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Martín Horacio Fugassa

*Consejo Nacional de Investigaciones Científicas y Técnicas, mfugassa@mdp.edu.ar*

N. H. Sardella

*Universidad Nacional de Mar del Plata*

V. Taglioretti

*Universidad Nacional de Mar del Plata,*

Karl J. Reinhard

*University of Nebraska-Lincoln, kreinhard1@mac.com*

Adauto Araujo

*Fundação Oswaldo Cruz, adauto@ensp.fiocruz.br*

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## Eimeriid Oocysts From Archaeological Samples in Patagonia, Argentina

M. H. Fugassa, N. H. Sardella, V. Taglioretti\*, K. J. Reinhard†, and A. Araújo‡, CONICET – Laboratorio de Zoonosis Parasitarias, Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata. Funes 3350, Mar del Plata, Argentina, CP 7600; \*Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, Calle Funes 3350, Mar del Plata, Argentina, CP: 7600; †School of Natural Resources, University of Nebraska–Lincoln, 719 Hardin Hall, Lincoln, Nebraska 68583-0987; ‡Laboratorio de Paleoparasitología, Departamento de Endemias Samuel Pessoa, Escola Nacional de Saúde Pública, Fundação Oswaldo Cruz. Rua Leopoldo Bulhões 1480, Manguinhos 21041-210, Rio de Janeiro, RJ – Brazil. e-mail: mfugassa@mdp.edu.ar

**ABSTRACT:** Oocysts attributable to *Eimeria macusaniensis* Guerrero et al. 1971, were found in coprolites and in archaeological sediments dating to the Holocene of Patagonia, Argentina. By means of a nonparametric regression using a generalized additive model, a significant relationship was found between the size of the oocysts and their antiquity. Specifically, a reduction in oocyst size over time was discovered, probably due to a parasite response to host replacement, to an extinct eimeriid species common during the Pliocene–Holocene transition, or to environmental changes known for the Holocene. Explanations regarding coevolution between parasites, hosts, and paleoenvironmental conditions are discussed herein.

Paleoparasitological studies focus on parasite remains such as cysts, eggs, and larvae in organic deposits derived from archaeological or paleontological contexts (Bouchet et al., 2003). Interpretations of this evidence are based on knowledge of cultural, ecological, and biogeographical aspects of the human populations and their accompanying fauna (Reinhard, 1990, 1992). In meridional Patagonia, there is evidence of human occupation extending to at least 11,000 yr ago (Miotti and Saleme, 2004). Archaeological reconstruction indicates that camelids were a main resource for Patagonian hunter–gatherer populations. Several extinct camelid species, i.e., *Lama gracilis* and *Paleolama* sp., have been identified in fossil faunal remains at the Pleistocene transition (Borrero, 2001). Later, and up to the present, only *L. guanicoe* is reported in the zooarchaeological literature. At present, *Eimeria macusaniensis* Guerrero et al., 1971 (Protozoa, Coccidia) and *E. ivitaensis* Leguía and Casas 1998 are the coccidians with the largest oocyst size parasitizing South American camelids. In the Peruvian Andes, Leguía (1999) found *E. macusaniensis* in feces of *L. alpaca*, *L. guanicoe*, and *Vicugna vicugna*. In Patagonia, Beldomenico et al. (2003) reported only *E. macusaniensis* in *L. guanicoe* feces from Chubut, Argentina (Patagonia).

Host specificity of these coccidians is a useful indicator for the presence of camelids in archaeological deposits and coprolites (Fugassa and Barberena, 2006; Fugassa, 2007; Fugassa et al., 2007). Recently, a large, morphometric variability was observed in oocyst sizes in *E. macusaniensis* examined from different time periods in Patagonia. The aim of the present study was to determine if a temporal trend could be established for *E. macusaniensis* oocyst dimensions recovered from coprolites and archaeological sediments of the region.

Sixty-two oocysts, each with a thick wall, brown-reddish coloration, and prominent micropyle, and all compatible with *E. macusaniensis* (Fig. 1), were measured in length and width using a microscope equipped with an ocular micrometer. Oocysts were recovered from coprolites in the archaeological sites of Cerro Casa de Piedra 5 and 7 (CCP5 and CCP7), located in Perito Moreno National Park, Santa Cruz Province, Argentina, in strata dated from 10,000 yr BP (before present). Oocysts found in noncoprolite sediments of the archaeological sites Nombre de Jesús (500 yr BP) and Orejas de Burro I (3,500 yr BP), situated in the province of Santa Cruz, Argentina, and La Arcillosa II located in Tierra del Fuego, Argentina (4,000 yr BP), were also examined. Eimeriid oocyst measurements, arranged by date–time period and mean length and width, are presented in Table I. Because of the difference in sources, i.e., coprolites versus sediments, it could be argued that the oldest cysts might be larger because of better preservation conditions. However, alterations in oocyst structure between coprolites and sediments were not observed. Therefore, the preservation conditions of the coprolites versus sediments did not alter the morphology of the oocysts. For this analysis, the oocysts from coprolites and sediments were comparable.

For the statistical analysis, a nonparametric regression based on a generalized additive model (Hastie and Tibshirani, 1990) was used for

length and width. The smooth function was computed using cubic splines, and the link with the variable response was calculated by the identity function.

Results obtained suggest that both of the nonparametric regressions (for length and width) have fit well. The  $R^2$  was 0.83 for length and 0.81 for width, and the incorporation of the independent variable to both additive models was highly significant ( $P < 0.001$ ). The plots show the final fitted cubic spline function for length (Fig. 2a) and width (Fig. 2b), along with the observed predictor values, plotted against the partial residuals (this figure permitted an evaluation of the nature of the relationship between the respective predictor [age] and the response variables length [Fig. 2a] and width [Fig. 2b] in the final model). In both plots, there was a general decay tendency in each dependent variable with respect to oocyst age. This tendency was greater between 10,000–8,000 yr BP, decreasing until 3,000 yr BP for length and increasing to 5,000 yr BP for width.

The oocysts from coprolites and sediments measured in the present study were attributable to *E. macusaniensis*, according to descriptions provided by Leguía (1999) in Perú and by Beldomenico et al. (2003) and C. Beldomenico (pers. comm.) in Patagonia. *Eimeria macusaniensis* has been reported from different species of *Lama* (Jarvinen, 1999). Le-



FIGURE 1. Eimeriid oocyst from archaeological site CCP7, Perito Moreno National Park, Santa Cruz Province, Argentina. Bar = 40  $\mu$ m.

TABLE I. Age and measurement of eimeriid oocysts examined in the present study.

Age (years before present)		Width ( $\mu\text{m}$ )			Length ( $\mu\text{m}$ )			N
Calibrated	Noncalibrated	Mean	SD	Range	Mean	SD	Range	
507	515*	45.0	—	—	75.0	—	—	1
3,775	3,490†	61.0	2.4	57.5–63.75	87.0	5.42	82.5–95.0	5
3,978	3,565‡	50.0	3.53	47.5–52.5	77.5	3.53	75.0–80.0	2
6,007	5,205‡	65.0	—	—	90.0	—	—	1
7,434	6,540§	67.39	6.42	60.0–80.0	89.76	8.25	81.25–112.5	14
8,742	7,880	80.0	—	—	116.25	—	—	1
8,988	8,110	68.26	4.35	62.5–80.0	93.3	4.92	85.0–107	18
9,990	8,920	95.0	—	—	117.5	—	—	1
10,635	9,370	97.51	4.9	87.5–108.75	121.32	4.76	110.0–127.5	18
11,032	9,730	73.75	—	—	138.75	—	—	1
Modern sample (C. Beldomenico, pers. comm.)#		67.0	2.7	53.3–70.5	85.1	7.2	71.0–94.0	—
Modern sample (Leguía 1999)¶		67.4	—	61.0–80.0	93.6	—	81–107	—

\* Archaeological sites Nombre de Jesús, Santa Cruz Province.

† Orejas de Burro I, Santa Cruz Province.

‡ La Arcillosa II, Tierra del Fuego Province.

§ CCP5.

|| CCP7.

# Santa Cruz Province. Modern samples from Patagonia.

¶ Perú.

guía (1999) cited the presence of *E. macusaniensis* oocysts ( $93.6 \times 67.4 \mu\text{m}$ ) in Peruvian camélids. In South America, eimeriids with cysts of similar dimensions, with respect to those of the present study, were assigned to *E. ivitaensis* ( $88.8 \times 51.86 \mu\text{m}$  as in Leguía [1999]).

Paleoparasitological studies carried out on mummified Peruvian camélids revealed oocysts of *E. macusaniensis* and *E. ivitaensis* dated 1,000 yr BP (Leguía, 1999; Leguía et al. 1995). Paleoparasitological findings in sediment and coprolites in Patagonia were dated from 3,500 to 8,300 yr BP (Fugassa and Barberena, 2006; Fugassa, 2007; Fugassa et al., 2007).

The oldest fossil representatives of American camélids belonged to the Lamini tribe, including species of *Pliauchenia*, which inhabited North America  $11 \times 10^6$  yr ago; it probably differentiated into 2 genera, *Alforjas* and *Hemiauchenia*. Species of *Hemiauchenia* migrated to South America during the Pleistocene–Holocene transition (Wheeler, 1995). During the Pleistocene, a descendant of *Hemiauchenia*, i.e., *Pa-*

*leolama*, was found in South America up to the Pleistocene–Holocene transition (Miotti and Salemme, 1999). Among the extant South American camélids, i.e., *L. glama*, *L. guanicoe*, *L. vicugna*, and *L. alpaca*, only *L. guanicoe* is found in Patagonia.

Paleoparasitological results for the Pleistocene transition to middle Holocene can be reasonably interpreted as a parasite response to host replacement. It is also plausible that the “large-size” oocysts are those of an extinct eimeriid-like species common to camélids during the Pleistocene–Holocene transition. Changing environmental conditions may have selected against the survival of these species, and it was succeeded by *E. macusaniensis*. Likewise, the major size of the oocysts during the pleistocenic transition and their minimal size during the middle-Holocene may be related to environmental changes known for the area in these periods (Miotti and Salemme, 2004). These hypotheses will guide future research.

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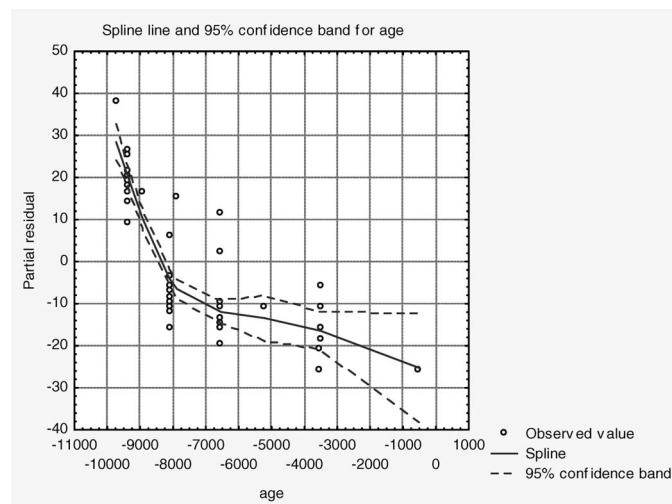


FIGURE 2. Oocyst length (a) and width (b) of eimeriid, by time. The plots show the final fitted cubic spline function for length and width, along with the observed predictor values, plotted against the partial residuals.

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