammatory reaction composed of macrophages, lymphocytes, and a few basophils and eosinophils in the lamina propria of the villi of the small intestine. In addition, we observed an atrophy of the villi.

Co-infections Endogenous stages (n = 84) were observed in tissue sections of the individual that was eliminating oocysts of *E. jansenae* and *E. fosteri* in the feces. Developmental stages were observed in the epithelium of the villi, and one single oocyst was observed in the external muscle layer (Fig. 3a). A moderate to intense mixed inflammatory reaction, mainly composed of macrophages, lymphocytes, plasmocytes, and eosinophils, diffusely distributed, was seen in the lamina propria. Hyperplasia of the mucosal epithelium (Fig. 3b) and atrophy of the villi were also observed.

In the individuals parasitized by *E. nhecolandensis* and *E. jansenae*, all the endogenous coccidian stages were observed (ranging from 1 to 109). The inflammatory reaction in the lamina propria was mild to intense (Fig. 3c), multifocal to diffuse, and composed of macrophages, fewer lymphocytes, eosinophils, and some interspersed plasmocytes. The most prominent morphological changes in the villi were epithelial hyperplasia, atrophy, incipient necrosis of the apical region, merger (Fig. 3d), and destruction.

We found a very large number of endogenous developing coccidian stages in the small intestines of the two individuals that were eliminating concomitantly the oocysts of *E. nhecolandensis*, *E. jansenae*, and *E. fosteri* in the feces. In the individual with 131 developmental forms, we only observed meronts containing merozoites and immature gametocytes in the villi enterocytes. In the lamina propria, a multifocal, mild to intense inflammatory infiltrate consisting of macrophages, lymphocytes, and eosinophils was evident. In the other animal, we found that 596 developmental forms, including immature gametocytes, different stages of microgamonts and macrogamonts, and oocysts (Fig. 3e), had invaded most of the epithelial cells of the villi, displacing the nucleus peripherally, and they were also present in the lamina propria (Fig. 3f) and in the lumen. In this animal, the inflammatory reaction was intense and diffuse, composed predominantly of macrophages, lymphocytes, and some plasmocytes, located in the lamina propria (Fig. 3g).

An enlargement of some villi by inflammatory cell accumulation as well as architecture loss due to the destruction of the epithelium of the villi and the presence of numerous inflammatory cells were also observed (Fig. 3h). In addition, we observed fibrosis foci and the absence of some villi.

Host: Clyomys laticeps

All endogenous coccidian stages at different phases of development (n = 124) were observed in the villi and the crypts of Lieberkühn enterocytes as well as in the lumen of the small intestine of the individual that showed *E. nhecolandensis* and *E. laticeps* oocysts in the feces. Another *C. laticeps* that was found co-infected by three eimerian species presented 58 developmental forms including meronts containing merozoites, immature gametocytes, and macrogamonts and microgamonts in the epithelium of the villi.

Overall, the animals presented a mild to moderate multifocal inflammatory reaction in the lamina propria (Fig. 4a), composed of mononuclear cells (lymphocytes, macrophages, and a few plasmocytes). The morphological changes observed in both individuals were denudation, hyperplasia, and merger of the villi (Fig. 4b). In addition, atrophy and epithelial destruction were observed in the animal parasitized by two eimerian species, and incipient necrosis of the apical region of the villi was found in the other.

Discussion

Our study has documented five new eimerian species infecting echimyid rodents in their natural environment. Furthermore, our histopathological analysis showed that these eimerians can threaten the health of the parasitized animals. Although *Eimeria* spp. have a high specificity (Kogut 1990), Duszynski and Wilber (1997) indicated that the identification of coccidia species should be performed using all species found in the host family. Nevertheless, to date, only a single study was conducted in South America describing species of *Eimeria* (*E. proechimyi* and *E. caripensis*) infecting the cayenne spiny rat (Echimyidae) *P. guyanensis* in Venezuela (Arcay-de-Peraza 1964). Other studies carried out in Europe described six species of *Eimeria* infecting the rodent *M. coypus*: *E. myopotami*, *E. pellucida*, *E. coypi*, *E. seideli*, *E. nutriae*, and *E. myocastori*. However, only three of these have an informative description (Table 1).

The comparison of eimerian oocysts observed in our study with oocysts of *E. proechimyi* and *E. caripensis* found in Venezuela was difficult because only mean oocyst and sporocyst width and length measurements were reported. In addition, it was quite impossible to visualize the morphological characteristics described for these species due to the absence of detailed images.

Due to the scarcity of knowledge on coccidia in echimyid rodents, and in order to increase the number of comparisons, we also compared our findings with those reported from other members of the Octodontoidea superfamily, due to their phylogenetic proximity to the family Echimyidae. Octodontoidea is composed by the families Abrocomyidae (including

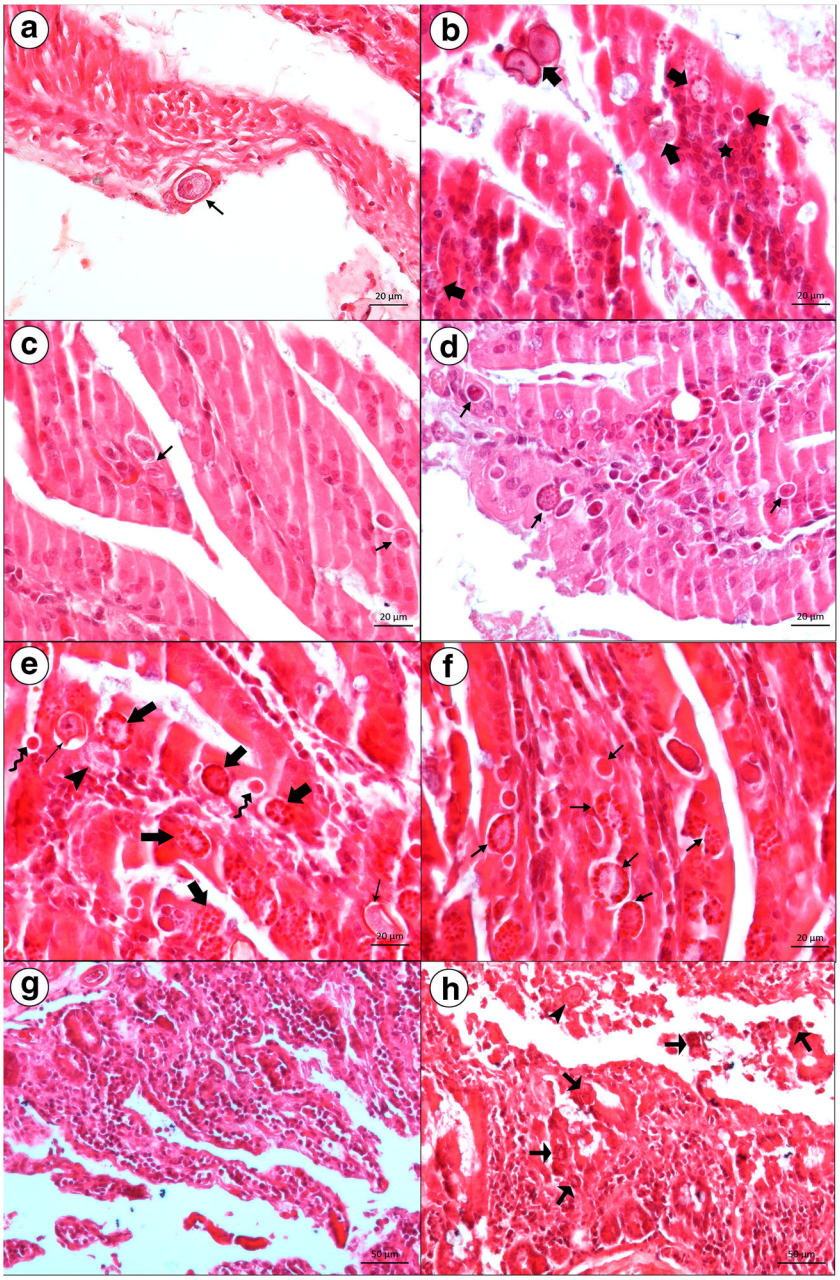

Fig. 3 Photomicrographs of small intestine of *Thrichomys fosteri* from Brazilian Pantanal naturally co-infected by two (**a**–**d**) and three (**e**–**h**) *Eimeria* spp. **a** Oocyst in the muscular external layer (arrow). **b** Hyperplasia of the epithelium of the villi (star) and endogenous stages (oocyst, macrogamont, and immature gametocyte) in the epithelium and lumen (arrows). **c** Villi with endogenous stages (arrows) without lymphocytic infiltration. **d** Merging of the villi; note the fused villi, endogenous stages (arrows) and inflammatory reaction. **e** Macrogamonts in different stages of development with eosinophilic wall-forming bodies (large arrow), microgamont containing many microgametes (arrowhead), immature gametocytes (curve arrow), and oocysts (thin arrow). Note the inflammatory reaction in the lamina propria. (H&E, ×40). **f** Endogenous stages developing in the epithelium of the villus and in the lamina propria (arrows). (H&E, ×20). **g** Intense inflammatory reaction diffusely distributed. (H&E, ×10). **h** Destruction of the villi and an intense mononuclear inflammatory reaction. Various macrogamonts (arrows) of *Eimeria* spp. and an oocyst (arrowhead) can be seen in the inflammatory reaction and in the lumen. (H&E, ×20)

Cuscomys), Ctenomyidae, Octodontidae, Capromyidae, and Echimyidae (including *Myocastor*) (Upham and Patterson 2015). Despite the great diversity of this superfamily, only two studies have been reported describing infection by *Eimeria* spp. in Ctenomyidae rodents (Lambert et al. 1988; Gardner and Duszynski 1990), in addition to the studies on echimyid rodents (Yakimoff 1933; Obitz and Wadowski 1937; Seidel 1954; Prasad 1960; Arcay-de-Peraza 1964). Among the four species of *Eimeria* from *Ctenomys* spp., *E. opimi* most closely resembled *E. laticeps* as described in

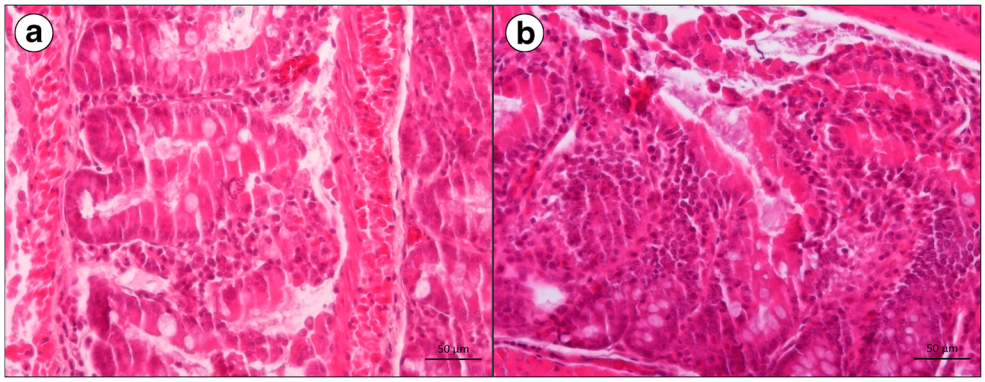

Fig. 4 Photomicrographs of small intestine of *Clyomys laticeps* from the Brazilian Pantanal naturally co-infected by *Eimeria* spp. **a** Note the mononuclear inflammatory reaction in the lamina propria associated with endogenous stages (arrows). **b** Inflammatory reaction and epithelial hyperplasia. (H&E, ×10)

our study, but with differences in the oocyst wall and oocyst residuum.

Since the late 1960s, phenotypic characters and host specificity data have been the main parameters for the description of eimeriid coccidia (Duszynski and Wilber 1997; Tenter et al. 2002). However, the development of molecular techniques has contributed to the more precise taxonomic classification (Hafeez et al. 2015; Tan et al. 2017). Moreover, studies have demonstrated variation in the size of *Eimeria* oocysts across their host range (Duszynski 1971; Parker and Duszynski 1986; Gardner and Duszynski 1990; Flausino et al. 2014). In fact, polymorphism among oocysts has already been reported in different species (e.g., Gardner and Duszynski 1990; Berto et al. 2008; Flausino et al. 2014). This characteristic was also observed in the present study. We detected no polymorphism in only one new species of coccidian, *E. fosteri*. Our analysis showed polymorphism in oocysts of *E. nhecolandensis*, *E. jansenae*, *E. corumbaensis*, and *E. laticeps*. Polymorphism has been associated with the physiological conditions of the hosts, as well as with environment conditions (Duszynski 1971; Catchpole et al. 1975; Fayer 1980; Joyner 1982; Parker and Duszynski 1986; Gardner and Duszynski 1990).

In nature, some free-living individuals may accidentally ingest oocysts from other true natural hosts, and these individuals may thereby develop a simple pseudoparasitism, which is rarely reported in the scientific literature. To avoid these mistakes, it is advisable to include in the description of the parasites at least the endogenous stages and their location in the hosts (Levine 1988; Tenter et al. 2002; Yang et al. 2013). In our study, endogenous developmental stages were seen in most of the histological samples of animals that were positive in the coprological analysis, which led us to infer that the rodents in our study are natural hosts for the *Eimeria* species described here.

Endogenous development occurred in most cases in the epithelium of the villi of the small intestine, which is in agreement with the findings of Arcay-de-Peraza (1964) on eimerians found in echimyid rodents. However, we also found an immature gametocyte developing in the crypts of Lieberkühn, stages of gametogony in the lamina propria, and an oocyst in the muscularis externa layer of the small intestine. The development of endogenous stages of *Eimeria* spp. has been reported in different animal species as occurring within epithelial cells at the site of entry. Other studies have described eimerian coccidians developing in both epithelial and non-epithelial cells across the small intestine; for example, endogenous stages found in the lamina propria, crypts of Lieberkühn, and endothelium of the lacteal cells (Stockdale 1976; Hammond 1982; Dubey et al. 2008).

Some samples that were positive at coprological analysis did not display developmental endogenous stages in any of the histological sections evaluated. In these cases, development may have been occurring in a segment of intestine that had not been prepared for histology, given the length of the enteric tract. In addition, inflammatory responses, necrosis, and destruction of the epithelium of the villi were observed in some animals that did not show endogenous stages. In those cases, we can hypothesize that development has occurred and just the lesions consequent to the parasitism remained. Also, four animals coprologically negative had endogenous stages of a coccidian (meronts and immature gametocytes) in the tissue, which we could not identify to genus. This finding demonstrates that parasitism should not be defined only by the presence or absence of oocysts in the feces, since an infection could be in its initial stage and the development cycle would have not been completed.

The parasite load in the small intestine was more intense in co-infected animals. *Thrichomys fosteri* co-infected by three *Eimeria* spp. (*E. nhecolandensis*, *E. jansenae*, and *E. fosteri*) presented the highest number of endogenous stages and large areas of tissue damage. By contrast, *C. laticeps* infected by two morphotypes (*E. nhecolandensis* and *E. laticeps*) had more endogenous stages than those infected by three morphotypes (*E. nhecolandensis*, *E. corumbaensis*, and *E. laticeps*), although the tissue damage was similar in both

individuals. A single species may be the major pathogenic agent, but associations with others may contribute to tissue damage, high numbers of oocysts eliminated in feces, and disease development. Oocyst production may be increased when co-infections occur or may remain at the same level as in a single infection. The occurrence of associated infections and the intensity of the lesions are dependent on the parasite species involved and their pathogenicity as well as on factors inherent to the host (Duszynski 1972; Marquardt 1976; Joyner and Norton 1983; Gregory 1990; Répérant et al. 2012; Naciri et al. 2014). Nevertheless, species interactions are important in the pathogenesis and epidemiology of coccidia infections and should be studied in more detail since little is known about the pathogeny of co-infections.

Tissue damage was variable in the different combinations of infections. The lesions observed are in agreement with those described from coccidia infections in other animal groups (Friend and Stockdale 1980; Gregory and Catchpole 1990; Kheirandish et al. 2014), but it is not possible to affirm that particular morphological changes were associated with one or another species of *Eimeria* since most individuals were parasitized by more than one species. The mechanism of the pathologic effect of the coccidia is not entirely clear; besides the damage caused by the parasites themselves, a severe host reaction may be more harmful (Gregory 1990). In fact, the vascular and cellular responses of inflammation are mediated by chemical factors that act singly, in combination, or in sequence, and then amplify the inflammatory response, leading in turn to villi epithelium destruction and hyperplasia (Jubb and Kennedy 1970; Gregory 1990), changes that were demonstrated in our study. In addition, in the case of natural infection, aspects of pathogenesis such as lesion extent and inflammatory pattern cannot be attributed exclusively to parasitism by eimerians, since associations with other parasites may also be occurring. The effects of parasitism by different enteric coccidian species on host health may be unpredictable and may depend on individual characteristics such as age, sex, and/or reproductive status, as well as on co-infections and environmental conditions (Gregory 1990; Ruff and Allen 1990; Gibson et al. 2011).

Conclusion

This is the first report of infection by *Eimeria* spp. in the rodents *T. fosteri* and *C. laticeps*. We identified five new eimerian species and described the morphological, morphometrical, and pathological aspects of simple and concomitant infections. Our results showed that the echimyid rodents *T. fosteri* and *C. laticeps* from the Brazilian Pantanal play an important role in the maintenance of enteric coccidian parasites. Furthermore, this parasitism may result in important tissue lesions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All applicable international, national, and institutional guidelines for the care and use of animals were followed.

All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

This article does not contain any studies with human participants performed by any of the authors.

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