

Biometric identification of capillariid eggs from archaeological sites in Patagonia

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Abstract

Numerous eggs of capillariid nematodes have been found in coprolites from a wide range of hosts and in raptor pellets in archaeological samples from Patagonia. The structure and sculpture of the eggshell of these nematodes and their biometry are commonly used for identification. The aim of this study was to determine whether eggs of the genus *Calodium* with similar morphology, found in different archaeological samples from Patagonia, belong to the same species. For this purpose, capillariid eggs ($N = 843$) with thick walls and radial striations were studied by permutational multivariate analysis of variance (PERMANOVA). Eggs exhibiting similar shape and structure also showed similar biometry, regardless of the zoological origin of coprolites ($P = 0.84$), host diet ($P = 0.19$), character of the archaeological sites ($P = 0.67$) and chronology ($P = 0.66$). Thus, they were attributed to the same species. We suggest that an unidentified zoonotic species of the genus *Calodium* occurred in the digestive tract of a wide range of hosts in Patagonia during the Holocene and that both human and animal populations were exposed to this parasite during the Holocene in the study area.

Introduction

The family Capillariidae includes numerous species of nematodes parasitizing a wide range of domestic and wild animals worldwide (Read, 1949; Moravec, 2001; Spratt, 2006; San Martín-Órdenes, 2009). Representatives of this family have been cited as parasites of the alimentary canal, respiratory system, urinary and genital tract and subcutaneous tissues of various vertebrates, including humans (Read, 1949; Anderson, 2000; Moravec, 2000; Spratt, 2006). Many species of this family are zoonotic, mostly with low specificity at host level but high specificity regarding their location in the host (Read, 1949; Moravec, 2001; San Martín-Órdenes, 2009). The family includes *Calodium hepaticum*, which causes liver illness, *Paracapillaria philippinensis*, which causes intestinal capillariosis, and *Eucoleus aerophilus*, a parasite of the respiratory system (Galvão, 1981; Cross, 1992; Moravec,

2001; San Martín-Órdenes, 2009; Fuehrer *et al.*, 2011; Traversa *et al.*, 2011).

The taxonomy of capillariids is difficult to address due to insufficient knowledge about their morphology and life cycles (Read, 1949; Butterworth & Beverly-Burton, 1980; Moravec, 1982; Anderson, 2000; Spratt, 2006). The large number of species belonging to this family explains the large number of species not yet identified or incorrectly cited (Butterworth & Beverly-Burton, 1980). There are different views on the taxonomy of capillariids. Here, we followed the system proposed by Moravec (1982).

Capillariid eggs have been found in human coprolites and latrine sediments from archaeological sites in the Old World (Bouchet *et al.*, 2003; Dittmar & Teejen, 2003; Fernandes *et al.*, 2005). In Patagonia, eggs compatible with different species of capillariids (Fugassa *et al.*, 2008a), and numerous eggs of nematodes with similar morphology attributable to the same capillariid species, have been found in coprolites from a wide range of hosts

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Table 1. Coprolite samples from archaeological sites in Alero Destacamento Guardaparque (ADG), Cerro Casa de Piedra, caves 5 and 7 (CCP5 and CCP7), relative to date, host diet, zoological origin and number of eggs per sample.

Archaeological sites	Years ago	Host diet	Zoological origin	No. of eggs	
CCP5	6540	Omnivore	Human	118	
		Omnivore	Human	8	
		Herbivore	Camelid	10	
		Herbivore	Camelid	35	
		Predator	Birds of prey	11	
		Predator	Birds of prey	29	
		Predator	Feline	387	
		Predator	Feline	12	
		Predator	Canid	20	
		Predator	Canid	20	
CCP5	2740	Herbivore	Camelid	12	
		Predator	Birds of prey	44	
		Predator	Birds of prey	10	
CCP7	9730	Omnivore	Human	14	
	9640	Herbivore	Camelid	7	
	7880	Omnivore	Human	26	
	3080	Omnivore	Human	7	
ADG	6700	Herbivore	Camelid	17	
		Herbivore	Rodent	7	
		4900	Herbivore	Rodent	17
		4900	Herbivore	Rodent	37
ADG	3440	Herbivore	Rodent	15	
		Herbivore	Rodent	15	

(Fugassa *et al.*, 2006, 2008a, b; Fugassa, 2007; Taglioretti *et al.*, 2009; Sardella *et al.*, 2010; Beltrame *et al.*, 2010, 2011).

The aim of this study was to determine whether eggs from capillariids with similar morphology found both in raptor pellets and in coprolites of different hosts with different dietary habits, collected from archaeological sites of Patagonia, belong to the same species. For this purpose, eggs were biometrically analysed and the life cycles of known capillariids were taken into account.

Materials and methods

Samples originated from different stratigraphic levels dated from the Pleistocene–Holocene transition to the late Holocene (from 9730 to 2740 radiocarbon years before present (BP)). Coprolites were collected from the archaeological sites Cerro Casa de Piedra, caves 5 and 7 (CCP5 and CCP7), and Alero Destacamento

Guardaparque (ADG), located in Perito Moreno National Park, Santa Cruz, Argentina (table 1). A total of 21 coprolite samples (12 collected from CCP5, 5 from CCP7 and 4 from ADG) were examined. For palaeoparasitological analysis, coprolites were rehydrated with 0.5% trisodium phosphate (Callen & Cameron, 1960) and processed by spontaneous sedimentation (Lutz, 1919).

Thick-walled eggs with uncleaved content attributable to capillariids ($N = 843$) were found in coprolites of humans, rodents, felines, canids and camelids, as well as in pellets of regurgitation of birds of prey (fig. 1). The morphology and sculpture of the eggshell was similar in all eggs examined.

Biometric analysis of capillariid eggs

Three different researchers took measurements of the eggs. Therefore, to test the reliability of these measurements, biometric variables (length and width) of 15 eggs of *Calodium* sp. measured by each of the three observers were analysed using repeated measures multivariate analysis of variance (MANOVA) (Potvin & Schutz, 2000).

The number of eggs found per sample was highly variable (table 1). Therefore, to obtain a balanced design for subsequent morphometric analysis, even in samples in which the number of eggs was over 20, we selected only 20 eggs by simple random sampling without replacement. We also tested whether subsamples were representative of the original sample. To this end, we obtained ten random subsamples (20 eggs each) from a single sample, and tested whether there were significant differences in the mean and the standard deviation of the egg biometric variables by permutational MANOVA (PERMANOVA) and permutational analysis of multivariate dispersions (PERMDISP) (Anderson, 2001, 2006) using the R software version 2.13.1 (R Development Core Team, 2011).

Morphometric analyses of eggs were undertaken to determine, first, whether there was any variation in the biometry of eggs through a time scale. Eggs found in rodent coprolites collected from different layers from ADG were selected and biometric variables were subjected to PERMANOVA, considering the radiocarbon age as a factor. Second, any variation in egg biometry, relative to the zoological origin of coprolites, host diet and samples from collecting sites, was analysed using a nested

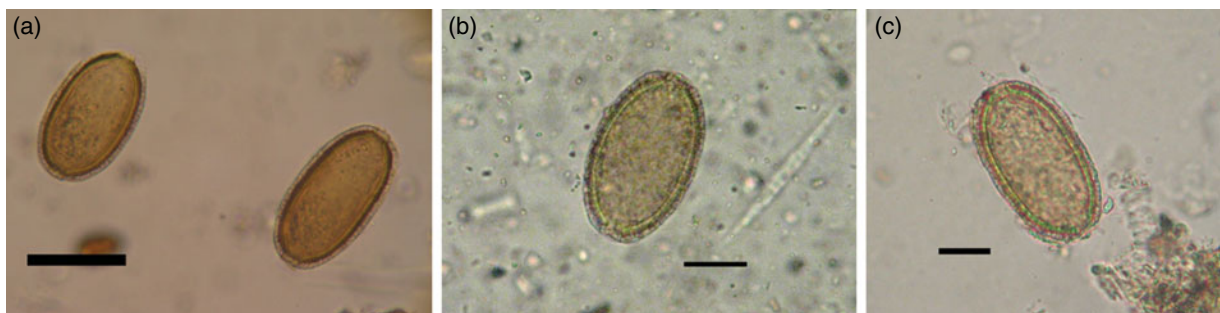


Fig. 1. (colour online) Capillariid eggs from (a) feline, (b) rodent and (c) camelid hosts. Scale bars: (a) = 40 μ m, (b) and (c) = 20 μ m.

Table 2. Random sampling without replacement of capillariid eggs from archaeological samples in which the number of eggs found was over 20.

No. of eggs	Sig. ^a	Sig. ^b	Zoological origin
118	0.96	0.18	Human
35	0.99	0.98	Camelid
29	1.00	0.99	Regurgitated pellet
387	0.87	0.24	Feline
44	0.98	0.98	Regurgitated pellet
26	0.99	0.92	Human
37	0.99	0.98	Rodent

Sig.^a: *P* value of permutational multivariate analysis of variance (PERMANOVA); Sig.^b: *P* value of permutational analysis of multivariate dispersions (PERMDISP).

PERMANOVA. This involved (a) selecting samples from CCP5 dated from 6540 years BP, in which factors considered were diet, zoological origin and samples from collecting sites; (b) taking into account all samples belonging to different archaeological sites, in which factors considered were the same as in the previous case; and (c) determining whether there were any differences in the biometry of eggs on a spatial scale where all samples from all sites were considered in the analysis and the factor selected was the archaeological site.

Results

The repeated measures MANOVA applied detected no significant differences between the biometric variables (length, width) measured by the three different observers (Pillai's trace = 0.118, *P* = 0.542). Random subsamples were representative of the original samples, because neither the dispersion nor the average of ten subsamples considered from each sample showed significant differences (table 2).

Descriptive statistics of capillariid egg morphometry according to host diet, zoological origin of samples, collecting site and time period are shown in table 3. The sizes of eggs from a sample of 843 ranged between 55 and 77.5 µm in length (mode = 65 µm) and between 35 and 45 µm in width (mode = 40 µm). Average sizes were 66.1 µm in length and 38.9 µm in width.

No significant differences (*P* = 0.66) were found in the biometric characteristics of the capillariid eggs present in rodents from the archaeological site ADG as a function of time (fig. 2). In addition, neither the different diets (*P* = 0.25) nor the zoological origin of coprolites (*P* = 0.58) led to significant differences in the biometry of eggs when eggs recovered from samples dated 6540 years BP from CCP5 were analysed statistically. Similarly, when capillariid eggs collected from all samples belonging to the different archaeological sites were analysed as a whole, no significant difference according to the host diet was found (*P*_{pooled} = 0.19; because of the lack of evidence to refuse the null hypothesis related to the zoological origin of coprolites and because the variance of the zoological origin of samples was negative, this term was removed from the model by pooling it, as suggested by Anderson, 2001) (fig. 3). Nor was a significant difference found for the zoological origin of the samples (*P* = 0.84) (fig. 4). In addition, no significant differences were found

Table 3. Morphometrics (µm) of capillariid eggs, relative to host diet and zoological origin of the samples, in sites ADG (Alero Destacamento Guardaparque), CCP5 (Cerro Casa de Piedra cave 5) and CCP7 (Cerro Casa de Piedra cave 7) and at time period corresponding to the archaeological site ADG.

Parameters	Archaeological site			Time period (years ago)					Host diet					Zoological origin				
	ADG	CCP5	CCP7	6700	4900	3440	H	O	P	Hu	Can	Ro	Br	Ca	Fe			
No. of eggs	76	696	71	7	54	15	157	173	513	20	76	94	81	399				
Length ± SD	65.7 ± 3.3	66.2 ± 3.8	64.8 ± 3.3	63.9 ± 2	65.8 ± 3.5	66.5 ± 2.6	65.8 ± 3.9	65.2 ± 3.8	66.5 ± 3.6	63.7 ± 4.5	65.7 ± 3.3	67.4 ± 3.9	65.8 ± 4.4	66.4 ± 3.3				
Width ± SD	38.9 ± 2.6	39 ± 2.3	38.7 ± 2.9	37.3 ± 3.1	39.4 ± 2.6	37.9 ± 2.2	38.7 ± 2.6	38.3 ± 2.8	39.3 ± 2.1	38.1 ± 2.3	38.9 ± 2.6	39.2 ± 2.2	38.6 ± 2.7	39.4 ± 2.1				

SD, Standard deviation; H, herbivore; O, omnivore; P, predator; Hu, human; Can, canid; Ro, rodent; Br, birds of prey; Ca, camelid; Fe, feline.

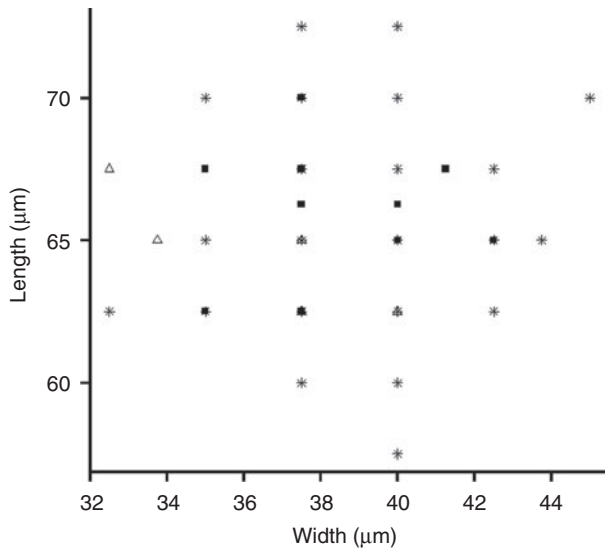


Fig. 2. Dispersion of biometric variables of capillariid eggs from rodents belonging to ADG as a function of time: *, 4900 years BP; ■, 3400 years BP; △, 6700 years BP.

in the biometry of eggs according to the collecting site ($P = 0.67$) (fig. 5).

Discussion

The study of the morphology and morphometry of nematode eggs is a useful tool to identify intestinal parasites (Benbrook & Sloss, 1965; Confalonieri *et al.*, 1985). The structure and ornamentation of the outer layer of the eggshell of capillariids are very often typical of each species and can be used as a taxonomic key (Moravec & Fajer-Avila, 2000; Moravec, 2001; Carballo & Navone, 2007).

Eggs used for this kind of study should be fully developed, or at least at the same stage of development, because the morphology of mature eggs differs from that of immature ones (Moravec & Fajer-Avila, 2000; Moravec, 2001), and although there is sometimes interspecific differentiation in egg size, this feature usually varies considerably, and may thus be considered as a complementary specific characteristic (Moravec, 2001).

Additional data to distinguish capillariid species and genera involve geographical distribution, organ preference and range of definitive hosts, since capillariids exhibit a high degree of organ specificity (Moravec & Fajer-Avila, 2000; Moravec, 2001). However, molecular studies carried out by Zhu *et al.* (2000) suggest that host and tissue specificity of the examined species of *Capillaria sensu lato* were highly variable.

Eggs examined had similar shape, size and superficial structure, regardless of zoological origin of coprolites, host diet, spatial and temporal origin, and were attributed to an unidentified species of capillariid.

Because of their shape and general structure, eggs found in the present study resemble those of *Paracapillaria malayensis* and *Capillostrongyloides arapaimae*, differing

from the former mainly in the polar plug, more irregular sculpture, size and host range (Moravec *et al.*, 2007), and from the latter in the superficial net-like sculpture, size and host range (Santos *et al.*, 2008). Additionally, egg shape and ornamentation are similar to those of eggs belonging to the genus *Calodium*, including *C. hepaticum*. The size range of eggs found in the present study includes the average size for *C. hepaticum* eggs reported by Carvalho-Costa *et al.* (2009) from stool examination (60 µm in length by 37.5 µm in width), but the average size for the present study exceeds that previously cited.

It is worth mentioning that most researchers have reported egg sizes from eggs collected from the liver, and although there is discrepancy in the biometry, eggs from various hosts overlap in their size range. Freeman & Wright (1960) occasionally found larger atypical eggs up to 69 by 35 µm, with an unusually thick outer shell. However, representatives of the genus *Calodium* are located in host tissues, not usually in intestines, and are sometimes released into the environment via faeces (Anderson, 2000; Moravec, 2001). *Calodium hepaticum* eggs can be found in faeces of carnivores that have eaten parasitized prey, indicating parasitism in transit (Freeman & Wright, 1960; Farhang-Azad, 1977; Camargo *et al.*, 2010; Li *et al.*, 2010; Fuehrer *et al.*, 2011). However, because of the life cycle of *C. hepaticum*, the probability of finding eggs in faeces of herbivores, as in the case of camelids, by accidental ingestion of non-embryonated eggs, is negligible. Experiments carried out by Freeman & Wright (1960) revealed that only a small percentage of non-embryonated eggs of *C. hepaticum* provided orally to rodents were collected from faeces. Thus, although eggs studied here are morphologically attributable to *C. hepaticum*, their location in the host does not correspond to this species. Whereas capillariids inhabiting the gut release their eggs in the environment along with faeces and exhibit a high degree of specificity in

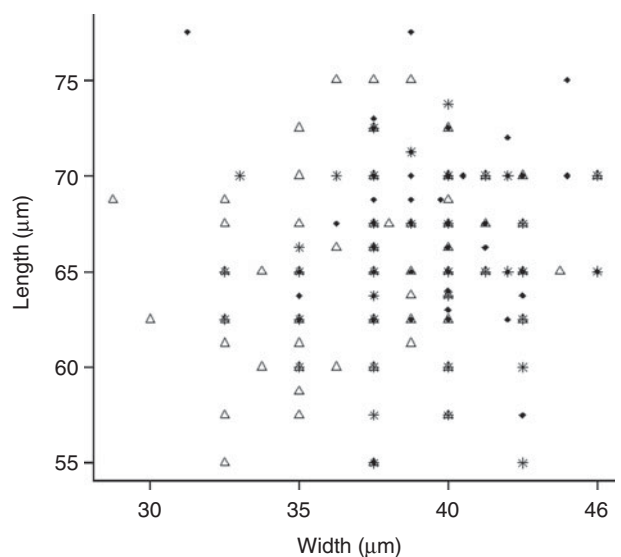


Fig. 3. Dispersion of biometric variables of capillariid eggs relative to host diet: ◆, predator; *, herbivore and △, omnivore.

function of the organ where they are located (Moravec, 2001), eggs found in this study could correspond to a capillariid of intestinal or stomach location in the host, not yet identified.

Current capillariids of intestinal and/or stomach location in mammals include the genera *Baruscapillaria*, *Eucoleus*, *Pterothominx*, *Aonchoteca* and *Capillaria* (Moravec, 2001). Because of their location in hosts, eggs found here could belong to any of these genera; however, none of these representatives has eggs morphologically similar to the ones found in this study.

Based on the results previously stated, we propose that during the Holocene in Patagonia, there was some parasite of the genus *Calodium* not yet identified, of intestinal or stomach location. In general, contact-transmitted parasites are expected to be more host-specific than parasites acquired via ingestion (Poulin *et al.*, 2006). Although this parasite was found in a wide range of hosts, this is not necessarily indicative that the parasite had infected all of them. In the cases of predators or omnivores, such as felines, birds of prey or humans, the presence of these capillariid eggs in coprolites or regurgitated pellets could be the result of parasitism in transit by the ingestion of infected prey. Moravec (2001) suggested that paratenic hosts can occur in the life cycle of capillariids. Nevertheless, there is no doubt that humans and animals were an important component of the epidemiological scenario for this unidentified capillariid, since soils of caves were contaminated with these eggs by direct release of eggs by definitive hosts, decomposition of infected hosts, or release of eggs through the faeces of hosts in transit. Both human and animal populations were exposed to this parasite during the Holocene in the study area. This may indicate its possible zoonotic role.

Caves, attracting successive use by diverse organisms, functioned as centres of dispersion for this parasite (Fugassa & Barberena, 2006; Fugassa *et al.*, 2009). Although

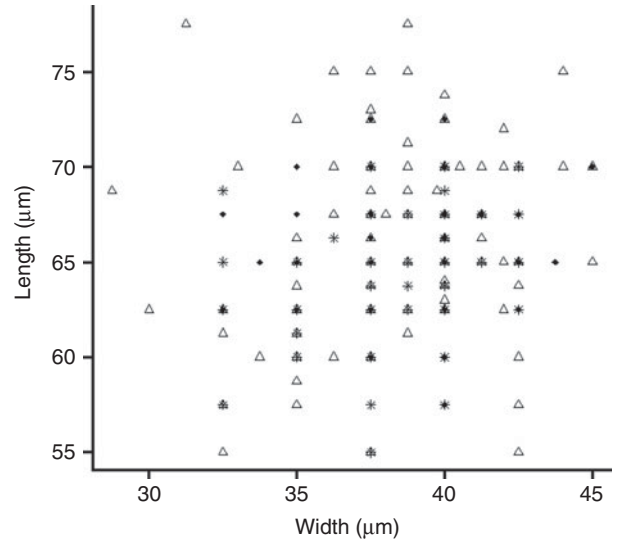


Fig. 5. Dispersion of biometric variables in terms of space (archaeological sites): Δ , CCP5; *, CCP7; and \bullet , ADG.

archaeological sites of Patagonia might not have been occupied simultaneously by animals and humans, eggs of capillariids such as *C. hepaticum* are very resistant and can remain viable in the environment at room temperature for up to 25 months (Luttermoser, 1938; Galvão, 1981).

Because of the large number of species belonging to the family Capillariidae, the taxonomic confusion and the numerous reports of species not yet identified or incorrectly cited, this study highlights the importance of biometric analysis as a potential tool to identify eggs of these nematodes collected from both archaeological and current samples.

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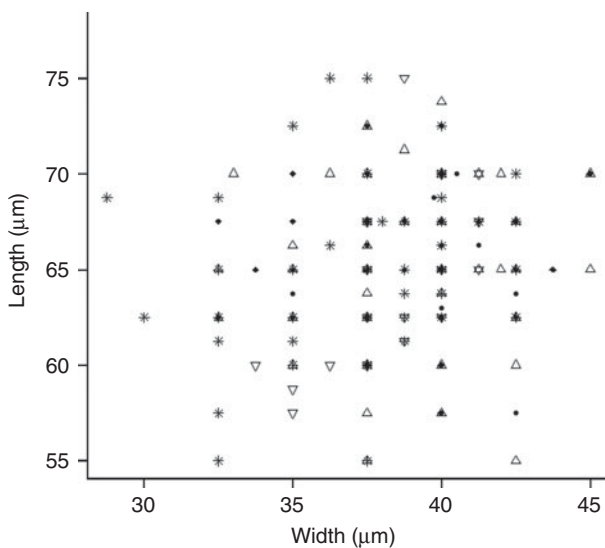


Fig. 4. Dispersion of biometric variables of capillariid eggs relative to the origin of samples: *, human; \bullet , feline; Δ , camelid; \circ , pellet of bird of prey; \blacklozenge , rodent; and ∇ , canid.

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