Paleontologia em Destaque
PALEODEST
ISSN 1807-2550 – Sociedade Brasileira de Paleontologia

PALEOPARASITOLOGICAL CONTRIBUTIONS TO THE STUDY ON ANCIENT INFECTIONS OF HOMINIDS AND OTHER VERTEBRATES IN BRAZIL: A REVIEW

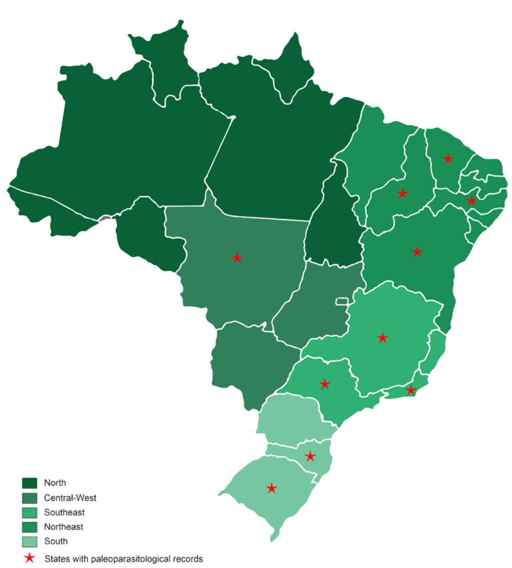
GUSTAVO MACÊDO DO CARMO[1,*]
SUELI DE SOUZA LIMA[2]
HERMÍNIO ISMAEL DE ARAÚJO-JÚNIOR[3]
FELIPE BISAGGIO PEREIRA[1]

[1]Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Presidente Antônio Carlos Ave., 31270-901, Belo Horizonte, Brazil.
[2]Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas, José Lourenço Kelmer Str., 36036-900, Juiz de Fora, Brazil.
[3]Universidade do Estado do Rio de Janeiro, Faculdade de Geologia, São Francisco Xavier Str., 20550-013, Rio de Janeiro, Brazil.
E-mails: *gugaatwts@hotmail.com; suelisouza.lima@ufjf.br; herminio.ismael@yahoo.com.br; felipebisaggiop@hotmail.com*

*Autor Correspondente: *gugaatwts@hotmail.com*

v. 38, n. 79, p. 45-61, 2023. doi:10.4072/paleodest.2023.38.79.04

Recebido em: 22 de janeiro de 2023
Aceito em: 06 de fevereiro de 2024



Carmo *et al.*, 2023. *Paleontologia em Destaque*, v. 38, n. 79, p. 48, Figure 1.

Paleontologia em Destaque – *Paleodest*, v. 38, n. 79, p. 45-61, 2023
Sociedade Brasileira de Paleontologia

PALEOPARASITOLOGICAL CONTRIBUTIONS TO THE STUDY ON ANCIENT INFECTIONS OF HOMINIDS AND OTHER VERTEBRATES IN BRAZIL: A REVIEW

GUSTAVO MACÊDO DO CARMO[1*]
SUELI DE SOUZA LIMA[2]
HERMÍNIO ISMAEL DE ARAÚJO-JÚNIOR[3]
FELIPE BISAGGIO PEREIRA[1]

[1]Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Presidente Antônio Carlos Ave., 31270-901, Belo Horizonte, Brazil.
[2]Universidade Federal de Juiz de Fora, Instituto de Ciências Biológicas, José Lourenço Kelmer Str., 36036-900, Juiz de Fora, Brazil.
[3]Universidade do Estado do Rio de Janeiro, Faculdade de Geologia, São Francisco Xavier Str., 20550-013, Rio de Janeiro, Brazil.
E-mails: *gugaatwts@hotmail.com; suelisouza.lima@ufjf.br; herminio.ismael@yahoo.com.br; felipebisaggiop@hotmail.com*

*Autor Correspondente: *gugaatwts@hotmail.com*

ABSTRACT

Paleoparasitology is an interdisciplinary science that studies the parasitic infections in the past, using fossils and subfossils recovered from archeological and paleontological lithostratigraphic units. During the 20th and 21st centuries, it has improved the biological knowledge on helminths and protozoans, as well as provided numerous sociocultural insights into the past civilizations. Here, we present an updated review of the paleoparasitological contributions to the analyses of ancient infections in vertebrate remains recovered from different regions of Brazil. Since its emergence, the Paleoparasitology has been important to a multidisciplinary knowledge related to sociocultural aspects of the American Pre-Columbian civilizations and may provide an important ecological, evolutionary, and biogeographical understanding of parasites of vertebrates other than humans throughout the geological time. The present data compilation suggests a prominent role in the scientific community assumed by paleoparasitological approaches, since they have been contributing to a better understanding of helminth and protozoan distribution in South America, during the Phanerozoic eon and consolidating the Paleoparasitology as a global science.

Keywords: Coprolite, mummy, helminth, protozoa.

RESUMO

Contribuições paleoparasitológicas para o estudo de infecções pretéritas de hominídeos e outros vertebrados no Brasil: uma revisão. A Paleoparasitologia é uma ciência interdisciplinar que estuda as infecções parasitárias do passado, utilizando fósseis e subfósseis recuperados de unidades litoestratigráficas arqueológicas e paleontológicas. Durante os séculos XX e XXI, a área supracitada não só aprimorou o conhecimento biológico sobre helmintos e protozoários, como também forneceu numerosas informações socioculturais sobre as civilizações antigas. Apresentamos aqui uma revisão atualizada das contribuições paleoparasitológicas para a análise de infecções antigas em fósseis e subfósseis de vertebrados recuperados de diferentes regiões do Brasil. Desde o seu surgimento, a Paleoparasitologia tem sido importante para a construção do conhecimento multidisciplinar relacionado aos povos pré-colombianos, fornecendo também uma importante compreensão ecológica, evolutiva e biogeográfica de parasitos de outros vertebrados não humanos ao longo do tempo geológico. A presente compilação de dados sugere um papel de destaque na comunidade científica assumido pelos esforços paleoparasitológicos, uma vez que eles contribuíram para uma melhor compreensão da distribuição de helmintos e protozoários na América do Sul, durante o éon Fanerozoico e consolidaram a Paleoparasitologia como uma ciência global.

Palavras-chave: Coprólito, múmia, helminto, protozoário.

INTRODUCTION

The first report of *Schistosoma haematobium* eggs in the kidney tissues of Egyptian mummies from the 20th dynasty (1250 to 1100 BC), by Sir Marc Armand Ruffer in the first half of the 20th century, represented the genesis of Paleoparasitology, and also triggered the emergence of new perspectives for studies pertaining to helminths and protozoans all over the world (Ruffer, 1910). The identification of parasites in fossils and subfossils recovered from paleontological and archaeological sites during the last decades has improved the evolutionary and biogeographical understanding of

https://doi.org/10.4072/paleodest.2023.38.79.04

these organisms in a broader time scale, making it possible to study the spread of host populations over the Phanerozoic eon (Reinhard *et al*., 1987; Gonçalves *et al*., 2002a).

Reports of parasites in Amerindian ancient remains from the South and North Americas has been clarifying the archeological comprehension of the first migratory routes of humans to the New World, as well as providing important information on the development of their economic, political, cultural, and social history (Darling 1920; Soper, 1927; Ferreira *et al*., 1983; Reinhard *et al*., 1987; Reinhard, 1988; Faulkner *et al*., 1989; Faulkner, 1991; Santoro *et al*., 2003; Souza *et al*., 2018; Montenegro *et al*., 2006). Paleoparasitological studies on hookworms have contributed to the refutation of the "*Clovis first and only*" hypothesis[1] (Darling 1920; Soper, 1927; Ferreira *et al*., 1983; Montenegro *et al*., 2006).

Furthermore, through the identification of parasites in trace fossils from american archaeological sites marked by social, cultural, political and commercial reorganizations, it is possible to observe the increase of parasitic infections in this continent due to the emergence of the agriculture, the sedentarization and the birth of great civilizations and large cities with poor sanitary conditions (Reinhard *et al*., 1987; Reinhard, 1988; Faulkner *et al*., 1989; Faulkner, 1991; Santoro *et al*., 2003; Souza *et al*., 2018).

In this sense, the Paleoparasitology has expanded the biological knowledge about the parasitic infections and provided sociocultural insights into the past civilizations, since helminths and protozoans can be used as biological indicators of behavioral, socioeconomic and environmental conditions in the present (Flammer & Smith, 2020).

Although the first paleoparasitological studies were focused on the description of infections in ancient humans (Ruffer, 1910; Szidat, 1944), efforts to identify helminths and protozoans in other vertebrate remains throughout the Phanerozoic eon have been noted in the literature. Reports of parasites in fossils and subfossils are uneven, and records from the Cenozoic are by far the most numerous (Araújo *et al*., 1981; Ferreira *et al*., 1989b, 1991, 1992, 1993; Schmidt *et al.,* 1992; Noronha *et al.,* 1994; Jouy-Avantin *et al.,* 1999; Verde & Ubilla, 2002; Sardella & Fugassa, 2009; Beltrame *et al.,* 2011, 2012, 2013, 2015a, b, 2017, 2018, 2020, 2022; Fugassa *et al.,* 2013, 2022; McConnell & Zavada, 2013; Wood *et al.,* 2013, 2019; Taglioretti *et al.,* 2015; Sianto *et al.,* 2016; Nunes *et al.,* 2017; Perri *et al.,* 2017; Dentzien-Dias *et al.,* 2018; Leles *et al*., 2018; Tietze *et al.,* 2019, 2020; Souza *et al.,* 2020; Agustín *et al*., 2021; Cardia *et al.,* 2021; Oyarzún-Ruiz *et al.,* 2021; Petrigh *et al.,* 2021; Sivkova & Kosintsev, 2021; Carmo *et al*., 2023; Ramirez *et al*., 2023). Nevertheless, paleoparasitologists have expanded the studies to animal remains dated from the Paleozoic (Dentzien-Dias *et al.,* 2013) and Mesozoic Eras (Poinar & Boucot, 2006; Hugot *et al.,* 2014; Silva *et al.,* 2014; Brachaniec *et al.,* 2015; Tweet *et al.,* 2016; Francischini *et al*., 2017; Cardia *et al.,* 2018, 2019a, b; Pedro *et al.,* 2020; Aureliano *et al.,* 2021).

In Brazil, the first paleoparasitological studies were conducted during the 1970s, by Dr. Luiz Fernando Rocha Ferreira da Silva and Dr. Adauto José Gonçalves de Araújo, from the Instituto Oswaldo Cruz (FIOCRUZ) (Novo & Ferreira, 2016). The identification of parasites in fossils and subfossils of fish, reptiles, birds, and mammals, including humans, from Brazilian lithostratigraphic units, have been presented for the States of Rio Grande do Sul and Santa Catarina (South Region), São Paulo, Minas Gerais and Rio de Janeiro (Southeast Region), Ceará, Piauí and Pernambuco (Northeast Region), and Mato Grosso (Central-West Region) (Figure 1) (Ferreira *et al*., 1979, 1980, 1983, 1987, 1989a, b, 1991, 1992, Araújo *et al*., 1981, 1984, 1989; Confalonieri *et al*., 1981; Noronha *et al*., 1994; Gonçalves *et al*., 2003; Sianto *et al*., 2005, 2012, 2014, 2016; Fernandes *et al*., 2008; Leles *et al*., 2008, 2018; Lima *et al*., 2008; Camacho *et al*., 2013; Dentzien-Dias *et al*., 2013; Jaeger *et al*., 2013a, b; Hugot *et al*., 2014; Silva *et al*., 2014; Novo *et al*., 2015; Francischini *et al*., 2017; Cardia *et al*., 2018, 2019a, b, 2021; Guedes *et al*., 2020; Souza *et al*. 2020; Aureliano *et al*., 2021; Iñiguez *et al*., 2022; Carmo *et al*., 2023). Therefore, the present review aimed to access and compile all the scientific publications reporting endoparasites in ancient remains collected in different paleontological and archaeological sites from Brazil, published during the 20th and 21st centuries.

The survey was carried out from 2020 to 2023, using the combination of the following descriptors "pre-columbian", "paleoparasitology", "coprolite", "archaeology", "archeology", "archaeoparasitology", "archeoparasitology", "mummy", "parasite" and "Brazil", with the logical operators "AND" and "OR", in five databases: Science Direct, Web of Science, Scopus, Scientific Electronic Library (Scielo) and Google Scholar. After the analysis of the "Abstract", the articles were

[1] According to this theory, all inhabitants of pre-Columbian America, except those from the northern part of the continent, would have descended from one or more groups of hunters from the Clovis Culture, whom migrated across the Beringian land bridge during the last ice age (Montenegro *et al*., 2006). More recent archaeological evidences from Mexico, reveal that the dispersal of humans to the New World may have happened more than 30,000 years ago (Ardelean *et al*., 2020).

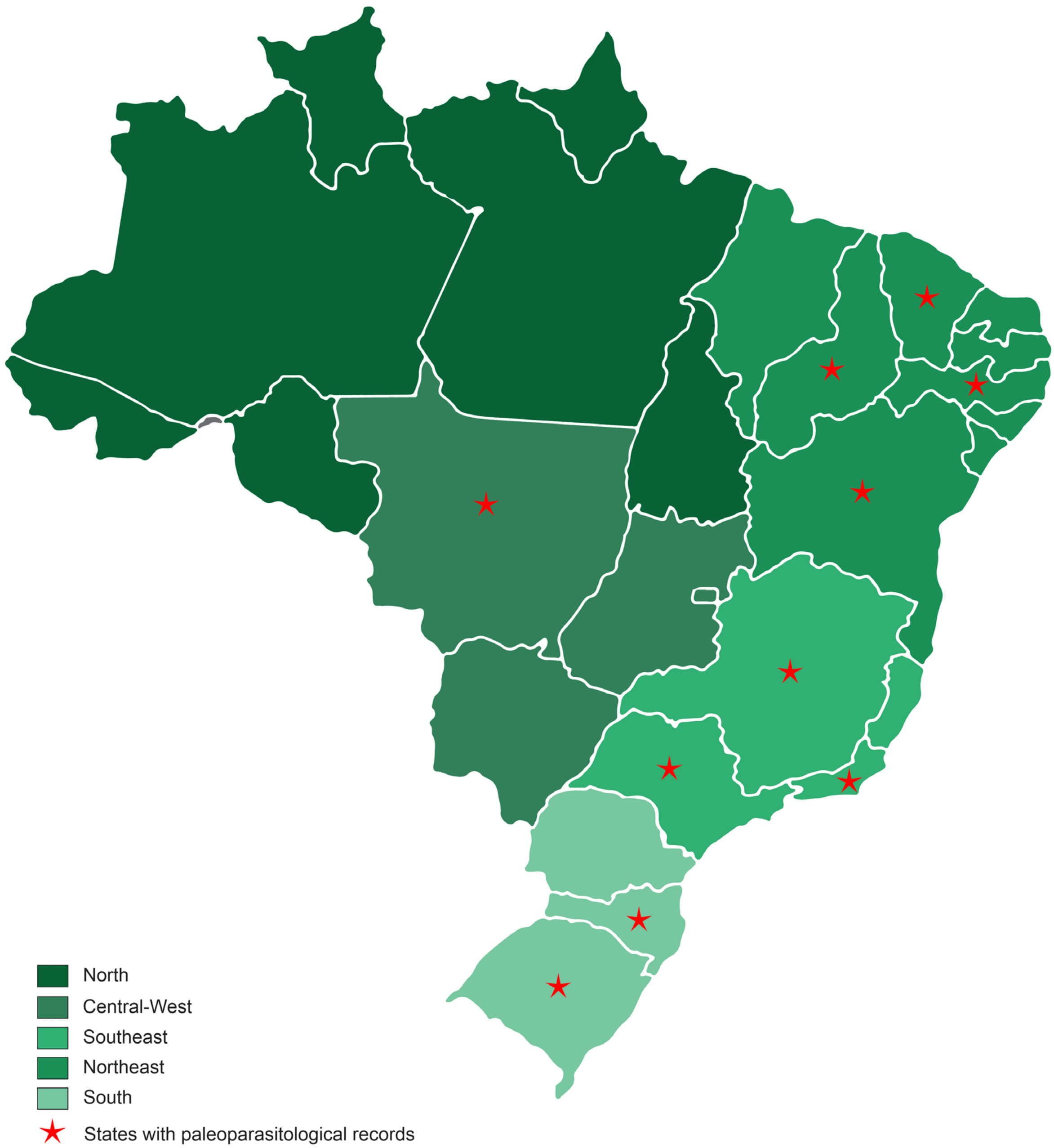


Figure 1. Brazilian states in which endoparasites were reported in fossils and subfossils during the 20th and 21st centuries. Different colors correspond to the five Brazilian regions.
Figura 1. Estados brasileiros nos quais foram registrados endoparasitos em fósseis e subfósseis durante os séculos XX e XXI. As diferentes cores correspondem às cinco regiões brasileiras.

selected according to their relevance and their consonance with the present theme. Some paleoparasitological references that are not included in the previously mentioned databases, but cited in the present articles and considered important for the present approach, were obtained representing non-probabilistic sampling methodology (Zar, 2010). Forty scientific papers were gathered from the databases and a single scientific conference abstract was selected, due to its importance. We also provide new Protozoa records unpublished yet. Detailed information on parasite, host, time period or age, locality and reference are given in Table 1.

Table 1. Endoparasites reported in archaeological and paleontological sites from Brazil. Question marks indicate information that could not be confirmed.
Tabela 1. Endoparasitos registrados em sítios arqueológicos e paleontológicos do Brasil. Interrogações indicam informações que não puderam ser confirmadas.

Parasite taxa	Host taxa	Period/Epoch	Lithostratigraphic unit/ Site (State)	Reference
Tetraphyllidea (Cestoda)	Elasmobranchii (Chondrichthyes)	Permian	Rio do Rasto Formation (Rio Grande do Sul)	Dentzien-Dias *et al.*, 2013
Ascarites rufferi (Nematoda)	Cynodontia (Synapsida, Therapsida)	Triassic	Santa Maria Formation (Rio Grande do Sul)	Silva *et al.*, 2014
Paleoxyuris cockburni (Nematoda)	Terrestrial Tetrapoda	Triassic	Santa Maria Formation (Rio Grande do Sul)	Francischini *et al.*, 2017
Paleoxyuris cockburni (Nematoda)	Traversodontidae gen. sp. (Synapsida, Therapsida)	Triassic	Santa Maria Formation (Rio Grande do Sul)	Hugot *et al.*, 2014
Acanthocephala; Ascaridoidea, *Bauruascaris adamantinensis* e *B. cretacicus* (Nematoda)	Crocodyliformes (Reptilia, Eusuchia)	Cretaceous	Adamantina Formation (São Paulo)	Cardia *et al.*, 2018; 2019a; 2019b
Trypanosomatidae gen. sp. (Protozoa)	Titanosaur (Sauropoda, Titanosauria)	Cretaceous	Adamantina Formation (São Paulo)	Aureliano *et al.*, 2021
Archamoebae gen. sp. (Amoebozoa); Eimeriidae gen. sp. (Apicomplexa)	Neornithes	Oligocene	Tremembé Formation (São Paulo)	Unpublished data
Ascaridina, Spirurina, Trichocephalida (Nematoda)	Neornithes	Oligocene	Tremembé Formation (São Paulo)	Carmo *et al.*, 2023
Ancylostomatidae? gen. sp. (Nematoda); Eucoccidiorida (Apicomplexa)	Carnivora (Mammalia)	Pleistocene	Touro Passo Formation (Rio Grande do Sul)	Cardia *et al.*, 2021
Giardia duodenalis (Protozoa)	*Nothrotherium maquinense* (Xenarthra, Nothrotheriidae), *Palaeolama major* (Artiodactyla, Camelidae)	Pleistocene?	Northeast Brazil	Leles *et al.*, 2018
Strongyloides ferreirai, Trichuris sp. (Nematoda)	*Kerodon rupestris* (Rodentia, Caviidae)	Pleistocene–Holocene	Pedra Furada (Piauí)	Ferreira *et al.*, 1991
Acanthocephala; Ascaridoidea, Heterakoidea (Nematoda)	Sedimento de Sambaqui	Holocene	Sambaqui de Guapi (Rio de Janeiro)	Camacho *et al.*, 2013

Table 1. Cont.
Tabela 1. Cont.

Parasite taxa	**Host taxa**	**Period/Epoch**	**Lithostratigraphic unit/ Site (State)**	**Reference**
Acanthocephala	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Boqueirão Soberbo (Minas Gerais)	Gonçalves *et al.*, 2003
Acanthocephala	*Homo sapiens sapiens* (Primates, Hominidae)?	Holocene	Gruta do Gentio (Minas Gerais)	Gonçalves *et al.*, 2003
Ancylostomatidae gen. sp. (Nematoda); *Echinostoma* sp. (Trematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Lapa do Boquete – Vale do Peruaçu (Minas Gerais)	Sianto *et al.*, 2005
Ancylostomatidae gen. sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Boqueirão do Sítio da Pedra Furada (Piauí)	Ferreira *et al.*, 1987
Ancylostomatidae gen. sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene?	Sítio do Meio (Piauí)	Gonçalves *et al.*, 2003
Ancylostomatidae gen. sp., Nematoda, *Trichuris* sp., (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)?	Holocene	Gruta do Gentio II (Minas Gerais)	Ferreira *et al.*, 1979
Ancylostomatidae gen. sp., *Trichuris trichiura* (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Gruta do Gentio II (Minas Gerais)	Araújo *et al.*, 1981
Ancylostomatidae gen. sp., *Trichuris trichiura* (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Gruta do Gentio II (Minas Gerais)	Ferreira *et al.*, 1983
Ascaris lumbricoides (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Gruta do Gentio (Minas Gerais)	Gonçalves *et al.*, 2003
Ascaris lumbricoides (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Gruta do Gentio II (Minas Gerais)	Leles *et al.*, 2008
Ascaris lumbricoides (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Toca do Meio (Piauí)	Leles *et al.*, 2008
Ascaris sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Cemitério dos Pretos Novos (Rio de Janeiro)	Guedes *et al.*, 2020
Ascaris sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Sambaqui Jabuticabeira II (Santa Catarina)	Iñiguez *et al.*, 2022
Ascaris sp., *Trichuris* sp. (Nematoda); *Entamoeba coli*? (Protozoa); *Taenia* sp. (Cestoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Cemitério Praça XV (Rio de Janeiro)	Jaeger *et al.*, 2013b

Table 1. Cont.
Tabela 1. Cont.

Parasite taxa	**Host taxa**	**Period/Epoch**	**Lithostratigraphic unit/ Site (State)**	**Reference**
Ascaris sp., *Trichuris trichiura* (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Igreja de Nossa Senhora do Carmo (Rio de Janeiro)	Jaeger *et al.*, 2013a
Aspidoderidae gen. sp., Nematoda, Strongylida (Nematoda); *Entamoeba* cf. sp. (Protozoa); *Gigantorhynchus echinodiscus*, *Macracanthorhynchus hirudinaceus*, *Oligacanthorhynchus* sp. (Acanthocephala)	*Tamandua tetradactyla* (Pilosa, Myrmecophagidae)	Holocene	Toca do Enoque (Piauí)	Souza et *al.* 2020
Calodium cf. *C. hepaticum*, Nematoda, Oxyuroidea, *Physaloptera* sp., *Toxocara cati*, Trichuridae gen. sp., *Trichuris* cf. *T. muris* (Nematoda), *Spirometra* sp. (Cestoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca do Morcego (Piauí)	Sianto *et al.*, 2014.
Cestoda	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Santa Elina (Mato Grosso)	Gonçalves *et al.*, 2003
Echinopardalis sp. (Acanthocephala)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	São Raimundo Nonato (Piauí)	Noronha *et al.*, 1994
Echinostomatidae gen. sp. (Trematoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Furna do Estrago (Pernambuco)	Sianto *et al.*, 2016
Eimeria lobatoi (Protozoa)	*Mazama* sp. (Mammalia, Cervidae)	Holocene	Perna I (Piauí)	Ferreira *et al.*, 1992
Enterobius vermicularis (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)?	Holocene	Sítio BA RC 28 - Serra do Ramalho (Bahia)	Lino *et al.*, 2018
Gigantorhynchus echinodiscus (Acanthocephala)	*Tamandua tetradactyla* or *Myrmecophaga tridactyla* (Pilosa, Myrmecophagidae)	Holocene	Baixão da Vaca (Piauí)	Ferreira *et al.*, 1989b
Gigantorhynchus echinodiscus (Acanthocephala)	*Tamandua tetradactyla* or *Myrmecophaga tridactyla* (Pilosa, Myrmecophagidae)	Holocene	Boqueirão Soberbo (Minas Gerais)	Ferreira *et al.*, 1989b
Gigantorhynchus echinodiscus (Acanthocephala)	*Tamandua tetradactyla* (Pilosa, Myrmecophagidae)	Holocene	Toca dos Coqueiros (Piauí)	Souza et *al.* 2020

Table 1. Cont.
Tabela 1. Cont.

Parasite taxa	Host taxa	Period/Epoch	Lithostratigraphic unit/ Site (State)	Reference
Hymenolepis nana (Cestoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Santa Elina (Mato Grosso)	Gonçalves *et al.*, 2003
Leishmania tarentolae (Protozoa)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Igreja de Sant'Antonio Aparecido - Itacambira (Minas Gerais)	Novo *et al.*, 2015
Macracanthorhynchus hirudinaceus (Acanthocephala)	*Tamandua tetradactyla* (Pilosa, Myrmecophagidae)	Holocene	Toca da Passagem (Piauí)	Souza et *al.* 2020
Necator americanus, *Trichuris trichiura* (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Gruta do Gentio II (Minas Gerais)	Ferreira *et al.*, 1980
Oncicola sp. (Acanthocephala); *Spirometra* spp. (Cestoda).	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca da Baixa dos Caboclos (Piauí)	Sianto *et al.*, 2014.
Oxyuroidea, *Toxocara cati* (Nematoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca do Enoque (Piauí)	Sianto *et al.*, 2014.
Parapharyngodon sp. (Nematoda)	Sauria (Lacertilia) (Reptilia, Squamata)	Holocene	Grande abrigo de Santana do Riacho (Minas Gerais)	Araújo *et al.*, 1981
Pharyngodonidae gen. sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Furna do Estrago (Pernambuco)	Sianto *et al.*, 2012
Pharyngodonidae gen. sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Toca dos Coqueiros (Piauí)	Sianto *et al.*, 2012
Pharyngodonidae gen. sp. (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Toca da Baixa dos Caboclos (Piauí)	Sianto *et al.*, 2012
Syphacia sp. (Nematoda)	*Kerodon rupestris* (Rodentia, Caviidae)	Holocene	Toca dos Coqueiros (Piauí)	Souza *et al.*, 2012
Spirometra sp. (Cestoda); *Toxocara cati* (Nematoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca dos Coqueiros (Piauí)	Sianto *et al.*, 2014.
Strongyloides ferreirai, *Trichuris* sp. (Nematoda)	*Kerodon rupestris* (Rodentia, Caviidae)	Holocene	São Raimundo Nonato (Piauí)	Araújo *et al.*, 1989

Table 1. Cont.
Tabela 1. Cont.

Parasite taxa	Host taxa	Period/Epoch	Lithostratigraphic unit/ Site (State)	Reference
Trichostrongylidae, *Trichuris trichiura* (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Itacambira (Minas Gerais)	Araújo *et al.*, 1984
Trichuris cf. *T. muris* (Nematoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca do Gongo I (Piauí)	Sianto *et al.*, 2014.
Trichuris cf. *T. muris* (Nematoda), *Spirometra* sp. (Cestoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca do Paraguaio (Piauí)	Sianto *et al.*, 2014.
Trichuris sp. (Nematoda)	Felidae gen. sp. (Mammalia, Carnivora)	Holocene	Toca do Sítio do Meio (Piauí)	Sianto *et al.*, 2014.
Trichuris trichiura (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Furna do Estrago (Pernambuco)	Ferreira *et al.*, 1989a
Trichuris trichiura (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Itacambira (Minas Gerais)	Confalonieri *et al.*, 1981
Trichuris trichiura (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Lapa Pequena (Minas Gerais)	Gonçalves *et al.*, 2003
Trichuris trichiura (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene?	Pedra Furada (Piauí)	Gonçalves *et al.*, 2003
Trichuris trichiura (Nematoda)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Santa Elina (Mato Grosso)	Gonçalves *et al.*, 2003
Trypanossoma cruzi (Protozoa)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Vale do Peruaçu (Minas Gerais)	Fernandes *et al.*, 2008
Trypanossoma cruzi (Protozoa)	*Homo sapiens sapiens* (Primates, Hominidae)	Holocene	Abrigo do Malhador – Vale do Peruaçu (Minas Gerais)	Lima *et al.*, 2008

SOUTHEAST

The Southeast Region has a relevant number of paleoparasitological studies. Parasites of the phyla Nematoda and Acanthocephala have been reported in Holocene coprolites and consumulites from the archaeological site Gruta do Gentio, municipality of Unaí, State of Minas Gerais (Ferreira *et al.*, 1979, 1980, 1983; Araújo *et al.*, 1981; Gonçalves *et al.*, 2003; Leles *et al.*, 2008). It is worth noting that Ferreira *et al.* (1979), studying helminths in coprolites from Gruta Gentio, introduced the term "Paleoparasitology".

Despite the adverse conditions for mummification in Brazil (Ferreira *et al.*, 1983), in the State of Minas Gerais, nematodes and protozoans were identified in mummies dated from the colonial period and collected in Itacambira (Confalonieri *et al.*, 1981; Araújo *et al.*, 1984; Novo *et al.*, 2015), as well as infections by digenetic, nematode and trypanosomatid in mummies from the Vale do Peruaçu (Sianto *et al.*, 2005; Fernandes *et al.*, 2008; Lima *et al.*, 2008). Araújo *et al.* (1981) reported nematodes from coprolites of lizards collected in Grande Abrigo de Santana do Riacho, municipality of Santana do Riacho. Other studies carried out in the State of Minas Gerais recorded acanthocephalans in archaeological material from Boqueirão Soberbo, municipality of Varzelândia, and nematodes from Lapa Pequena (Ferreira *et al.*, 1989b; Gonçalves *et al.*, 2003).

Regarding the State of São Paulo, paleoparasitological studies have been carried out in the Adamantina Formation (Bauru Basin), where hemoparasites were reported in vascular regions of the bone tissues from a titanosaur fibula (Aureliano *et al.*, 2020), and nematodes and acanthocephalans observed in coprolites of Crocodyliformes (Cardia *et al.*, 2018, 2019a, 2019b), all from the Cretaceous. Protozoans and nematodes were also found in coprolites of birds from the Tremembé Formation, which represents the Oligocene of the Taubaté Basin, in the Paraíba Valley (Carmo *et al.*, 2023).

Several parasites in human subfossils have been reported in the State of Rio de Janeiro. Sacral and pelvic sediments of bodies from the Cemitério Pretos Novos (1769-1830), which was built to bury enslaved Africans who died upon arrival at Rio de Janeiro municipality, or before being sold in slave market, were analyzed by Guedes *et al.* (2020). These authors detected a helminthic infection by Nematoda that was acquired in Africa. The bodies of slaves were accumulated for days, being dismembered, placed in mass graves and even cremated, presenting a high level of degradation (Guedes *et al.*, 2020). These results indicate great potential for detection of parasitic infections in archaeological sites, despite high level of sample degradation. In this same municipality (Rio de Janeiro), pelvic sediments were also extracted from bodies collected in the archaeological site of Igreja de Nossa Senhora do Carmo, being positive for nematodes (Jaeger *et al.*, 2013a). The paleoparasitological studies in Rio de Janeiro also include records of eggs of Cestoda and Nematoda, as well as Archamoebea cysts found in human sacral sediments, collected in the archaeological site of Cemitério Praça XV (Jaeger *et al.*, 2013b). Finally, the study of sediments from the Sambaqui de Guapi, municipality of Guapimirim, revealed the presence of eggs of Nematoda and Acanthocephala (Camacho *et al.*, 2013).

In an attempt to detect *Giardia duodenalis* in ancient human remains from Gruta do Gentio (Minas Gerais), Gonçalves *et al.* (2002b) analyzed the material that was previously studied by Ferreira *et al.* (1980, 1983, 1987), but found no trace of this protozoan parasite.

NORTHEAST

A wide diversity of endoparasitic infections have been recorded in the Brazilian Northeast region. In the archaeological site of Furna do Estrago, municipality of Brejo da Madre de Deus, State of Pernambuco, nematode and trematode eggs have been reported in human and feline coprolites, respectively (Ferreira *et al.*, 1989a; Sianto *et al.*, 2012, 2016). Interestingly, Sianto *et al.* (2012) collected eggs from human coprolites that, according to the authors, resemble those of nematodes parasitic in reptiles. The study was conducted in the archaeological site of Furna do Estrago (State of Pernambuco) and São Raimundo do Nonato (State of Piauí) and, also according to these researchers, may be an indicative of reptile consumption by ancient humans in the region, a habit that persists in Northeast Brazil until the present.

In addition, there are several reports of parasitic infections in mammals caused by Nematoda, Cestoda, Acanthocephala, Archamoebea and Coccidiomorphea from the Pleistocene to the Holocene, in the State of Piauí (Ferreira *et al.*, 1987, 1989b, 1991, 1992; Araújo *et al.*, 1989; Noronha *et al.*, 1994; Gonçalves *et al.*, 2003; Leles *et al.*, 2008; Souza *et al.*, 2012; Sianto *et al.*, 2012, 2014). Lino *et al.* (2018) also reported a nematode taxon in a coprolite from the Coribe municipality, Bahia State. Other paleoparasitological records from Northeastern Brazil include protozoa found in coprolites of representatives of the families Camelidae and Nothrotheriidae (Leles *et al.*, 2018; Lino *et al.*, 2018).

It should be noted that, in the same previously mentioned study by Gonçalves *et al.* (2002b), samples from Boqueirão do Sítio da Pedra Furada (State of Piauí) were also analyzed for *G. duodenalis* without positive results.

SOUTH

Paleoparasitological studies in the State of Rio Grande do Sul report several parasite infections during ancient times. Cestodes were recorded in Elasmobranchii coprolites dating from the Permian (Paleozoic Era), collected in Rio do Rasto Formation (Dentzien-dias *et al.*, 2013). Nematodes were observed in coprolites of cynodonts and other terrestrial tetrapods from the Triassic (Mesozoic Era), collected in Santa Maria Formation (Hugot *et al.*, 2014; Silva *et al.*, 2014; Francischini *et al.*, 2017). Coccidia and Nematodes infecting carnivores from the Quaternary period (Cenozoic Era) were also reported (Cardia *et al.*, 2021). Regarding human remains, studies on pelvic and sacral sediments exhumed from the Sambaqui Jabuticabeira II, municipality of Jaguaruna, State of Santa Catarina, revealed the presence of Nematoda parasitic forms (Iñiguez *et al.*, 2022).

CENTRAL-WEST

The only paleoparasitological approach in Central-West Brazil was performed in the State of Mato Grosso. Cestodes and nematodes were observed in human subfossils from Santa Elina (Gonçalves *et al.*, 2003).

DISCUSSION

The parasitological studies from the current time are crucial for the development of public policies regarding prophylaxis and control of parasitic infections, especially in underdeveloped endemic areas (Holland *et al.*, 2022). Similarly, reports of helminth and protozoan in ancient human remains make it possible to better understand how the socioeconomic and sociopolitical traces have evolved or persisted until the present (Reinhard *et al.*, 1987; Reinhard, 1988; Faulkner *et al.*, 1989; Faulkner, 1991; Santoro *et al.*, 2003; Souza *et al.*, 2018). Therefore, since its emergence in the 20th century, the Paleoparasitology has been important to a multidisciplinary knowledge pertaining to sociocultural aspects, related to the American Pre-Columbian civilizations, associating parasitology, archeology and anthropology.

The preservation of parasites in paleontological material is rare (Dentzien-Dias *et al.*, 2013), which may explain the greater number of records dating from the Holocene in comparison to other geological time intervals (Figs. 2 and 3). In relation to fossils and subfossils of vertebrates other than humans, the identification of protozoans and helminths in such materials may provide an important ecological, evolutionary, and biogeographical understanding of parasites throughout the geological time (Reinhard *et al.*, 1987; Gonçalves *et al.*, 2002a).

The southeast region has the greatest number of paleoparasitological records due to the efforts carried out with a large amount of ancient material, collected in the State of Minas Gerais. Helminth eggs, especially those of Nematoda, have been the most common parasitic forms described in fossils and subfossils, since they are resistance stages for environmental variables (Gonçalves *et al.*, 2003; Flammer & Smith, 2020). In some cases, genera and even new species are identified based on this material. It is worth noting that the taxonomic identification of this isolated material, without the presence of adult parasites, may be fragile, since eggs keep ancestral ontogenetic characteristics and show rather homogeneous morphology, which almost always prevents the specific identification (Gonçalves *et al.*, 2003; Loreille & Bouchet, 2003; Flammer & Smith, 2020). Furthermore, some morphological features used for diagnosing certain taxa are problematic, complicating the establishment of boundaries between genera, for example (Pereira *et al.*, 2018). Morphometric aspects of the eggs can also vary according to the parasite load and its ecological strategy (Goater *et al.*, 2014). Therefore, researches should be more conservative when dealing with the taxonomic identification of ancient immature forms of parasites, especially in cases when genetic material is not available for use.

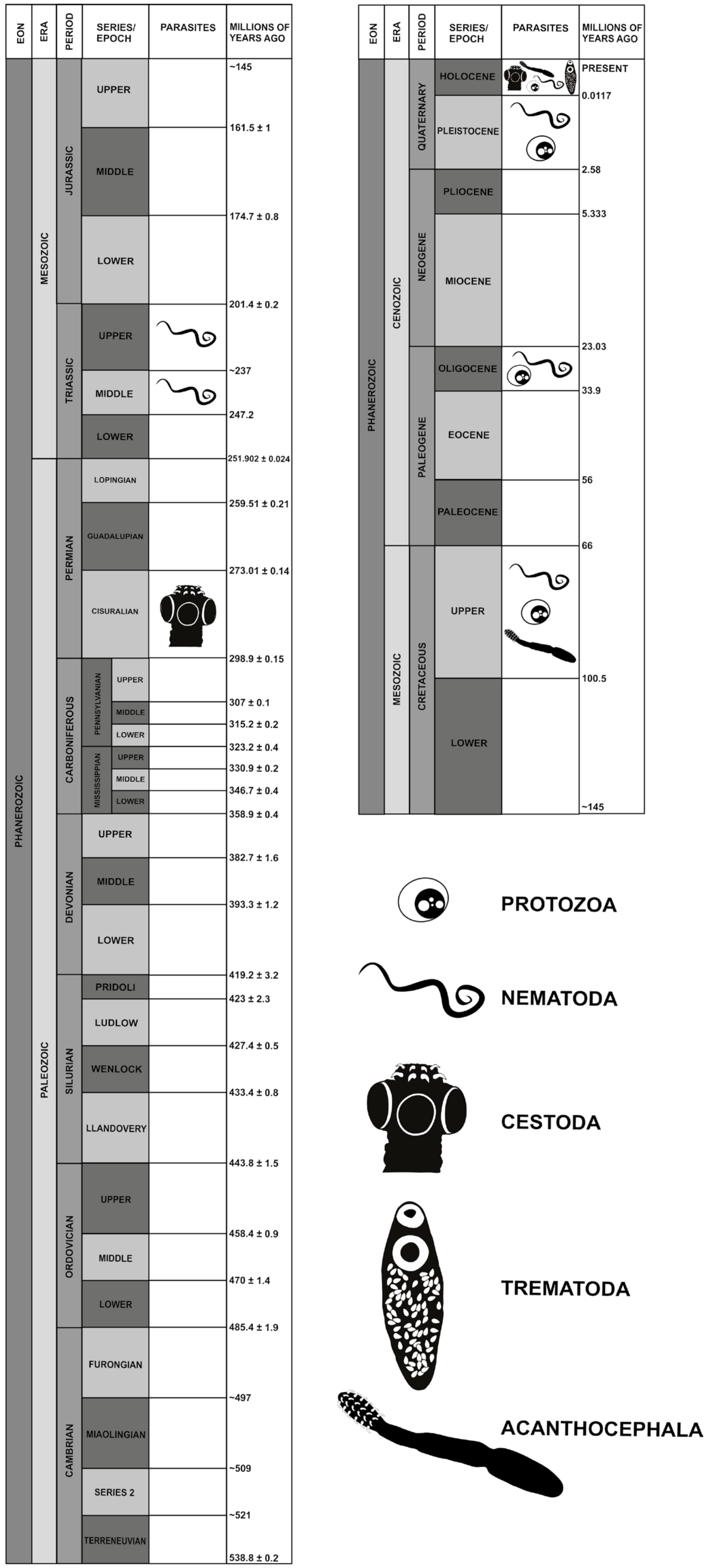


Figure 2. Parasite taxa reported throughout the Phanerozoic Eon. Modified from Cohen *et al.* (2023).
Figura 2. Grupos taxonômicos de parasitos registrados ao longo do Éon Fanerozoico. Modificado de Cohen *et al.* (2023).

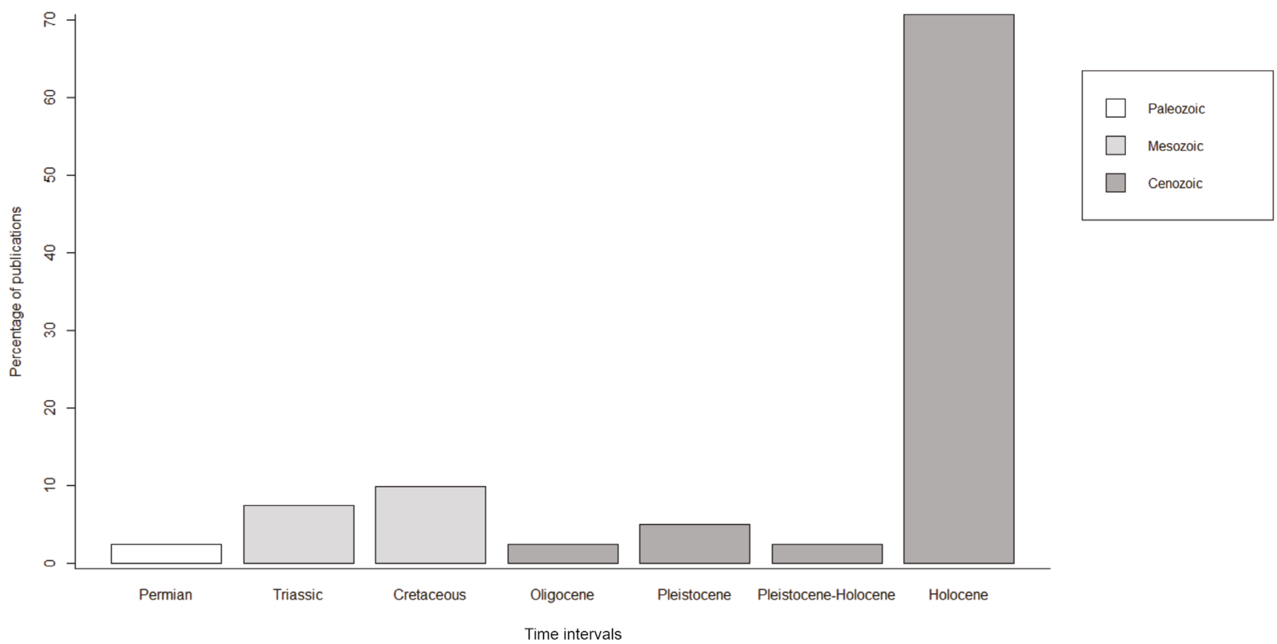


Figure 3. Percentage of publications per time intervals.
Figura 3. Porcentagem de publicações por intervalos de tempo.

CONCLUSION

Studies on fossils and subfossils collected in Brazil play an important role in the scientific community, since they improve the current knowledge about parasite distribution in South America during the Phanerozoic eon and have been consolidating Paleoparasitology as a global science during the last two centuries. It is noteworthy that the lack of studies in certain states, lithostratigraphic units or geological time intervals does not necessarily reflect the absence of samples, but issues related to low paleoparasitological researcher efforts. Furthermore, the present study was specifically focused on the analysis of 40 published and peer-reviewed scientific articles and a single conference abstract. There is still a huge number of master's dissertations, doctoral theses and other conference abstracts describing results that have not been formally published and, therefore, were not considered here as object of our study. This leads to a subnotification of occurrences and may indicates that the record is even wider than that reported here. It is crucial to highlight the importance of Paleoparasitology both inside and outside academic means, taking advantage of scientific papers and of teaching actions directed to the general public. Such actions will help disseminating the growing prominence of Paleoparasitology, turning it less hermetic and attracting new researchers to the study of previously unexplored parasites in national unearthed fossils and subfossils.

REFERENCES

Agustín, B.; Julián, F.F.; Ornela, B.M. 2021. Carnivore coprolites from "Gruta del Indio" site as source of paleoparasitological and paleoecological evidences (late Pleistocene-Holocene, Mendoza, Argentina). *Archaeological and Anthropological Sciences*, **13**:1-14. *doi: 10.1007/s12520-021-01272-w*

Araújo, A.; Ferreira, L.F.; Confalonieri, U.; Chame, M.; Ribeiro, B. 1989. *Strongyloides ferreirai* Rodrigues, Vicente & Gomes, 1985 (Nematoda, Rhabdiasoidea) in rodent coprolites (8.000-2.000 years BP), from archaeological sites from Piauí, Brazil. *Memórias do Instituto Oswaldo Cruz*, **84**:493-496. *doi: 10.1590/S0074-02761989000400006*

Araújo, A.J.G.; Confalonieri, U.E.C.; Ferreira, L.F. 1984. Encontro de ovos de trichostrongylideo e *Trichuris trichiura* em corpo mumificado do período colonial brasileiro. *CBS - Centro de Ciências Biológicas e da Saúde, Universidade Gama Filho*. 11-16.

Araújo, A.J.G.; Ferreira, L.F.; Confalonieri, U.E.C. 1981. A contribution to the study of helminth findings in archaeological material in Brazil. *Revista Brasileira de Biologia*, **41**:873-881.

Ardelean, C.F. *et al.* 2020. Evidence of human occupation in Mexico around the Last Glacial Maximum. *Nature*, **584**:87-92.

Aureliano, T.; Nascimento, C.S.I.; Fernandes, M.A.; Ricardi-Branco, F.; Ghilardi, A.M. 2021. Blood parasites and acute osteomyelitis in a non-avian dinosaur (Sauropoda, Titanosauria) from the Upper Cretaceous Adamantina Formation, Bauru Basin, Southeast Brazil. *Cretaceous Research*, **118**:1-11. *doi: 10.1016/j.cretres.2020.104672*

Beltrame, M.O.; Bellusci, A.; Andrade, A. 2018. First paleoparasitological study of micromammal coprolites from the holocene of the Somuncurá Plateau Protected Natural Area (Patagonia Argentina). *Parasitology International*, **67**:362-365. *doi: 10.1016/j.parint.2018.02.005*

Beltrame, M.O.; Cañal, V.; Llano, C.; Barberena, R., 2020. Macroparasites of megamammals: The case of a Pleistocene-Holocene extinct ground sloth from northwestern Patagonia, Argentina. *Quaternary International*, **568**:36-42. *doi: 10.1016/j.quaint.2020.09.030*

Beltrame, M.O.; Fernández, F.J.; Sardella, N.H., 2015a. Reptile and rodent parasites in raptor pellets in an archaeological context: the case of Epullan Chica (northwestern Patagonia, Argentina). *Quaternary Science Reviews*, **119**:1-10. *doi: 10.1016/j.quascirev.2015.04.014*

Beltrame, M.O.; Fernández, F.J.; Sardella, N.H. 2015b. First paleoparasitological record of acanthocephalan eggs from Northwestern Patagonia (Late Holocene, Argentina). *Acta Tropica*, **146**:33-35. *doi: 10.1016/j.actatropica.2015.02.019*

Beltrame, M.O.; Fugassa, M.H.; Barberena, R.; Sauthier, D.E.U.; Sardella, N.H. 2013. New record of anoplocephalid eggs (Cestoda: Anoplocephalidae) collected from rodent coprolites from archaeological and paleontological sites of Patagonia, Argentina. *Parasitology International*, **62**:431-434. *doi: 10.1016/j.parint.2013.04.004*

Beltrame, M.O.; Fugassa, M.H.; Sardella, N.H.; Civalero, M.T.; Aschero, C. 2011. Raptor pellets as zooarchaeological material for paleoparasitological studies in Patagonia. *Journal of Archaeological Science*, **38**:1511-1515. *doi: 10.1016/j.jas.2011.02.016*

Beltrame, M.O.; Sardella, N.H.; Fugassa, M.H.; Barberena, R. 2012. A palaeoparasitological analysis of rodent coprolites from the Cueva Huenul 1 archaeological site in Patagonia (Argentina). *Memórias do Instituto Oswaldo Cruz*, **107**:604-608. *doi: 10.1590/S0074-02762012000500006*

Beltrame, M.O.; Tietze, E.; Cañal, V.; Barberena, R.; Quintana, S. 2022. Paleogenetic and microscopic studies of Eimeria spp. (Apicomplexa: Eimeriidae) as a tool to reveal the zoological origin of coprolites: The case of study of artiodactyl coprolites from an archeological site from Patagonia, Argentina. *The Holocene*, **32**:1-7. *doi: 10.1177/09596836221114287*

Beltrame, M.O.; Tietze, E.; Pérez, A.E.; Bellusci, A.; Sardella, N.H. 2017. Ancient parasites from endemic deer from "CUEVA PARQUE DIANA" archeological site, Patagonia, Argentina. *Parasitology Research*, **116**:1523-1531. *doi: 10.1007/s00436-017-5429-7*

Brachaniec, T.; Niedzwiedzki, R.; Surmik, D.; Krzykawski, T.; Szopa, K.; Gorzelak, P.; Salamon, M.A. 2015. Coprolites of marine vertebrate predators from the Lower Triassic of southern Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **435**:118-126. *doi: 10.1016/j.palaeo.2015.06.005*

Camacho, M.; Pessanha, T.; Leles, D.; Dutra, J.M.F.; Silva, R.; Souza, S.M.; Araujo, A. 2013. Lutz's spontaneous sedimentation technique and the paleoparasitological analysis of sambaqui (shell mound) sediments. *Memórias do Instituto Oswaldo Cruz*, **108**:155-159. *doi: 10.1590/0074-0276108022013005*

Cardia, D.F.F.; Bertini, R.J.; Camossi, L.G.; Letizio, L.A. 2018. The first record of Ascaridoidea eggs discovered in Crocodyliformes hosts from the Upper Cretaceous of Brazil. *Revista Brasileira de Paleontologia*, **21**:238–244. *doi: 10.4072/rbp.2018.3.04*

Cardia, D.F.F.; Bertini, R.J.; Camossi, L.G.; Letizio, L.A. 2019a. First record of Acanthocephala parasites eggs in coprolites preliminary assigned to Crocodyliformes from the Adamantina Formation (Bauru Group, Upper Cretaceous), São Paulo, Brazil. *Anais da Academia Brasileira de Ciências*, **91**:1-10. *doi: 10.1590/0001-3765201920170848*

Cardia, D.F.F.; Bertini, R.J.; Camossi, L.G.; Letizio, L.A. 2019b. Two new species of ascaridoid nematodes in Brazilian Crocodylomorpha from the Upper Cretaceous. *Parasitology International*, **72**:1-5. *doi: 10.1016/j.parint.2019.101947*

Cardia, D.F.F.; Bertini, R.J.; Camossi, L.G.; Richini-Pereira, V.B.; Losnak, D.O.; Francischini, H.; Dentzien-Dias, P. 2021. Paleoparasitological analysis of a coprolite assigned to a carnivoran mammal from the Upper Pleistocene Touro Passo Formation, Rio Grande do Sul, Brazil. *Anais da Academia Brasileira de Ciências*, **93**:1-13. *doi: 10.1590/0001-3765202120190876*

Carmo, G.M.; Garcia, R.A.; Vieira, F.M.; Lima, S.S.; Araújo-Júnior, H.I.; Pinheiro, R.M. 2023. Paleoparasitological study of avian trace fossils from the Tremembé Formation (Oligocene of the Taubaté Basin), São Paulo, Brazil. *Journal of South American Earth Sciences*, **125**:1-8. *doi: 10.1016/j.jsames.2023.104319*

Cohen, K.M.; Harper, D.A.T.; Gibbard, P.L. 2023. ICS International Chronostratigraphic Chart 2023/06. International Commission on Stratigraphy, IUGS. Available at www.stratigraphy.org; accessed on 10/20/2023.

Confalonieri, U.E.; Araújo, A.J.G.; Ferreira, L.F. 1981. *Trichuris trichiura* infection in colonial Brazil. *Paleopathology newsletter*, 13-14.

Darling, S.T. 1920. Observations on the geographical and ethnological distribution of hookworms. *Parasitology*, **12**:217-233. *doi: 10.1017/S0031182000014207*

Dentzien-Dias, P.; Carrillo-Briceño, J.D.; Francischini, H.; Sánchez, R. 2018. Paleoecological and taphonomical aspects of the Late Miocene vertebrate coprolites (Urumaco Formation) of Venezuela. *Palaeogeography, Palaeoclimatology, Palaeoecology*. **490**:590-603. *doi: 10.1016/j.palaeo.2017.11.048*

Dentzien-Dias, P.C.; Poinar Jr, G.; Figueiredo, A.E.Q.; Pacheco, A.C.L.; Horn, B.L.D.; Schultz, C.L. 2013. Tapeworm Eggs in a 270 Million-Year-Old Shark Coprolite. *PLoS ONE*, **8**:1-4. *doi: 10.1371/journal.pone.0055007*

Faulkner, C.T.; Patton, S.; Johnson, S.S. 1989. Prehistoric Parasitism in Tennessee: Evidence from the Analysis of Desiccated Fecal Material Collected from Big Bone Cave, Van Buren County, Tennessee. *The Journal of Parasitology*, **75**:461-463. doi: *10.2307/3282606*

Faulkner, C.T. 1991. Prehistoric Diet and Parasitic Infection in Tennessee: Evidence from the Analysis of Desiccated Human Paleofeces. *American Antiquity*, **56**:687-700. *doi: 10.2307/281546*

Fernandes, A.; Iñiguez, A.M.; Lima, V.S.; Souza, S.M.F.M.; Ferreira, L.F.; Vicente, A.C.P.; Jansen, A.M. 2008. Pre-Columbian Chagas disease in Brazil: *Trypanosoma cruzi* I in the archaeological remains of a human in Peruaçu Valley, Minas Gerais, Brazil. *Memórias do Instituto Oswaldo Cruz*, **103**:514-516. *doi: 10.1590/S0074-02762008000500021*

Ferreira, L.F.; Araújo, A.; Confalonieri, U.; Chame, M. 1989b. Acanthocefalan eggs in animal coprolites from archaeological sites from Brazil. *Memórias do Instituto Oswaldo Cruz*, **84**:201-203. *doi: 10.1590/S0074-02761989000200007*

Ferreira L.F.; Araújo, A.; Confalonieri, U.; Lima, J.M.D. 1989a. *Trichuris trichiura* eggs in human coprolites from the archaeological site of "Furna do Estrago", Brejo da Madre de Deus, Pernambuco, Brazil. *Memórias do Instituto Oswaldo Cruz*, Rio de Janeiro, **84**:581. *doi: 10.1590/S0074-02761989000400020*

Ferreira, L.F.; Araújo, A.; Confalonieri, U.; Chame, M.; Gomes, D.C. 1991. *Trichuris* eggs in animal coprolites dated from 30,000 years ago. *Journal of Parasitology*, **77**:491-493. *doi: 10.2307/3283143*

Ferreira, L.F.; Araújo, A.; Confalonieri, U.; Chame, M.; Ribeiro, B. 1992. *Eimeria* oocysts in deer coprolites dated from 9000 years BP. *Memórias do Instituto Oswaldo Cruz*, **87**:105-106. *doi: 10.1590/S0074-02761992000500021*

Ferreira, L.F.; Araújo, A.; Confalonieri, U.; Chame, M.; Ribeiro, B.M. 1987. Encontro de ovos de ancilostomídeos em coprólitos humanos datados de 7230 ± 80 anos, Piauí, Brasil. *Anais da Academia Brasileira de Ciências*, **59**:280-281.

Ferreira, L.F.; Araújo, A.J.G.; Confalonieri, U.E.C. 1980. The finding of eggs and larvae of parasitic helminths in archaeological material from Unai, Minas Gerais, Brazil. *Transactions of The Royal Society of Tropical Medicine and Hygiene*, **74**:798-800. *doi: 10.1016/0035-9203(80)90205-9*

Ferreira, L.F.; Araújo, A.J.G.; Confalonieri, U.E.C. 1983. The finding of helminth eggs in a Brazilian mummy. *Transactions of The Royal Society of Tropical Medicine and Hygiene*, **77**:65-67. *doi: 10.1016/0035-9203(83)90017-2*

Ferreira, L.F.; Araujo, A.J.G.; Confalonieri, U. 1979. Subsídios para a paleoparasitologia do Brasil - I. Parasitos encontrados em coprólitos no município de Unaí, MG. *In*: CONGRESSO DA SOCIEDADE BRASILEIRA DE PARASITOLOGIA, 4, 1979. Campinas, p. 66.

Ferreira, L.F.; Araújo, A.; Duarte, A.N. 1993. Nematode Larvae in Fossilized Animal Coprolites from Lower and Middle Pleistocene Sites, Central Italy. *The Journal of Parasitology*, **79**:440-442. *doi: 10.2307/3283583*

Flammer, P.G.; Smith, A. L. 2020. Intestinal helminths as a biomolecular complex in archaeological research. *Philosophical Transactions of the Royal Society B.*, **375**:1-9. *doi: 10.1098/rstb.2019.0570*

Francischini, H.; Dentzien-Dias, P.; Schultz, C.L. 2017. A fresh look at ancient dungs: the Brazilian Triassic coprolites revisited. *Lethaia*, **51**:389–405. *doi: 10.1111/let.12251*

Fugassa, M.H.; Fernández, P.M.; Bellelli, C.; Calatayud, M.C. 2022. Assessing parasite epidemiology in the epidemiological importance of Patagonian Late Holocene rockshelters using carnivore coprolites in the past: new data from Piedra Parada, Argentina. *Parasitology*, **149**:1556-1564. *doi: 10.1017/S0031182022001020*

Fugassa, M.H.; Olivera, E.A.G.; Petrigh, R.S. 2013. First palaeoparasitological record of a dioctophymatid egg in an archaeological sample from Patagonia. *Acta Tropica*, **128**:175-177. *doi: 10.1016/j.actatropica.2013.06.001*

Goater, T.M.; Goater, C.P.; Esch, G.W. 2014. Parasitism The Diversity and Ecology of Animal Parasites. 2nd Edition. USA, Cambridge University Press, 510 p. *doi: 10.1111/bij.12526*

Gonçalves, M.L.C.; Araújo, A.; Duarte, R.; Silva, J.P.; Reinhard, K.; Bouchet, F.; Ferreira, L.F. 2002b. Detection of *Giardia duodenalis* antigen in coprolites using a commercially available enzyme-linked immunosorbent assay. *Transactions of the Royal Society of tropical medicine and hygiene*, **96**:640-643. *doi: 10.1016/s0035-9203(02)90337-8*

Gonçalves, M.L.C.; Araújo, A.; Ferreira, L.F. 2002a. Paleoparasitologia no Brasil. *Ciência Saúde Coletiva*, **7**:191–196. *doi: 10.1590/S1413-81232002000100018*

Gonçalves, M.L.C.; Araújo, A.; Ferreira, L.F. 2003. Human Intestinal Parasites in the Past: New Findings and a Review. *Memórias do Instituto Oswaldo Cruz*, Rio de Janeiro, **98**:103-118. *doi: 10.1590/S0074-02762003000900016*

Guedes, L.; Borba, V.H.; Camacho, M.; Neto, J.; Dias, O.; Iñiguez, A.M. 2020. African helminth infection out of Africa: Paleoparasitological and paleogenetic investigations in Pretos Novos cemetery, Rio de Janeiro, Brazil (1769–1830). *Acta Tropica*, **205**:1-6. *doi: 10.1016/j.actatropica.2020.105399*

Holland, C. *et al*. 2022. Global prevalence of *Ascaris* infection in humans (2010–2021): a systematic review and meta-analysis. *Infectious Diseases of Poverty*, **11**:113. *doi: 10.1186/s40249-022-01038-z*

Hugot, J.P.; Gardner, S.L.; Borba, V.; Araujo, P.; Leles, D.; Da-Rosa, A.A.S.; Dutra, J.; Ferreira, L.F.; Araújo, A. 2014. Discovery of a 240 million year old nematode parasite egg in a cynodont coprolite sheds light on the early origin of pinworms in vertebrates. *Parasites & Vectors*, **7**:1-8. *doi: 10.1186/s13071-014-0486-6*

Iñiguez, A.M.; Brito, L.; Guedes, L.; Chaves, S.A.M. 2022. Helminth infection and human mobility in sambaquis: Paleoparasitological, paleogenetic, and microremains investigations in Jabuticabeira II, Brazil (2890±55 to 1805±65 BP). *The Holocene*, **32**:200-207. *doi: 10.1177/09596836211060490*

Jaeger, L.H.; Taglioretti, V.; Dias, O.; Iñiguez, A.M. 2013a. Paleoparasitological analysis of human remains from a European cemetery of the 17th–19th century in Rio de Janeiro, Brazil. *International Journal of Paleopathology*, **3**:214-217. *doi: 10.1016/j.ijpp.2013.04.001*

Jaeger, L.H.; Taglioretti, V.; Fugassa, M.H.; Dias, O.; Neto, J.; Iñiguez, A.M. 2013b. Paleoparasitological results from XVIII century human remains from Rio de Janeiro, Brazil. *Acta Tropica*, **125**:282-286. *doi: 10.1016/j.actatropica.2012.11.007*

Jouy-Avantin, F.; Combes, C.; Lumley (De), H.; Miskovsky, J-C.; Moné, H. 1999. Helminth Eggs in Animal Coprolites from a Middle Pleistocene Site in Europe. *The Journal of Parasitology*, **85**:376-379. *doi: 10.2307/3285652*

Leles, D.; Araújo, A.; Ferreira, L.F.; Vicente, A.C.P.; Iñiguez, A.M. 2008. Molecular paleoparasitological diagnosis of *Ascaris* sp. from coprolites: new scenery of ascariasis in pre-Columbian South America times. *Memórias do Instituto Oswaldo Cruz*, **103**:106-108. *doi: 10.1590/s0074-02762008005000004*

Leles, D. *et al*. 2018. Methodological innovations for the study of irreplaceable samples reveal giardiasis in extinct animals (*Nothrotherium maquinense* and *Palaeolama major*). *Parasitology International*, **67**:776-780. *doi: 10.1016/j.parint.2018.07.011*

Lima, V.S.; Iñiguez, A.M.; Otsuki, K.; Ferreira, L.F.; Araújo, A.; Vicente, A.C.P.; Jansen, A.M. 2008. Chagas Disease in Ancient Hunter-Gatherer Population, Brazil. *Emerging Infectious Diseases*, **14**:1001–1002. *doi: 10.3201/eid1406.0707*

Lino, M.; Leles, D.; Peña, A.P.; Vinaud, M.C. First description of *Enterobius vermicularis* egg in a coprolite dated from the pre-contact in Brazil. *Journal of Archaeological Science: Reports*, **17**, 2018. *doi: 10.1016/j.jasrep.2017.10.038*

Loreille, O.; Bouchet, F. 2003. Evolution of Ascariasis in Humans and Pigs: a Multi-disciplinary Approach. *Memórias do Instituto Oswaldo Cruz*, **98**:39-46. *doi: 10.1590/S0074-02762003000900008*

McConnell, S.M.; Zavada, M.S. 2013. The occurrence of an abdominal fauna in an articulated tapir (*Tapirus polkensis*) from the Late Miocene Gray Fossil Site, northeastern Tennessee. *Integrative Zoology*, **8**:74–83. *doi: 10.1111/j.1749-4877.2012.00320.x*

Montenegro, A.; Araújo, A.; Eby, M.; Ferreira, L.F.; Hetherington, R.; Weaver, A.J. 2006. Parasites, Paleoclimate, and the Peopling of the Americas: Using the Hookworm to Time the Clovis Migration. *Current Anthropology*, **47**:193-200. *doi: 10.1086/499553*

Noronha, D.; Ferreira, L.F.; Rangel, A.; Araujo, A.; Gomes, D.C. 1994. *Echinopardalis* sp. (Acanthocephala, Oligacanthorhynchidae) eggs in felid coprolites dated from 9,000 years before present, found in the Brazilian northeast. *Memórias do Instituto Oswaldo Cruz*, **89**:119-120. *doi: 10.1590/S0074-02761994000100022*

Novo, S.P.C.; Ferreira, L.F. 2016. The Paleoparasitology in Brazil and Findings in Human Remains from South America: A Review. *Korean Journal of Parasitology*, **54**:573-583. *doi: 10.3347/kjp.2016.54.5.573*

Novo, S.P.C.; Leles, D.; Bianucci, R.; Araujo, A. 2015. *Leishmania tarentolae* molecular signatures in a 300 hundred-years-old human Brazilian mummy. *Parasites & Vectors*, **8**:1-8. *doi: 10.1186/s13071-015-0666-z*

Nunes, V.H.B.; Alcover, J.A.; Silva, V.L.; Cruz, P.B.; Machado-Silva, J.R.; Araújo, A.J.G. 2017. Paleoparasitological analysis of the extinct *Myotragus balearicus* Bate 1909 (Artiodactyla, Caprinae) from Mallorca (Balearic Islands, Western Mediterranean). *Parasitology International*, **66**:7-11. *doi: 10.1016/j.parint.2016.11.009*

Oyarzún-Ruiz, P.; Pérez-Espinosa, S.A.; González-Saldías, F.; Martin, F.; Moreno, L. 2021. Paleoparasitological survey of coprolites of Darwin's ground sloth *Mylodon darwini* (Xenarthra, Folivora: Mylodontidae) from Cueva del Milodón Natural Monument, Chilean Patagonia. *Archaeological and Anthropological Sciences*, **13**:1-8. *doi: 10.1007/s12520-021-01383-4*

Pedro, S.B.; Osuna, A.; Buscalioni, A.D. 2020. Helminth eggs from early cretaceous faeces. *Scientific reports*, **10**:1-8. *doi: 10.1038/s41598-020-75757-4*

Pereira, F.B.; Luque, J.L.; Tavares, L.E.R. 2018. Integrative approach on Pharyngodonidae (Nematoda: Oxyuroidea) parasitic in reptiles: Relationship among its genera, importance of their diagnostic features, and new data on *Parapharyngodon bainae*. *PLoS ONE*, **13**:1-16. *doi: 10.1371/journal.pone.0200494*

Perri, A.R.; Heinrich, S.; Gurarieh, S.; Saunders, J.J. 2017. Earliest Evidence of *Toxocara* sp. in a 1.2-Million-Year-Old Extinct Hyena (*Pachycrocuta brevirostris*) Coprolite from Northwest Pakistan. *The Journal of Parasitology*, **103**:138-141. *doi: 10.1645/16-71*

Petrigh, R.S.; Velázquez, N.J.; Fugassa, M.H.; Burry, L.S.; Mondini, M.; Korstanje, M.A. 2021. Herbivore coprolites from the South-Central Andes. A multiproxy study at Los Viscos Archaeological Site, Catamarca, Argentina. *Journal of Archaeological Science*, **38**:1-12. *doi: 10.1016/j.jasrep.2021.103063*

Poinar, G.; Boucot, J. 2006. Evidence of Intestinal Parasites of Dinosaurs. *Parasitology*, **133**:245-249. *doi: 10.1017/S0031182006000138*

Ramirez, D.A.; Herrera-Soto, M.J.; Andreu, J.G.; Santana-Sagredo, F.; Rodríguez, M.U.; Nores, R. 2023. Gastrointestinal parasites in ancient South American camelid feces from the Atacama Desert (Pampa del Tamarugal, Tarapacá, northern Chile). *Archaeometry*, **65**:1073–1089. *doi: 10.1111/arcm.12862*

Reinhard, K.J. 1988. Cultural Ecology of Prehistoric Parasitism on the Colorado Plateau as Evidenced by Coprology. *American Journal of Physical Anthropology*, **77**:355-366. *doi: 10.1002/ajpa.1330770308*

Reinhard, K.J.; Hevly, R.H.; Anderson, G.A. 1987. Helminth Remains from Prehistoric Indian Coprolites on The Colorado Plateau. *Journal of Parasitology*, **73**:630-639. *doi: 10.2307/3282147*

Ruffer, M.A. 1910. Note on The Presence of "*Bilharzia haematobia*" in Egyptian Mummies of the Twentieth Dynasty [1250-1000 B.C.]. *The British Medical Journal*, **1**:2557. *doi: 10.1136/bmj.1.2557.16-a*

Santoro, C.; Vinton, S.D.; Reinhard, K.J. 2003. Inca Expansion and Parasitism in the Lluta Valley: Preliminary Data. *Memórias do Instituto Oswaldo Cruz*, Rio de Janeiro, **98**:161-163. *doi: 10.1590/s0074-02762003000900024*

Sardella, N.H.; Fugassa, M.H. 2009. Paleoparasitological Analysis of Rodent Coprolites in Holocenic Samples from Patagonia, Argentina. *Journal of Parasitology*, **95**:646-651. *doi: 10.1645/GE-1809.1*

Schmidt, G.D.; Duszynski, D.W.; Martin, P.S. 1992. Parasites of the Extinct Shasta Ground Sloth, *Nothrotheriops shastensis*, in Rampart Cave, Arizona. *The Journal of Parasitology*, **78**:811-816. *doi: 10.2307/3283310*

Sianto, L.; Duarte, A.N.; Borba, V.H.; Magalhães, J.G.; Souza, S.M.; Chame, M. 2016. Echinostomes in Felid Coprolites from Brazil. *Journal of Parasitology*, **102**:385-387. *doi: 10.1645/15-819*

Sianto, L.; Reinhard, K.J.; Chame, M.; Chaves, S.; Mendonça, S.; Gonçalves, M.L.C.; Fernandes, A.; Ferreira, L.F.; Araújo, A. 2005. The Finding of *Echinostoma* (Trematoda: Digenea) and Hookworm Eggs in Coprolites Collected from a Brazilian Mummified Body Dated 600–1,200 Years Before Present. *Journal of Parasitology*, **91**:972-975. *doi: 10.1645/GE-3445RN.1*

Sianto, L.; Souza, M.V.; Chame, M.; Luz, M.F.; Guidon, N.; Pessis, A.; Araújo, A. 2014. Helminths in feline coprolites up to 9000 years in the Brazilian Northeast. *Parasitology International*, **63**:851-857. *doi: 10.1016/j.parint.2014.08.002*

Sianto, L.; Teixeira-Santos, I.; Chame, M.; Chaves, S.M.; Souza, S.M.; Ferreira, L.F.; Reinhard, K.; Araujo, A. 2012. Eating lizards: a millenary habit evidenced by Paleoparasitology. *BMC Research Notes*, **5**:1-4. *doi: 10.1186/1756-0500-5-586*

Silva, P.A.; Borba, V.H.; Dutra, J.M.F.; Leles, D.; Da-Rosa, A.A.S.; Fereira, L.F.; Araujo, A. 2014. A new ascarid species in cynodont coprolite dated of 240 million years. *Anais da Academia Brasileira de Ciências*, **86**:265-269. *doi: 10.1590/0001-3765201320130036*

Sivkova, T.N.; Kosintsev, P.A. 2021. First Find of Eggs of the Nematode *Baylisascaris transfuga* Rudolphi, 1819 (Ascaridoidea, Nematoda) in the Late Pleistocene. *Doklady Biological Sciences*, **499**:103–104. *doi: 10.1134/S0012496621040062*

Soper, F. L. 1927. The Report of a Nearly Pure *Ancylostoma duodenale* Infestation in Native South American Indians and a Discussion of its Ethnological Significance. *American Journal of Hygiene*, **7**:174-184. *doi: 10.1093/oxfordjournals.aje.a120409*

Souza, M.V.; Chame, M.; Souza, S.M.F.M.; Felice, G.D.; Guildon, N.; Sianto, L. 2020. New parasite occurences in *Tamandua tetradactyla* (Pilosa: Myrmecophagidae) in the northeast of Brazil: a paleoparasitological study. *Oecologia Australis*, **2**:141–153. *doi: 10.4257/oeco.2020.2401.11*

Souza, M.V.; Sianto, L.; Chame, M.; Ferreira, L.F.; Araújo, A. 2012. *Syphacia* sp. (Nematoda: Oxyuridae) in coprolites of *Kerodon rupestris* Wied, 1820 (Rodentia: Caviidae) from 5,300 years BP in northeastern Brazil. *Memórias do Instituto Oswaldo Cruz*, **107**:539-542. *doi: 10.1590/S0074-02762012000400015*

Souza, M.V.; Silva, L.G.R.; Silva-Pinto, V.; Mendez-Quiros, P.; Chaves, S.A.M.; Iñiguez, A. M. 2018. New Paleoparasitological

Investigations from the Pre-Inca to Hispanic Contact Period in northern Chile. *Acta Tropica*, **178**:290-296. *doi: 10.1016/j.actatropica.2017.11.021*

Szidat, L. 1944. Über die Erhaltungsfähigkeit von Helmintheneierm in vor-und Fühgeschichtlichen Moorleichen. *Zeitschrift für Parasitenkunde*, **13**:265-274.

Taglioretti, V.; Fugassa, M.H.; Sardella, N.H. 2015. Parasitic diversity found in coprolites of camelids during the Holocene. *Parasitology Research*, **114**:2459-2464. *doi: 10.1007/s00436-015-4442-y*

Tietze, E.; Barberena, R.; Beltrame, M.O. 2019. Parasite Assemblages from Feline Coprolites through the Pleistocene-Holocene Transition in Patagonia: Cueva Huenul 1 Archaeological Site (Argentina). *Environmental Archaeology*, **0**:1-11. *doi: 10.1080/14614103.2019.1689893*

Tietze, E.; Tommaso, D.; Beltrame, M.O. 2020. Parasites in micromammal fecal pellets throughout the Late Holocene ("Cueva Peligro" paleontological site, Patagonia, Argentina). *Parasitology International*, **78**:1-8. *doi: 10.1016/j.parint.2020.102147*

Tweet, J.; Chin, K.; Ekdale, A.A. 2016. Trace fossils of possible parasites inside the gut contents of a hadrosaurid dinosaur, Upper Cretaceous Judith River Formation, Montana. *Journal of Paleontology*, **90**:279–287. *doi: 10.1017/jpa.2016.43*

Verde, M.; Ubilla, M. 2002. Mammalian Carnivore Coprolites from the Sopas Formation (Upper Pleistocene, Lujanian Stage), Uruguay. *Ichnos*, **9**:77-80. *doi: 10.1080/10420940216406*

Wood, J.R.; Díaz, F.P.; Latorre, C.; Wilmshurst, J.M.; Burge, O.R.; González, F. Gutiérrez, R.A. 2019. Ancient parasite DNA from late Quaternary Atacama Desert rodent middens. *Quaternary Science Reviews*, **226**:1-12. *doi: 10.1016/j.quascirev.2019.106031*

Wood, J.R.; Wilmshurst, J.M.; Rawlence, N.J.; Bonner, K.I.; Worthy, T.H.; Kinsella, J.M.; Cooper, A. 2013. A Megafauna's Microfauna: Gastrointestinal Parasites of New Zealand's Extinct Moa (Aves: Dinornithiformes). *PLoS ONE*, **8**:1-9. *doi: 10.1371/journal.pone.0057315*

Zar, J.H. 2010. Biostatistical Analysis. 5th Edition. USA, Pearson Prentice Hall, 944 p.