Gastrointestinal parasite diversity of South American camelids (Artiodactyla: Camelidae): First review throughout the native range of distribution

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ABSTRACT

In South America inhabit an endemic group of ungulates adapted to extreme environments: the South American camelids (SAC), a key component of the Andean biocultural heritage. Until today, SAC are the most important factor of Andean economies and social and ritual life. SAC include two wild species, the guanaco (Lama guanicoe) and the vicuña (Vicugna vicugna), and two domestic species, the llama (Lama glama) and the alpaca (Vicugna pacos). Endoparasitosis are one of the most common diseases in SAC, and have great economic and health relevance. Despite this, there is a lack of knowledge on this concern. The main objective of this work was to conduct the first systematic review of the diversity of gastrointestinal parasites of SAC throughout the entire native range of distribution and to identify several gaps in knowledge. The PRISMA protocol was performed and a total of 101 documents were summarized. At least 36 parasitic helminths and five Eimeria spp. were registered. This work highlights the need for a greater number of works to know with more certainty the parasitic fauna of camelids in the past and present, in order to achieve predictions that allow proper management of camelids for their future conservation. Furthermore, concerted research efforts are needed to understand the biology, epidemiology, diagnosis and distribution of the parasitosis of SAC along the entire distribution range to guide conservation decisions.

1. Introduction

The South American camelids (SAC) (Artiodactyla, Camelidae) are a key component of the Andean biocultural heritage (Vilá and Arzamendia, 2020) and have occupied a central role in the development of Andean societies, both for ancient hunter-gatherers and for more recent pastoralists and farmers. SAC were the most important factor in Andean economies and social and ritual life throughout time. SAC include two wild species, the guanaco (Lama guanicoe) and the vicuña (Vicugna vicugna); and two domestic species, the llama (Lama glama) and the alpaca (Vicugna pacos) (Wheeler et al., 2006; Yacobaccio, 2021). This is an endemic group of ungulates adapted to extreme environments with a wide distribution in arid and semiarid ecosystems from Argentina, Bolivia, Chile, Ecuador and Peru, mainly from 3000 to 5000 m.a.s.l. (Franklin, 2011). The original distribution of SAC includes the Andean high-altitude grasslands, the Altiplano and the Patagonian arid steppes (Vilá and Arzamendia, 2020). The distribution of guanacos includes a wide diversity of open habitats and temperate forest environments of Peru, Bolivia, Chile and Argentina, including Patagonian steppes. The distribution of vicuñas is limited to Northern Argentina, Chile, Peru and Bolivia, restricted to high-altitude Puna environments, above 3400 m.a.s.l. (Vilá, 2012). In pre-Hispanic times, llamas inhabit the Andean regions of Peru, Bolivia, Argentina and Chile and the alpacas were restricted to high and humid environments from the Puna of Peru, Bolivia and Chile (Yacobaccio, 2021). Under the dominion of the Incas (1470–1532), the llama distribution reached the southern Colombia and central Chile. There is no evidence of the presence of alpacas in pre-Columbian sites from Argentina (Olivera and Grant, 2009) and Ecuador (Miller and Gill, 1990) being introduced in these regions later.

Today, husbandry of SAC is an important socioeconomic activity for the Andean populations of South America. Recently, the breeding of domestic camelids also began to have great interest in other parts of the world. Numerous publications have been reported the relevance of parasites of SAC. Endoparasitosis are one of the most common diseases

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of SAC and have great economic and health relevance. Host-specific parasites and generalistic parasites shared with domestic ruminants such as sheep and goats are well known and have been widely described in the literature (e.g. Navone and Merino 1989; Leguia, 1991; Belo-
demenico et al., 2003; Aguirre and Cafrune, 2007; Arias-Pacheco et al., 2021). It is known that camelids are parasitized by gastrointestinal nematodes, trematodes and cestodes, and by coccidians, among other parasites. Many of them can cause serious diseases (Fowler, 2010) and can be transmitted to humans, including hydatidosis, fascioliasis, sarccystosis and toxoplasmosis. The knowledgement of the diversity, spread, and evolution of parasites of SAC play a very important role in the understanding of the behavioral ecology, health, and camels conservation. Despite this, there is a lack of knowledge about a global vision of gastrointestinal parasite diversity throughout the entire distribution range. The main objective of this work was to conduct the first systematic review of the diversity of gastrointestinal parasites of SAC throughout the native range of distribution and to identify several gaps in knowledge.

2. Materials and methods

The research was conducted using the systematic approach of the Preferred Reporting Items for Systematic Review and Meta-Analyses (PRISMA) protocol guidelines (Shamseer et al., 2015).

2.1. Selection criteria

The literature used in this review included publications reporting on gastrointestinal parasites of SAC. The following list gives the criteria used in the selection of publications.

The inclusion criteria were:
- Scientific peer-reviewed, scientific papers, conference proceedings and theses (PhD and MSc Thesis and Final Degree Projects) were included.
- Literature published in English and Spanish-written in order to include research with local, regional and global impact.
- Gastrointestinal parasite analysis of SAC in the natural range of distribution in order to conduct the first review in the subject and to identify gaps in knowledge.

The exclusion criteria were:
- Research papers conducted in SAC from sites outside the natural range of distribution.
- Research papers on topics other than gastrointestinal parasites of SAC.
Fig. 2. Geographical location of the documents compiled in the present review (red dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
Table 1
Gastrointestinal helminths and *Eimeria* spp. reported in alpacas (*Lama pacos*) across the entire nature distribution range. (* Calculated with published data, NR: no reported).

| Country      | Region         | No. tested samples | No. positive (%) | Reported parasites (%) | Remarks | Type of publication | Reference                  |
|--------------|----------------|--------------------|------------------|------------------------|---------|---------------------|----------------------------|
| Chile        | Valdivia       | 47                 | NR               | *Nematodirus spathiger* | Rectal samples | Scientific research  | Valenzuela et al. (1998)   |
|              | Arica-Parinacota | 494               | 52 (10.53)       | *Nematodirus filicolis*, *Ostertagia sp.* | Rectal samples | Only Fasciola study | Zamorano et al. (2012)     |
| Bolivia      | La Paz         | 22                 | (59.1)           | *Fasciola hepatica*    | Only abstract access | Scientific research | Ueno et al. (1975)         |
|              | Arica-Parinacota | 55                | 54 (98.0)        | *Eimeria punoensis (67.37)* | Fecal samples | Scientific research | Beltrán-Sanvedra et al. (2014) |
| Peru         | NR             | NR                 | NR               | *Nematodirus lamae*, *Lamanema chavezi*, *Nematodirus spathiger* | Only abstract access | Scientific research | Becklund (1963)           |
| Cuzco and Puno | 12              | NR                 | NR               | *Eimeria lama*, *Eimeria alpacae*, *Eimeria punoensis* | Rectal samples | Scientific research | Guerrero (1967)           |
| Puno         | NR             | NR                 | NR               | *Haemonchus sp.*, *Ostertagia sp.* | No access to original document | Scientific research | Guerrero (1970) (in Navone and Merino, 1989) |
| Cuzco        | 7              | NR                 | NR               | *Eimeria lama*, *Eimeria macusaniensis* | Fecal samples | First report E. macusaniensis | Guerrero et al. (1971) |
| Junín        | NR             | NR                 | NR               | *Eimeria punoensis*, *Eimeria ivitaensis*, *Eimeria macusaniensis* | Rectal samples | Only Eimeria study | Leguía and Casas (1998)   |
| Junín        | 280            | NR                 | NR               | *Fasciola hepatica (7.1)* | Rectal samples | First description | Neyra et al. (2002)       |
| Cuzco        | 7              | NR                 | NR               | *Eimeria lama*, *Eimeria macusaniensis* | Necropsy | Dead animals with clinical signs of diarrhea | Palacios et al. (2004) |
| Cuzco        | 48             | 11 (23.0)          | *Eimeria ivitaensis*, *Eimeria macusaniensis* | intestinal samples | Only Eimeria study | Palacios et al. (2005) |
| NR           | 40             | 12                 | *Fasciola hepatica* | Fecal samples | ELISA method | Scientific research | Li et al. (2005)           |

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Table 1 (continued)

| Country          | Region    | No. tested samples | No. positive (%) | Reported parasites (%)                                      | Remarks                                      | Type of publication | Reference                        |
|------------------|-----------|--------------------|------------------|------------------------------------------------------------|----------------------------------------------|---------------------|----------------------------------|
| Cuzco            | NR        | NR                |                  | Eimeria macusaniensis                                      | Only Fasciola study                         | Scientific research  | Palacios et al. (2006)           |
|                  |           |                   |                  | Eimeria ivitaensis                                          | Histopathological examination               |                     |                                  |
|                  |           |                   |                  | Fasciola hepatica                                           | Only Eimeria study                          |                     |                                  |
| Ayacucho         | 10        | (100)             |                  | Coccidia (25.44), Vermes (10.52), Dictyocaulus sp. (0.88)| Fecal and blood samples Necropsy            | Scientific research  | Ciprián (2007)                   |
| Puno             | NR        | (3.03)            |                  | Eimeria macusaniensis                                      | Necropsy                                     |                     | Paredes et al. (2009)            |
| Puno and Cuzco   | 108       | 33 (30.55)        |                  | Eimeria macusaniensis                                      | Intestinal samples                          | Scientific research  | Rosadio et al. (2010)           |
| South of Peru    | 316       |                   |                  | Eimeria macusaniensis                                      | Only Eimeria study                          | Scientific research  | Cordero et al. (2011) (in       |
|                  |           |                   |                  |                                                            |                                              |                     | Dubey, 2019)                   |
| Puno             | 60        | NR                |                  | Strongylus sp., Nematodirus sp., Lamanema chavezi          | Rectal samples                              | Scientific research  | Marino (2011)                   |
| Huancavelica     | 161       | NR                |                  | Eimeria spp. (31.37), Eimeria macusaniensis (4.3)         | Fecal samples Adults                        |                     | Rosadio et al. (2012)           |
| Puno             | 478       | 418 (87.5)        |                  | Eimeria lamae (60.4), Eimeria alpaca (45.6), Eimeria      | Fecal samples                               |                     | Rodríguez et al. (2012)         |
|                  |           |                   |                  | panoenuis (30.0), Eimeria macusaniensis (50.4), Eimeria   |                                              |                     |                                  |
|                  |           |                   |                  | ivitaeni (6.24)                                            |                                              |                     |                                  |
| Cuzco            | 30        | NR                |                  | Eimeria lamae, Eimeria alpaca, Eimeria panoenuis, Eimeria| Fecal samples                              | Thesis              | Mamani (2012)                   |
|                  |           |                   |                  | macusaniensis, Eimeria ivitaeni, Nematodirus spathiger,   |                                              |                     |                                  |
|                  |           |                   |                  | Lamanema chavezi, Trichures spp., Capillaria spp., Strongyliida |                        |                     |                                  |
| Huancavelica     | 366       | (59.02)           |                  | Eimeria spp.                                              | Rectal samples                              | Thesis              | Auris Bellido and Santiago      |
|                  |           |                   |                  |                                                            |                                              |                     | Cahuaus (2013)                  |
| Cuzco            | 1001      | Helminthes (68.4),|                  | Nematodirus (54.0), Strongylida (16.3), Trichures (17.5)| Rectal samples                              | Scientific research  | Pérez et al. (2014)            |
|                  |           | Eimeria spp. (61.5)|                  | Capillaria (5.1), Lamanema (4.5), Moniezia (6.3), Eimeria|                                              |                     |                                  |
|                  |           |                   |                  | alpaca (42.0), Eimeria panoenuis (31.0), Eimeria lamae (20.0)|                                              |                     |                                  |
|                  |           |                   |                  | Eimeria macusaniensis (7.0), Cooperia (40.0), Ostertagia (22.0)|                                              |                     |                                  |
|                  |           |                   |                  | Trichostrongylus (20.0), Oesophagostomum (16.0), Bonnotatum (2.0)|                                              |                     |                                  |
| Junín, Jauja     | 103       | (73.8)            |                  | Fasciola hepatica                                          | Rectal samples                              | Scientific research  | Flores et al. (2014)           |
| Puno             | 1319      | (63.9)            |                  | Nematodirus spp. (52.8), Strongylida (4.9), Trichures spp.| Rectal samples                              | Scientific research  | Contreras et al. (2014)         |
|                  |           |                   |                  | (10.8), Capillaria spp. (1.8), Lamanema spp. (0.7),       |                                              |                     |                                  |
|                  |           |                   |                  | Moniezia spp. (9.6), Cooperia spp. (37.0), Oesophagostomum spp. (23.0)|                                              |                     |                                  |

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| Country        | Region       | No. tested samples | No. positive (%) | Reported parasites (%) | Remarks                        | Type of publication | Reference                  |
|---------------|--------------|--------------------|------------------|------------------------|--------------------------------|---------------------|----------------------------|
| Cajamarca     |              | 10                 | 9 (90.0)         | Trichostrongylus spp.  (20.0)  
Ostertagia spp.  (14.0)  
Bunostomum spp.  (3.0)  
Haemonchus spp.  (3.0)  
Trichuris spp.  (20.0)  
Nematodirus spp.  (70.0)  
Bunostomum sp. (20.0)  
Ostertagia sp.  (30.0)  
Trichostrongylus sp.  (20.0) | Necropsy  
Sacrificed alpacas from slaughterhouse | Thesis | Roncal Narváez (2014) |
| Cajamarca     |              | 151                | 20 (13.25)       | Fasciola hepatica  
Trichostrongylus  
Trichuris sp.  
Moniezia benedeni  
Moniezia expansa  
Lamanema chavezi | Rectal samples | Thesis | López Mejía (2014) |
| Puno          |              | 369                | (54.20)          | Nematodirus lamae  
Lamanema chavezi  
Trichostrongylus  
Trichuris sp.  
Moniezia benedeni  
Moniezia expansa  
Lamanema chavezi | Rectal samples and intestinal segments  
Redescription  
Only Lamanema study | Scientific research | Angulo et al. (2015) |
| Puno          |              | 20                 | NR               | Eimeria spp.  
Eimeria macusaniensis  
Eimeria alpaca  
Eimeria posthuma  
Strongylus sp.  
Nematodirus spp.  
Nematodirus spathiger  
Nematodirus lamae  
Trichuris sp.  
Lamanema chavezi  
Capillaria sp.  
Moniezia benedeni  
Moniezia expansa  
Lamanema chavezi | Necropsy  
Intestinal samples  
Rectal samples and necropsy | Abstract of Scientific meeting  
Theis | Díaz et al. (2015) |
| Puno          |              | 51                 | 14 (27.5)        | Eimeria punoensis  
Eimeria lamae  
Eimeria macusaniensis  
Eimeria alpaca  
Eimeria posthuma  
Strongylus sp.  
Nematodirus spp.  
Nematodirus spathiger  
Nematodirus lamae  
Trichuris sp.  
Lamanema chavezi  
Capillaria sp.  
Moniezia benedeni  
Moniezia expansa  
Lamanema chavezi | Eimeria lamae  
Eimeria macusaniensis  
Eimeria posthuma  
Eimeria punoensis  
Strongylus sp. | Fecal samples from unweaned alpacas  
Only Eimeria study | Scientific research | Quina Quina (2015) |
| Pasco         |              | 160                | NR               | Strongylida (28.1)  
Eimeria posthuma (6.9)  
Eimeria macusaniensis (41.9)  
Nematodirus spp. (26.3)  
Trichuris sp. (20.0)  
Capillaria sp. (5.0)  
Lamanema chavezi (3.8)  
Cooperia spp.  
Oesophagostomum spp.  
Teladorsagia circumcincta  
Ostertagia ostertagi  
Trichostrongylus spp.  | Rectal samples | Scientific research | Masson et al. (2016) |
| Pasco and Junín |          | 60                 | (73.3)           | Eimeria spp. (43.3)  
Eimeria alpaca  
Eimeria macusaniensis  
Eimeria lamae  
Nematodirus sp. (40.0)  
Strongylida (18.3)  
Trichuris sp. (1.6)  | Rectal samples and necropsy  
Dead calves with diarrhea | Scientific research | Lucas et al. (2016) |
| Puno          |              | 1319               | (52.4)           | Eimeria alpaca (31.5)  
Eimeria lamae (2.3)  
Eimeria punoensis (66.2)  | Rectal samples  
Only Eimeria study | Scientific research | Camarena et al. (2016) |

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| Country     | Region          | No. tested samples | No. positive (%) | Reported parasites (%)                           | Remarks                  | Type of publication | Reference                |
|-------------|-----------------|--------------------|------------------|-------------------------------------------------|--------------------------|---------------------|--------------------------|
| Huancavelica|                 | 190 (81.88)        |                  | Eimeria macusaniensis (8.7)                      | Rectal samples           | Thesis              | Lizana Hilario (2016)   |
| Puno        |                 | 45 (69.65)         |                  | Eimeria macusaniensis (0.7)                      | Rectal samples           | Thesis              | Chirinos (2017)         |
| Arequipa, Tacna |            | 346                |                  | Eimeria spp.                                    | Intestinal sample        | Thesis              | Torres Huanca (2017)    |
|             |                 |                    |                  | Nematodirus spp. (46.53)                        | Rectal samples           |                    |             |
|             |                 |                    |                  | Capillaria spp. (15.61)                         |                          |                    |             |
|             |                 |                    |                  | Lamanema chavezi (1.45)                         |                          |                    |             |
|             |                 |                    |                  | Strongyloida (4.34)                             |                          |                    |             |
|             |                 |                    |                  | Moniezia expansa (6.65)                         |                          |                    |             |
|             |                 |                    |                  | Eimeria spp. (45.66)                            |                          |                    |             |
| Pasco       |                 | 238 (21.43)        | 7 (3.93)         | Eimeria macusaniensis (8.7)                      | Rectal samples           | Thesis              | Puicón (2018)          |
| Huancavelica|                 | 260 (45.8*)        |                  | Lamanema chavezi                                 | Necropsy                 | Thesis              | Gómez Escobar and Mallqui Saravia (2018) |
| Puno        |                 | 92 NR              |                  | Strongyloida spp.                               | Rectal samples           | Thesis              | quispe Pino (2019)      |
| Arequipa    |                 | 288 NR             |                  | Trichuris sp. Eimeria spp. (60.4)               | Rectal samples           | Scientific research | Frezzato et al. (2020) |
|             |                 |                    |                  | Eimeria macusaniensis (18.8)                    |                          |                    |             |
|             |                 |                    |                  | Trichuris spp. (5.6)                            |                          |                    |             |
|             |                 |                    |                  | Capillaria spp. (3.5)                           |                          |                    |             |
|             |                 |                    |                  | Moniezia spp. (3.5)                             |                          |                    |             |
|             |                 |                    |                  | Nematodirus spp.                                |                          |                    |             |
|             |                 |                    |                  | Teladorsagia circumanicta                        |                          |                    |             |
|             |                 |                    |                  | Oesophagostomum columbianum                      |                          |                    |             |
| Cuzco       |                 | 78 (87.18)         |                  | Eimeria lamae (85.90)                           | Rectal samples           | Scientific research | Gómez-Puerta et al. (2021) |
|             |                 |                    |                  | Eimeria punoensis (62.82)                       |                          |                    |             |
|             |                 |                    |                  | Eimeria alpaca (53.85)                          |                          |                    |             |
|             |                 |                    |                  | Eimeria macusaniensis (41.03)                    |                          |                    |             |
|             |                 |                    |                  | Eimeria ivitaensis (5.13)                       |                          |                    |             |
|             |                 |                    |                  | Eimeria sp. (67.50)                             |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (35.0)                         |                          |                    |             |
|             |                 |                    |                  | Cooperia (32.5)                                 |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (5.0)                          |                          |                    |             |
|             |                 |                    |                  | Nematodirus sp. (12.50)                         |                          |                    |             |
|             |                 |                    |                  | Trichuris sp. (12.50)                           |                          |                    |             |
| Ecuador     | Imbabura        | 40 NR              |                  | Nematodirus spp. (45.5)                         | Rectal samples           | Thesis              | Fierro Obregón (2010)   |
| Cotopaxi and Pichincha | | 406 NR       |                  | Bunostomum spp. (39.4)                          |                          |                    | Salazar et al. (2014) |
|             |                 |                    |                  | Haemonchus spp. (27.5)                          |                          |                    |             |
|             |                 |                    |                  | Cooperia spp. (14.5)                            |                          |                    |             |
|             |                 |                    |                  | Ostertagia spp. (13.7)                          |                          |                    |             |
|             |                 |                    |                  | Trichuris spp. (12.6)                           |                          |                    |             |
|             |                 |                    |                  | Marshallagia spp. (6.1)                         |                          |                    |             |
|             |                 |                    |                  | Strongyloides spp. (5.1)                        |                          |                    |             |
|             |                 |                    |                  | Moniezia benedeni (5.9)                         |                          |                    |             |
|             |                 |                    |                  | Moniezia expansa (4.4)                          |                          |                    |             |
|             |                 |                    |                  | Eimeria lamae (18.2)                            |                          |                    |             |
|             |                 |                    |                  | Eimeria macusaniensis (5.1)                     |                          |                    |             |
|             |                 |                    |                  | Eimeria ivitaensis (5.1)                        |                          |                    |             |
|             |                 |                    |                  | Eimeria sp. (70.7)                              |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (35.0)                         |                          |                    |             |
|             |                 |                    |                  | Cooperia (32.5)                                 |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (5.0)                          |                          |                    |             |
|             |                 |                    |                  | Nematodirus sp. (12.50)                         |                          |                    |             |
|             |                 |                    |                  | Trichuris sp. (12.50)                           |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (35.0)                         |                          |                    |             |
|             |                 |                    |                  | Cooperia (32.5)                                 |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (5.0)                          |                          |                    |             |
|             |                 |                    |                  | Nematodirus sp. (12.50)                         |                          |                    |             |
|             |                 |                    |                  | Trichuris sp. (12.50)                           |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (35.0)                         |                          |                    |             |
|             |                 |                    |                  | Cooperia (32.5)                                 |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (5.0)                          |                          |                    |             |
|             |                 |                    |                  | Nematodirus sp. (12.50)                         |                          |                    |             |
|             |                 |                    |                  | Trichuris sp. (12.50)                           |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (35.0)                         |                          |                    |             |
|             |                 |                    |                  | Cooperia (32.5)                                 |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (5.0)                          |                          |                    |             |
|             |                 |                    |                  | Nematodirus sp. (12.50)                         |                          |                    |             |
|             |                 |                    |                  | Trichuris sp. (12.50)                           |                          |                    |             |
| Pichicha    |                 | 201 (73.0)         |                  | Haemonchus spp. (77.9)                          | Rectal samples           | Thesis              | Salazar Robayo (2015)   |
|             |                 |                    |                  | Nematodirus spp. (77.6)                         |                          |                    |             |
|             |                 |                    |                  | Trichosiroga sp. (77)                           |                          |                    |             |
|             |                 |                    |                  | Bunostomum spp. (69.9)                          |                          |                    |             |
|             |                 |                    |                  | Cooperia spp. (55.8)                            |                          |                    |             |
|             |                 |                    |                  | Ostertagia spp. (50.4)                          |                          |                    |             |
|             |                 |                    |                  | Oesophagostomum spp. (45.1)                     |                          |                    |             |
|             |                 |                    |                  | Capillaria spp. (34.5)                          |                          |                    |             |
|             |                 |                    |                  | Trichuris spp. (29.2)                           |                          |                    |             |
|             |                 |                    |                  | Marshallagia sp. (25.6)                         |                          |                    |             |
|             |                 |                    |                  | Lamanema spp. (22.1)                            |                          |                    |             |
|             |                 |                    |                  | Strongyloides spp. (18.6)                       |                          |                    |             |
|             |                 |                    |                  | Strongyloides spp. (18.6)                       |                          |                    |             |
|             |                 |                    |                  | Eimeria sp. (70.7)                              |                          |                    |             |

(continued on next page)
| Country | Region  | No. tested samples | No. positive (%) | Reported parasites (%) | Remarks | Type of publication | Reference               |
|---------|---------|--------------------|------------------|------------------------|---------|---------------------|-------------------------|
| Cotopaxi| 114     | 114 (100.0)        | Eimeria macusaniensis (29.3) | Moniezia expansa (19.4) Moniezia benedeni (80.6) Marshallagia spp. (9.6) Nematodirus spp. (42.1) Strongylus spp. (14.9) Trichostrongylus spp. (28.9) Haemonchus spp. (13.2) Ostertagia spp. (8.8) Oesophagostomum spp. (9.6) Bunostomum spp. (0.9) Trichuris spp. (23.7) Cooperia spp. (10.5) Toxocara spp. (13.2) Capillaria spp. (7.9) Nematodirus spp. (89.0) Bunostomum spp. (78.0) Haemonchus spp. (43.0) Capillaria spp. (31.0) Trichostrongylus spp. (31.0) Oesophagostomum spp. (28.0) Laganema chavezi (27.0) Trichuris spp. (27.0) Ostertagia spp. (26.0) Cooperia spp. (20.0) Marshallagia spp. (20.0) Strongyloides spp. (10.0) Strongyloides (2.0) Eimeria spp. (81.0) Eimeria macusaniensis (25.0) Moniezia benedeni (61.0) Moniezia expansa (41.0) Ostertagia sp. (29.37) Nematodirus sp. (24.56) Trichostrongylus sp. (5.79) Haemonchus sp. (9.06) Strongyloides sp. (18.89) Trichuris tenius (12.99) Coccidia (83.75) | Rectal samples | Thesis | Condor Tapia (2015) |
| Cotopaxi| 204     | 71 (71.0)          | Eimeria macusaniensis | Moniezia benedeni (61.0) Moniezia expansa (41.0) Marshallagia spp. (9.6) Nematodirus spp. (42.1) Strongylus spp. (14.9) Trichostrongylus spp. (28.9) Haemonchus spp. (13.2) Ostertagia spp. (8.8) Oesophagostomum spp. (9.6) Bunostomum spp. (0.9) Trichuris spp. (23.7) Cooperia spp. (10.5) Toxocara spp. (13.2) Capillaria spp. (7.9) Nematodirus spp. (89.0) Bunostomum spp. (78.0) Haemonchus spp. (43.0) Capillaria spp. (31.0) Trichostrongylus spp. (31.0) Oesophagostomum spp. (28.0) Laganema chavezi (27.0) Trichuris spp. (27.0) Ostertagia spp. (26.0) Cooperia spp. (20.0) Marshallagia spp. (20.0) Strongyloides spp. (10.0) Strongyloides (2.0) Eimeria spp. (81.0) Eimeria macusaniensis (25.0) Moniezia benedeni (61.0) Moniezia expansa (41.0) Ostertagia sp. (29.37) Nematodirus sp. (24.56) Trichostrongylus sp. (5.79) Haemonchus sp. (9.06) Strongyloides sp. (18.89) Trichuris tenius (12.99) Coccidia (83.75) | Rectal samples | Thesis | Regalado Valdivieso (2015) |
| Cotopaxi| 80      | NR                 | Eimeria macusaniensis | Moniezia benedeni (61.0) Moniezia expansa (41.0) Marshallagia spp. (9.6) Nematodirus spp. (42.1) Strongylus spp. (14.9) Trichostrongylus spp. (28.9) Haemonchus spp. (13.2) Ostertagia spp. (8.8) Oesophagostomum spp. (9.6) Bunostomum spp. (0.9) Trichuris spp. (23.7) Cooperia spp. (10.5) Toxocara spp. (13.2) Capillaria spp. (7.9) Nematodirus spp. (89.0) Bunostomum spp. (78.0) Haemonchus spp. (43.0) Capillaria spp. (31.0) Trichostrongylus spp. (31.0) Oesophagostomum spp. (28.0) Laganema chavezi (27.0) Trichuris spp. (27.0) Ostertagia spp. (26.0) Cooperia spp. (20.0) Marshallagia spp. (20.0) Strongyloides spp. (10.0) Strongyloides (2.0) Eimeria spp. (81.0) Eimeria macusaniensis (25.0) Moniezia benedeni (61.0) Moniezia expansa (41.0) Ostertagia sp. (29.37) Nematodirus sp. (24.56) Trichostrongylus sp. (5.79) Haemonchus sp. (9.06) Strongyloides sp. (18.89) Trichuris tenius (12.99) Coccidia (83.75) | Rectal samples | Thesis | Panchi Lema (2021) |
Table 2
Gastrointestinal helminths and Eimeria spp. reported in llamas (*Lama glama*) across the entire nature distribution range. (*Calculated with published data, NR: no reported*).

| Country | Region      | No. tested samples | No. positive (%) | Reported parasites (%) | Remarks | Type of publication | Reference                  |
|---------|-------------|---------------------|------------------|------------------------|---------|---------------------|-----------------------------|
| **Argentina** | Jujuy | 15                  | 15 (100.0)        | Fasciola hepatica      | Fecal samples Only Fasciola study | Scientific research | Cafrune et al. (1996a) |
|         | Jujuy      | 37                  | 35 (95.0)*        | Trichuris tenius       | Fecal samples and Necrospy Only Trichuris study | Scientific research | Cafrune et al. (1999) |
|         | Salta      | 2                   | 2 (100.0)         | Lamanema chavezi (100)* | Fecal samples and one Necrospy Farm llamas | Scientific research | Cafrune et al. (2001) |
| Jujuy   | Salta      | 708                 | 131 (18.5)        | Lamanema chavezi (13.9) | Rectal samples Only Lamanema study | Scientific research | Cafrune et al. (2009a) |
|         | Catamarca  | 626                 | 315 (50.3)        | Eimeria ivitaensis (0.4) | Rectal samples Only Eimeria study | Scientific research | Cafrune et al. (2009b) |
| Jujuy   | Salta      | 430                 |                   | Fasciola hepatica (21.6) | Fecal samples FAO project | Marin et al. (2009) |
|         |            |                     |                  | Lamanema chavezi (18.2) |                 |                     |                             |
|         |            |                     |                  | Trichuris sp. (70.5) | Fecal samples Clinical signs of diarrhea |              |                             |
|         |            |                     |                  | Capillaria sp. (10.2) |                     | Scientific research |                             |
|         |            |                     |                  | Nematodirus sp. (1.1) |                     |                             |                             |
|         |            |                     |                  | Strongylidae sp. (3.4)|                     |                             |                             |
|         |            |                     |                  | Strongylida (5.7) |               |                             |                             |
|         |            |                     |                  | Cestoda (17.0) |                     |                             |                             |
|         |            |                     |                  | Eimeria spp. (64.8) |                     |                             |                             |
|         |            |                     |                  | Eimeria lamae |                     |                             |                             |
|         |            |                     |                  | Eimeria alpaca |                     |                             |                             |
|         |            |                     |                  | Eimeria punoensis |                     |                             |                             |
|         |            |                     |                  | Eimeria ivitaeni |                     |                             |                             |
|         |            |                     |                  | Eimeria macusaniens |                     |                             |                             |
|         |            |                     |                  | Eimeria lamae |                     |                             |                             |
|         |            |                     |                  | Eimeria alpaca |                     |                             |                             |
|         |            |                     |                  | Eimeria punoensis |                     |                             |                             |
|         |            |                     |                  | Eimeria ivitaeni |                     |                             |                             |
| Mendoza |            | 2                   | 2 (100.0)         | Fasciola hepatica (100.0) | Fecal samples | Scientific research | Mera y Sierra et al. (2015) |
| Salta   | NR         | NR                  | Lamanema chavezi  |                     |                     | Scientific research | Petrich et al. (2019) |
| Catamarca | 97       | NR                  | Strongylida (1.0) |                     | Rectal samples and necrocy (+) indicates presence | Thesis | Cardozo (2019) |
|         | 60         |                     | (18.9)            | Trichuris sp. (15.50) |                     |                             |                             |
|         |            |                     | (23.3)            | Toxocara sp. (72.30) |                     |                             |                             |
|         |            |                     | (1.6)             | Lamanema chavezi (1.0)|                     |                             |                             |
|         |            |                     | (18.3)            |               |                     |                             |                             |
|         |            |                     |                  | Moniezia (+) |                     |                             |                             |
|         |            |                     |                  | Strongyloides papillosus |                  |                             |                             |
|         |            |                     |                  | (1.6)         |                     |                             |                             |
|         |            |                     |                  | Nematodirus sp. (0.0) |                     |                             |                             |
|         |            |                     |                  | (11.6)       |                     |                             |                             |
|         |            |                     |                  | Camelostrongylus sp. (0.0)|                   |                             |                             |
|         |            |                     |                  | (5.0)        |                     |                             |                             |
|         |            |                     |                  | Eimeria lamae (4.1)|                     |                             |                             |
|         |            |                     |                  | (6.7)        |                     |                             |                             |
|         |            |                     |                  | Eimeria alpaca (7.2)|                     |                             |                             |
|         |            |                     |                  | (26.7)       |                     |                             |                             |
|         |            |                     |                  | Eimeria punoensis (15.5)|                   |                             |                             |
|         |            |                     |                  | (36.7)       |                     |                             |                             |
|         |            |                     |                  | Eimeria macusaniensis (10.3)|                 |                             |                             |
|         |            |                     |                  | (28.3)       |                     |                             |                             |
|         |            |                     |                  | Eimeria ivitaensis (3.1)|                   |                             |                             |
|         |            |                     |                  | (5.0)        |                     |                             |                             |
|         |            |                     |                  | Fasciola hepatica (3.15)|                   |                             |                             |
|         |            |                     |                  | (2.6)        |                     |                             |                             |

(continued on next page)
Table 2 (continued)

| Country | Region | No. tested samples | No. positive (%) | Reported parasites (%) | Remarks | Type of publication | Reference |
|---------|--------|--------------------|------------------|------------------------|---------|---------------------|-----------|
| Chile   | I Chile Region | 150 | NR | Ostertagia sp. (100.0) + Trichostrongylus sp. (8.0) Coopera sp. (0.0) + Camelostrongylus mentulatus (73.3) Trichostrongylus axei (11.3) Ostertagia sp. (1.3) Graphinema aucheniae (1.3) Masamastrongylus (Spiculopteragia) peruvianus (1.3) Lamanema chavezi (61.3) Nematodirus sp. (18.7) Trichuris ovis (66.7) Moniezia expansa (6.7) | Only abstract description | Scientific research | Alcaino et al. (1991) |
| Araucania, Temuco | 45 | NR | Strongylida | Nematodirus sp. Ostertagia sp. Nematodirus spathiger Nematodirus filicola Trichostrongylus sp. Cooperia sp. Capillaria sp. Eimeria sp. Eimeria macusaniensis Fasciola hepatica Moniezia sp. Trichuris sp. Nematodirus sp. Strongylida | Rectal samples | Scientific research | Müller (1998) |
| Los Ríos, Valdivia | 32 | (100.0) | Lamanema chavezi (94.0) Nematodirus spathiger (55.0) Nematodirus lamae (12.0) Nematodirus abnormalis (15.0) Camelostrongylus mentulatus (33.0) Haemonchus contortus (15.0) Trichuris sp. (42.0) Graphinema aucheniae (12.0) Marshallagia occidentalis (6.0) Ostertagia ostertagi (12.0) Cooperia oncophora (9.0) Cooperia surnabada (3.0) Trichostrongylus coluberformis (6.0) Trichostrongylus varinus (3.0) Trichostrongylus probolurus (6.0) Skrjabinema sp. (3.0) Moniezia sp. (3.0) Fasciola hepatica (12.0) Eimeria spp. (82.0) | Fecal samples and necropsy | Scientific research | Oyarzún-Ruiz et al. (2017) |
| Bolivia | Oruro, Potosí, La Paz and Cochabamba | 33 | NR | Fasciola hepatica (9.7) Haemonchus sp. (18.0) Trichostrongylus axei (18.7) Ostertagia sp. (36.8)* Graphinema sp. (15.5)* Camelostrongylus sp. (11.0)* Nematodirus sp. (83.22)* Lamanema chavezi (45.2)* Cooperia sp. (16.12)* Trichostrongylus c. (15.5)* Bunostomum sp. (6.45)* Moniezia sp. (10.22)* Oesophagostomum sp. (21.3)* Oesophagostomum sp. (21.3)* | Rectal samples | Mother and brood | Thesis | Mamani (2012) |
| Peru | Cuzco | NR | NR | Eimeria lamae Eimeria alpaca Eimeria punensis Eimeria tritonis Eimeria macusaniensis Nematodirus spathiger Nematodirus lamae Lamanema chavezi Trichuris spp. Capillaria spp. Strongylida | Rectal samples | Thesis | Thesis | Fuentes Ríos (2013) |
| Huancavelica | 155 | 145 | (93.55) | Fasciola hepatica (9.7) Haemonchus sp. (18.0) Trichostrongylus axei (18.7) Ostertagia sp. (36.8)* Graphinema sp. (15.5)* Camelostrongylus sp. (11.0)* Nematodirus sp. (83.22)* Lamanema chavezi (45.2)* Cooperia sp. (16.12)* Trichostrongylus c. (15.5)* Bunostomum sp. (6.45)* Moniezia sp. (10.22)* Oesophagostomum sp. (21.3)* Oesophagostomum sp. (21.3)* | Necropsy | Thesis | Fuentes Ríos (2013) |
2.2. Search strategy and data

2.2.1. Identification

The study was focused on gastrointestinal helminths and *Eimeria* spp., hereafter “parasites”. The literature research was carried out on internet through the Google Scholar platform (https://scholar.google.com), the PubMed platform (https://pubmed.ncbi.nlm.nih.gov), and the SciELO platform (https://scielo.org/es/). The following keywords were used for the research: “endoparasites”, “gastrointestinal”, “intestinal”, “parasites”, “helminths”, “camelids”, “South American Camelids”, “SAC”, “endoparasitos”, “parásitos”, “intestinal”, “gastrointestinales”, “helmintos”, “camelidos”, “camelidos sudamericanos”, “CSA”, “guanaco”, “Lama”, “Vicugna”, “guanicoe”, “pacos”, “glama”, “llama”, “alpaca”, “vicuña”, “Eimeria”, “Coccidia”. The search rule used in English was (endoparasites OR gastrointestinal OR intestinal) AND (parasites OR helminths OR *Eimeria* OR coccidia) AND (camelids OR South American camelids OR SAC OR guanaco OR vicuña OR llama OR alpaca OR *Lama* OR *Vicugna*) AND (*guanicoe* OR glama OR vicugna OR pacos). The search rule used in Spanish was (endoparasitos OR parásitos OR helmintos OR *Eimeria*) AND (intestinal OR gastrointestinal) AND (camelidos OR camélidos sudamericanos OR CSA OR guanaco OR vicuña OR alpaca OR *Lama* OR *Vicugna*) AND (*guanicoe* OR glama OR vicugna OR pacos). The search was conducted in titles, abstracts and keywords in the above-cited databases, following the selection criteria. The snowball effect in the reference lists was used to increase the scope of the search. The initial search process generated 3960 academic papers from Google Scholar, and additional 285 papers from PubMed and 18 papers from SciELO. The publication retrieval from Google Scholar was scaled down to 237 after removing all parasite papers that did not represent the objective of this review. A flowchart of the PRISMA phases of the search is presented in Fig. 1.

2.2.2. Screening

After the initial search and paper retrieval, 540 academic papers were collected. After removing duplicate information, 482 publications remained. Subsequently, the generated papers were screened by applying the inclusion and exclusion criteria. A total of 98 academic papers were included for quality assessment.

2.2.3. Eligibility

The studies identified after applying the inclusion and exclusion criteria underwent further evaluation to ensure the quality of the research articles. The theses that contained only information published in scientific journals were eliminated. In total, 3 theses were excluded.

2.2.4. Included papers

A total of 95 publications were included in this review. From all reviewed documents, were extracted data regarding geographic location (country and region), number of samples evaluated, number of positive samples, taxa and prevalence of parasites reported, remarks (type of sample, animal characteristics, study remarks) and type of publication, being the data extraction performed by one author with verification by another, as the PRISMA protocol suggest (Shanmeeer et al., 2015).

3. Results

The present review includes documents from the period between 1963 and 2022. The information was retrieved from 95 publications and 6 more citations were added (there was no access to the original work), which makes a final number of 101 publications. A total of 74 scientific researchs, 27 theses (PhD and MSc Thesis and Final Degree Projects), four abstracts of scientific meetings and one FAO project were recopiled. The name of parasites was included exactly as reported in the retrieved publications.

The documents summarized belong to five countries (Argentina, Bolivia, Chile, Peru and Ecuador), with the alpaca being the most studied species of SAC, (49.5% of the total documents), followed by the guanaco (23.8%) and finally the llama and vicuña (both 18.8%). The geographical location of the documents summarized is shown in Fig. 2. The map was elaborated with the Google Earth platform.

The reports of parasites of alpacas are summarized in Table 1. The 80% of the documents refer to alpacas from Peru, 12% from Ecuador, 4% from Chile and 4% from Bolivia. The reports of parasites of llamas are summarized in Table 2. The 47.4% of the recopiled documents belong to Argentina, 21% to Peru, 15.8% to Chile, 10.5% to Ecuador and 5.3% belong to Bolivia. The Table 3 summarized the recopiled documents of parasites of vicuñas. The 42.1% of the documents refer to
Table 3
Gastrointestinal helminths and *Eimeria* spp. reported in vicuñas (*Vicugna vicugna*) across the entire distribution range. (* Calculated with published data, NR: no reported).

| Country     | Region                  | No. tested samples | No. positive (% | Reported parasites (%) | Remarks | Type of publication | Reference                  |
|-------------|-------------------------|--------------------|----------------|------------------------|---------|--------------------|-----------------------------|
| Argentina   | Jujuy                   | 187                | 30 (16.04)     | Fasciola hepatica      | Rectal samples Semi-captive | Scientific research | Cafrune et al., (1996b)    |
|             |                         |                    |                |                        | Only Fasciola study          |                    |                              |
|             |                         | 69                 | 45* (65.0)     | Trichuris tenus        | Fecal samples Semi-captive   | Scientific research | Cafrune et al. (1999)       |
|             |                         | 63                 | 14 (22.2)      | Eimeria macusaniensis  | Rectal samples Semi-captive  | Scientific research | Cafrune et al., (2009b)     |
|             | Salta                   | 98                 | 9 (9.2)        |                        | Only *Eimeria* study         |                    |                              |
|             |                         | 81 juveniles       | 81 (100.0)     | Eimeria punoensis (100)| Rectal samples Captive       | Scientific research | Cafrune et al. (2014)       |
|             |                         | 143 adults         | 143 (92.8)     | Eimeria alpaca (85.1)  | Only *Eimeria* study         |                    |                              |
|             |                         |                    |                | Eimeria macusaniensis (82.7) |                      |                    |                              |
|             |                         |                    |                |                        | (15.5)                      |                    |                              |
|             |                         |                    |                |                        | *Eimeria* lamae (48.1)       |                    |                              |
|             |                         |                    |                |                        | (27.2)                      |                    |                              |
|             |                         |                    |                |                        | *Eimeria* ivitainus (3.7)   |                    |                              |
|             |                         |                    |                |                        | (1.2)                       |                    |                              |
|             | Jujuy                   | 150                | NR             | Strongylida (40.66)    | Rectal samples               | Scientific research | Marcoppido et al. (2016)    |
|             |                         |                    |                | Nematodirus sp. (4.66) | Wild                        |                    |                              |
|             |                         |                    |                | Coccidia (7.33)       |                            |                    |                              |
|             |                         |                    |                | Cestoda (6.66)        |                            |                    |                              |
|             |                         | 40                 | (2.5)          | Capillaria sp.         | Fecal samples                | Thesis            | Cardozo (2019)               |
|             | Catamarca, Laguna Blanca|                    |                | Haemonchus sp.         |                            |                    |                              |
|             |                         |                    |                | Camelostrongylus sp.   |                            |                    |                              |
|             |                         |                    |                | *Eimeria* spp.         |                            |                    |                              |
|             |                         |                    |                | *Eimeria* lamae        |                            |                    |                              |
|             |                         |                    |                | *Eimeria* alpaca       |                            |                    |                              |
|             |                         |                    |                | *Eimeria* punoensis    |                            |                    |                              |
|             |                         |                    |                | *Moniezia* sp.         |                            |                    |                              |
|             | Bolivia                 |                    |                | Fasciola hepatica (12.5)|                            |                    |                              |
|             | La Paz, Apolobamba      | 7 juveniles        | 7 (100.0)      | Strongylida (28.6)    | Rectal samples               | Scientific research | Beltrán-Saravedra et al. (2011) |
|             |                         | 25 adults          | 22 (88.0)      | Wild                   |                            |                    |                              |
|             |                         |                    |                | Marshallagia sp.         |                            |                    |                              |
|             |                         |                    |                | (71.4)                 |                            |                    |                              |
|             |                         |                    |                | (32.0)                 |                            |                    |                              |
|             |                         |                    |                | Lamanema spp. (42.9)  |                            |                    |                              |
|             |                         |                    |                | (16.0)                 |                            |                    |                              |
|             |                         |                    |                | Nematodirus spp. (57.1)|                            |                    |                              |
|             |                         |                    |                | (28.0)                 |                            |                    |                              |
|             |                         |                    |                | *Capillaria* sp. (28.6)|                            |                    |                              |
|             |                         |                    |                | (0.0)                  |                            |                    |                              |
|             |                         |                    |                | Trichuris sp. (28.6)   |                            |                    |                              |
|             |                         |                    |                | (44.0)                 |                            |                    |                              |
|             |                         |                    |                | *Moniezia* benedeni (14.3)|                            |                    |                              |
|             |                         |                    |                | (0.0)                  |                            |                    |                              |
|             |                         |                    |                | *Eimeria* punoensis (100.0)|                            |                    |                              |
|             |                         |                    |                | (80.0)                 |                            |                    |                              |
|             |                         |                    |                | *Eimeria* alpaca (100.0)|                            |                    |                              |
|             |                         |                    |                | (88.0)                 |                            |                    |                              |
|             |                         |                    |                | *Eimeria* lamae        |                            |                    |                              |
|             |                         |                    |                | (42.9)                 |                            |                    |                              |
|             |                         |                    |                | (12.0)                 |                            |                    |                              |
|             |                         |                    |                | *Eimeria* macusaniensis (14.3)|                            |                    |                              |
|             |                         |                    |                | (8.0)                  |                            |                    |                              |
|             | La Paz, Apolobamba      | 54 fecal samples   | (100.0)        | Marshallagia sp.       | Fecal and dump samples       | Scientific meeting | Condori et al. (2012)       |
|             |                         | 8 dump samples     |                | Nematodirus sp.        | Wild                        |                    |                              |
|             |                         |                    |                | Trichuris sp.          |                            |                    |                              |
|             |                         |                    |                | *Capillaria* sp.       |                            |                    |                              |
|             |                         |                    |                | Lamanema chavezi       |                            |                    |                              |
|             |                         |                    |                | *Moniezia* benedeni    |                            |                    |                              |
|             |                         |                    |                | *Moniezia* expansa     |                            |                    |                              |
|             |                         |                    |                | *Eimeria* punoensis    |                            |                    |                              |
|             |                         |                    |                | *Eimeria* alpaca       |                            |                    |                              |
|             |                         |                    |                | *Eimeria* lamae        |                            |                    |                              |

(continued on next page)
| Country Region | No. tested samples | No. positive samples (%) | Reported parasites (%) | Remarks | Type of publication | Reference |
|----------------|--------------------|--------------------------|------------------------|---------|---------------------|------------|
| Potosí, Tarija and Cochabamba | 98 | (73.5) | *Trichostrongylus axei*  
*Marshallagia spp.* | Rectal samples  
Semi-captive | Thesis | Martela Mamani (2016) |
| La Paz and Oruro | 84 | (98.6) | *Lamanema chavezi*  
*Capillaria spp.*  
*Moniezia benedeni*  
*Trichuris spp.*  
*Fasciola hepatica*  
*Eimeria punoensis*  
*Eimeria lamae*  
*Eimeria macusaniensis*  
*Eimeria alpaca* | Rectal samples  
Semi-captive | Thesis | Ruiz Hurtado (2016) |
| Peru Cuzco | NR | NR | *Lamanema chavezi*  
*Nematodirus lamae* | First report  
Host: llama and vicuña  
no access to original document | Scientific research | Becklund (1963) |
| Ayacucho, Pampa Galeras | 39 | 15 (41.0) | *Eimeria lamae*  
*Eimeria punoensis* | NR | Scientific research | Bouts et al. (2003) (in Dubey, 2018) |
| Tacna | 120 | (80.83) | *Trichuris sp.*  
*Strongylus sp.*  
*Nematodirus sp.*  
*Capillaria sp.*  
*Moniezia lamae*  
*Eimeria spp.* | Rectal samples  
Semi-captive | Thesis | Quispe García (2011) |
| Huancavelica | 80 | (27.5) | *Fasciola hepatica* | Rectal and dump samples  
Only Fasciola study | Scientific research | Pizarro and Puray (2014) |
| Junín, Paccha | 143 | (32.9) | *Fasciola hepatica* | Rectal samples  
Only Fasciola study | Scientific research | Samamé et al. (2016) |
| Cajamarca | 208 | NR | *Strongylida*  
*Nematodirus sp.*  
*Capillaria sp.*  
*Moniezia lamae*  
*Cooperia sp.*  
*Oesophagostomum*  
*Haemonchus*  
*Bunostomum* | Rectal samples  
Semi-captive | Thesis | Curay Cabanillas (2018) |
| Cuzco | 147 | High NR | *Fasciola hepatica*  
*Strongylida*  
*Nematodirus sp.*  
*Nematodirus spathiger*  
*Trichuris sp.*  
*Eimeria spp.* | Rectal samples  
Wild and captive | Scientific research | Angulo-Tiscoc et al. (2021) |
| Cuzco | 115 | (84.4) | *Strongylida*  
*Nematodirus lamae*  
*Nematodirus spathiger*  
*Trichuris spp.*  
*Capillaria sp.*  
*Lamanema chavezi*  
*Eimeria alpaca*  
*Eimeria macusaniensis*  
*Eimeria lamae*  
*Eimeria panamensis*  
*Trichostrongylus spp.*  
*Haemonchus spp.* | Fecal samples  
Semi-captive | Scientific research | Arias-Pacheco et al. (2021) |

(continued on next page)
vicuñas from Peru, 31.6% from Argentina and 21% from Bolivia and only one document refers to vicuñas from Ecuador (5.3%). The reports of parasites of guanacos are summarized in Table 4. Most of the recopilated documents belong to Argentina (83.33%), while documents from Chile and Peru represent both 8.33%. The data collected through the entire native range of SAC distribution displayed that the highest species richness of gastrointestinal parasites are found in southern Peru, western Bolivia and central Patagonia. It is important to highlight that this data was elaborated from the information available to date. The parasitic richness found in SAC compiled from the information extracted is represented in Fig. 3.

The gastrointestinal parasites of each of the four SAC species compiled are summarized in Table 5. At least 36 parasitic helminths were registered. Twenty two genera of the Phylum Nematoda have been reported among the four species of SAC. Seventeen genera belong to the Order Strongyliida (including 28 taxa identified to the species level), one genus belong to the Order Ascaridida, one genus belong to the Order Oxyurida, one genus belong to the order Rhaditida and two genus belong to the Order Enopliida. Three genera of the Phylum Platyhelminthes were also reported. One of them belongs to Cestoda (with two identified species) and one species belong to Trematoda. Respects to Eimeria spp. (Apicomplexa), five species have been identified. The prevalence of the reported parasitic infestations in many cases was 100% (Tables 1–4). This review displays that there is no one species more prevalent than another, but rather that the prevalence varies in each of the studies.

4. Discussion

The present work is the first scientific review that provides detailed information about gastrointestinal parasite diversity of SAC throughout the entire native distribution range, encompassing a large number of documents. The records summarized here comprise documents dating from 1963 to 2022, with an increase in the last 10 years, whenever a wide production of scientific publications and graduate and postgraduate theses were produced. This point can be explained by the growing interest in recent years for SAC conservation and, in the other hand, for the economic interest on SAC around the world. The recopilated documents are focused mainly in gastrointestinal parasites studies from fecal samples or from necropsied animals, by microscopic techniques mostly. This implies that in many occasions it is not possible to identify the species. Molecular studies on cameldid parasites are scarce. Although 101 works were recopilated, results highlight that a large number of the documents summarized are not published in indexed journals and are not easily accessible to a wider audience.

The highest species richness of gastrointestinal parasites was found in southern Peru, western Bolivia and central Patagonia. This agrees with the regions with the highest population of SAC and with the regions where more studies have been carried out. The important population of Peru explain that this country produced a great number of the available knowledge. However, it is mainly focused on alpaca. Numerous studies considered that latitude is one of the main factors correlated to parasite diversity and richness. Parasite diversity is expected to decrease in high latitude areas as result of lack of intermediate hosts or high mortality rates due to harsh conditions in winter (Krasnov et al., 2004; Lindenfors et al., 2007; Bordes et al., 2010; Poulin and Leung, 2011). The data on parasitic richness of SAC summarized in this paper so far do not allow us to observe a decrease pattern in their distribution throughout their extensive distribution. However, the parasite diversity display in this review should be taken with caution as it is subject to the number and type of samples analyzed in each region. So far, all parasite genera appear to be represented throughout the distribution range.

Most wild and domestic ungulate species have few host-specific parasites, which make up less than half of the total number of nematode parasite species found in a given host; and mostly have generalist parasites (Walker and Morgan, 2014). Across vast areas, SAC coexist with domestic herbivores such as sheep, goat and cattle. Furthermore, domestic SAC coexist with human populations. This proximity facilitates the exchange of parasites between domestic and wild animals and humans. Walker and Morgan (2014) found that domestic cameldids (llamas and alpacas) have a high liability index (the degree to which a host species is vulnerable to infection with generalist parasites), with a value of 0.77. This index is designed to range from −1 (entirely host-specific parasites) to 1 (entirely parasites shared with the other group). This result displays that llamas and alpacas mostly generalist species. In the present study, 22 genera of nematodes were reported, with at least 33 species. Of all of them, only five are known as SAC-specific nematodes: Trichuris tenius, Graphinema aucheniae, Cameistrogenus mentulatus, Nematodirus lamae, and Lamanema chavesi. Most of the registered parasites in this review are generalist parasites, and are shared with domestic ungulates and wildlife species, such as Ostertagia spp., Haemonchus contortus, Trichostrongylus spp., Cooperia spp., and Oesophagostomum. From a sanitary point of view, it would be important to know if host-specific parasites dominate the communities of their hosts and generalist parasites tend to occur at lower abundances, or vice versa (Zaffaroni et al., 2000). In this review, is clear that there is not enough data to compare the abundance of different nematode species within a host. Further studies of the contribution of shared parasite species to total parasite burden than only species richness would be a step toward understanding the impact that generalist parasites have on SAC. In the other hand, several studies have looked at nematodes of wild ungulates in relation to domestic species. In the present review, domestic SAC displayed to have the same genera of parasites than wild SAC.

SAC have also been described as hosts for parasites of zoonotic importance such as Fasciola hepatica. This trematode was found in wild and domestic cameldids, from the north of its distribution to the north of Patagonia. It was generally assumed that entry of F. hepatica to America coincided with the first arrival of the Europeans and their associated livestock in the late 15th century. Throughout the 500 years since its introduction, the parasite gained new definitive hosts among native species. This trematode is now widespread in livestock and can be mapped across the whole South America and certain regions of North America. Nonetheless in Argentina, eggs of F. hepatica have been observed in deer and cameldid coprolites dating back to 2300 years B.P.
Table 4

Gastrointestinal helminths and *Eimeria* spp. reported in guanacos (*Lama guanicoe*) across the entire distribution range. (* Calculated with published data, NR: no reported).

| Country                     | Region                  | No. tested samples | No. positive (%) | Parasites reported (%)                                                                 | Remarks                                                                 | Type of publication            | Reference                                      |
|-----------------------------|-------------------------|--------------------|------------------|----------------------------------------------------------------------------------------|-------------------------------------------------------------------------|----------------------------------|------------------------------------------------|
| Argentina                   | Río Negro               | 3                  | NR               | *Skrjabinema* sp. *Trichuris ovis*. *Trichostrongylus sp.* *Trichostrongylus virens*  *Trichostrongylus axei*  *Ostertagia ostertagi*  *Nematodirus filicola*  *Nematodirus battus*  *Nematodirus lanceolatus*  *Nematodirus spathiger*  *Cooperia oncophora*  *Cooperia macmurrayi*  *Capillaria sp.*                                      | NR                                                                                 | Scientific research            | Larrieu et al. (1982) (in González-Rivas et al., 2019) |
|                             | Tierra del Fuego        | 58                 | NR               | *Haemonchus sp.* *Nematodirus sp.* *Marshallagia sp.* *Ostertagia sp.*  *Trichostrongylus sp.* *Oesophagostomum sp.*  *Chabertia sp.*  *Cooperia sp.*  *Eimeria sp.*                                      | Fecal samples                                                                 | Scientific research            | Navone and Merino (1989)                                                  |
|                             | Chubut                  | 20                 | 12 (60.0)*       | *Strongyloides sp.* *Nematodirus sp.* *Marshallagia sp.* *Trichostrongylus sp.*  *Oesophagostomum sp.*  *Chabertia sp.*  *Cooperia sp.*  *Eimeria sp.*                                      | Rectal samples Free-ranging Two animals in poor body conditions           | Scientific research            | Karesh et al. (1998)                                                      |
|                             | Chubut                  | 12                 | NR               | *Eimeria spp.* *Eimeria macusaniensis* *Nematodirus sp.*  *Marshallagia sp.*  *Trichostrongylus sp.*  *Dictyocaulus sp.*  *Dictyocaulus filaria*  *Trichuris tenus*  *Moniezia expansa*                                      | Feces from necropsied animals Animals dead by starvation Wild              | Scientific research            | Beldoméñico et al. (2003)                                                  |
| Mendoza and San Juan        |                         | 35                 | NR               | *Eimeria macusaniensis*                                                                 | Only access to abstract                                                    | Scientific research            | Borghi et al. (2004) (in Dubey, 2018)                                     |
| Mendoza                     |                         | 70                 | 1 (1.4)          | *Fasciola hepatica*                                                                    | Fecal samples First report Wild                                           | Scientific research            | Issia et al. (2007)                                                       |
| Neuquen, Río Negro and      |                         | NR                 | (84.2)           | *Fasciola hepatica*                                                                    | Only Fasciola study                                                       | Scientific research            | Larroza and Olaechea (2008)                                                 |
| Chubut                      | Salta                   | 4                  | 1 (25.0)         | *Eimeria macusaniensis*                                                                | Only Fasciola study                                                       | Scientific research            | Cafrune et al. (2009a)                                                     |
|                             | Salta                   | 4                  | 3 (75.0)         | *Lamanema chavezi*                                                                     | Dung samples Semi-captive Only Fasciola study                             | Scientific research            | Cafrune et al. (2009b)                                                     |
|                             | Mendoza                 | 224                | (0.5)            | *Fasciola hepatica*                                                                    | Fecal samples Wild Only Fasciola study Necropsized animals               | Scientific research            | Olaechea et al. (2011)                                                     |
|                             |                         | 622                | NR               | *Nematodirus spathiger*                                                                |                                                                          |                                 |                                                                                |

(continued on next page)
| Country          | Region                          | No. tested samples | No. positive (%) | Parasites reported (%)                                                                                                                                                                                                 | Remarks                           | Type of publication   | Reference                                      |
|------------------|---------------------------------|--------------------|------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------|----------------------|-----------------------------------------------|
| Neuquén, Chubut and Río Negro |                                |                    |                  | *Nematodirus oriatianus*  
* Nematodirus filicolis  
* Nematodirus abnormalis  
* Ostertagia ostertagi  
* Ostertagia trifurcata  
* Cooperia oncophora  
* Trichostrongylus colubriformis  
* Trichuris spp.  
* Dictyocaulus spp.  
* Moniezia spp.  
* Eimeria macusaniensis  
* Fasciola hepatica  
* Eimeria spp.  
* Eimeria macusaniensis  
* Nematodirus spp.  
* Trichuris sp.  
* Capillaria sp.  
* Strongyloides sp.  
* Moniezia benedeni  
* Eimeria lamae  
* Eimeria alpaca  
* Eimeria punoensis  
* Eimeria macusaniensis  
* Eimeria vitiaensis  
* Eimeria spp.  | Semi-captive                  |                    |                  |                                                                                                                                          |                                   |                      |                                               |
| Mendoza          | 75 rectal 600 field NR         |                    |                  | *Nematodirus oriatianus*  
* Nematodirus filicolis  
* Nematodirus abnormalis  
* Ostertagia ostertagi  
* Ostertagia trifurcata  
* Cooperia oncophora  
* Trichostrongylus colubriformis  
* Trichuris spp.  
* Dictyocaulus spp.  
* Moniezia spp.  
* Eimeria macusaniensis  
* Fasciola hepatica  
* Eimeria spp.  
* Eimeria macusaniensis  
* Nematodirus spp.  
* Trichuris sp.  
* Capillaria sp.  
* Strongyloides sp.  
* Moniezia benedeni  
* Eimeria lamae  
* Eimeria alpaca  
* Eimeria punoensis  
* Eimeria macusaniensis  
* Eimeria vitiaensis  
| Rectal and field samples  
| Wild                  | Scientific research            |                       | Moreno et al. (2013)                                                                                                                                                                                                 |                                   |                      |                                               |
| Mendoza          | 756 NR                         | 638 (84.4)*        |                  | *Nematodirus oriatianus*  
* Nematodirus filicolis  
* Nematodirus abnormalis  
* Ostertagia ostertagi  
* Ostertagia trifurcata  
* Cooperia oncophora  
* Trichostrongylus colubriformis  
* Trichuris spp.  
* Dictyocaulus spp.  
* Moniezia spp.  
| Rectal samples  
| Wild                  | Scientific research            |                       | Moreno et al. (2015)                                                                                                                                                                                                 |                                   |                      |                                               |
| Mendoza          | 4 NR                           | 1 (25.0)*          |                  | *Fasciola hepatica*  
| Semi-captive                  |                                           |                      | Moreno Sierrra et al. (2015)                                                                                                                                                                                                 |                                   |                      |                                               |
| Santa Cruz       | NR NR                          |                    |                  | *Nematodirus spathiger*                                                                                                                                            | Scientific research            |                       | Petrich and Fugassa (2014)                     |
| Santa Cruz       | 15 NR                          | (77.0)             |                  | *Nematodirus spp*  
|                  | (73.3)                        |                    | Only Nematodirus study                                                                                                                                            | Scientific research            |                       | Taglioretti (2015)                             |
| Chubut            | NR NR                          |                    |                  | *Lamanema chavezi*                                                                                                                                                    | Scientific research            |                       | Patrich et al. (2019)                           |
| San Juan          | 72 NR                          |                    |                  | *Eimeria spp.*  
|                  | *Eimeria macusaniensis*  
|                  | *Eimeria vitiaensis*  
|                  | *Nematodirus spp*  
|                  | *Trichuris sp.*                                                                                                                                                | Scientific research            |                       | Gonzalez-Rivas et al. (2019)                   |
| Santa Cruz        | 4 NR                           |                    |                  | *Capillarid eggs*                                                                                                                                                    | Scientific research            |                       | Velazquez et al. (2020)                         |
| Santa Cruz        | 10 NR                          | 10 (100.0)         |                  | *Lamanema chavezi (100.0)*  
|                  | *Nematodirus spp*  
|                  | (100.0)                        |                    | Only Lamanema study                                                                                                                                            | Scientific research            |                       | Santana et al. (2020)                           |
| Chile             | Magallanes NR NR               |                    |                  | *Ostertagia sp.*  
|                  | *Trichostrongylus sp.*  
|                  | *Nematodirus sp.*                                                                                                                                                | Scientific research            |                       | Cunazza (1982) (in Navone and Merino, 1998)     |

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prior to the arrival of the European cattle in the 15th century (Beltrame et al., 2020; Tietze et al., 2021). This shows that the presence of Fasciola in camelids is not only due to its transmission by European cattle.

Cestodes found in SACs are ruminant-related anoplocephalid of the genus Moniezia, identified in the four camelids species in a wide variety of environments with records that go from the north of its distribution reaching as far as northern Patagonia. Parasites of Moniezia expansa were identify in all SACs species, while Moniezia benedeni were identify in vicuñas, alpacas and guanacos. In the case of llamas, findings of cestodes were scarce, and in general it was only possible to identify the genus. Recently, Moniezia eggs were also found in coprolites from the middle to late-Holocene from the Argentinian Puna, evidencing the presence of this genus in SAC prior the European cattle arrival (Tietze et al., 2021).

There are five common species of Eimeria in SAC: E. lamae, E. alpacae, E. punoensis, E. macusaniensis and E. ivitaensis (Dubey, 2018). All Eimeria spp. were recorded in wild and domestic camels throughout its distribution range. The most prevalent Eimeria found in guanacos was E. macusaniensis, but in general the most prevalent in SAC was E. punoensis while the least prevalent was E. ivitaensis (Marin et al., 2009; Rodríguez et al., 2012; Cafrune et al., 2014; Moreno et al., 2015). Of the five Eimeria species registered in SAC, E. macusaniensis is considered the most pathogenic, clinical symptoms can develop even before oocysts are registered in the feces. The host specificity along with the characteristic morphology of its oocyst makes it an effective indicator when identifying the host in coprological studies (Dubey, 2018). The presence of E. macusaniensis is reported even in ancient samples from Argentina, Chile and Peru (Fugassa et al., 2008; Beltrame et al., 2010; Taglioret et al., 2015; de Souza et al., 2018; Le Bailly et al., 2020; Tietze et al., 2021).
Table 5
Review of gastrointestinal parasites of South American Camelids.

| Parasite species                        | Alpacas | Llamas | Vicuñas | Guanacos |
|----------------------------------------|---------|--------|---------|----------|
| NEMATODA                               |         |        |         |          |
| STRONGYLIDA/ANCYLOSTOMATIDAE           | + + + + |        |         |          |
| Bunostomum sp.                         | +       |        |         |          |
| Bunostomum phlebotomum                 | +       |        |         |          |
| MONILEPIDAE                            | + + + + | + + + +| + + + + | + + + +  |
| Strongyloides sp.                      | +       | + + + +| + + + + | + + + +  |
| Strongyloides papillosus               | +       | + + + +| + + + + | + + + +  |
| Strongyloides axei                     | +       | + + + +| + + + + | + + + +  |
| Strongyloides colubriformis            | +       | + + + +| + + + + | + + + +  |
| Strongyloides vitrinus                 | +       | + + + +| + + + + | + + + +  |
| Strongyloides probolorus               | +       | + + + +| + + + + | + + + +  |
| Strongyloides trichinoides             | +       | + + + +| + + + + | + + + +  |
| Strongyloides tenuis                   | +       | + + + +| + + + + | + + + +  |
| Strongyloides spp.                     | + + + + | + + + +| + + + + | + + + +  |
| Moniezia sp.                           | + + + + | + + + +| + + + + | + + + +  |
| Moniezia expansa                       | +       | + + + +| + + + + | + + + +  |
| Moniezia benedeni                      | +       | + + + +| + + + + | + + + +  |
| TROMATOIDE                             | + + + + | + + + +| + + + + | + + + +  |
| Oxyurida sp.                           | +       | + + + +| + + + + | + + + +  |
| Oxyurida spp.                          | +       | + + + +| + + + + | + + + +  |
| Oxyurida crassica                      | +       | + + + +| + + + + | + + + +  |
| Oxyurida circumcincta                  | +       | + + + +| + + + + | + + + +  |
| Oxyurida trifurcata                    | +       | + + + +| + + + + | + + + +  |
| Teladorsagia spp.                      | +       | + + + +| + + + + | + + + +  |
| Teladorsagia circumcincta              | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus sp.                   | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus colubriformis         | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus axei                  | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus vitrinus              | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus probolarius           | +       | + + + +| + + + + | + + + +  |
| Platyhelminthes                        | + + + + | + + + +| + + + + | + + + +  |
| CESTODA                                | +       | + + + +| + + + + | + + + +  |
| Moniezia sp.                           | + + + + | + + + +| + + + + | + + + +  |
| Moniezia expansa                       | +       | + + + +| + + + + | + + + +  |
| Moniezia benedeni                      | +       | + + + +| + + + + | + + + +  |
| TROMATOIDE                             | +       | + + + +| + + + + | + + + +  |
| Oxyurida sp.                           | + + + + | + + + +| + + + + | + + + +  |
| Oxyurida spp.                          | +       | + + + +| + + + + | + + + +  |
| Oxyurida crassica                      | +       | + + + +| + + + + | + + + +  |
| Oxyurida circumcincta                  | +       | + + + +| + + + + | + + + +  |
| Oxyurida trifurcata                    | +       | + + + +| + + + + | + + + +  |
| Teladorsagia spp.                      | +       | + + + +| + + + + | + + + +  |
| Teladorsagia circumcincta              | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus sp.                   | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus colubriformis         | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus axei                  | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus vitrinus              | +       | + + + +| + + + + | + + + +  |
| Trichostrongylus probolarius           | +       | + + + +| + + + + | + + + +  |
| Strongyloides sp.                      | + + + + | + + + +| + + + + | + + + +  |
| Moniezia sp.                           | + + + + | + + + +| + + + + | + + + +  |
| Moniezia expansa                       | +       | + + + +| + + + + | + + + +  |
| Moniezia benedeni                      | +       | + + + +| + + + + | + + + +  |
| TROMATOIDE                             | +       | + + + +| + + + + | + + + +  |
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Nematodirus lamae
sp. n.
Fasciola hepatica
Lama guanicoe
Lama pacos
Lama vicugna
Lama pacos (Protozoa: Eimeriidae) of the alpaca
Fasciola hepatica
Vicus pacos
Vicugna vicugna
Vicugna pacos
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