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Echinococcus granulosus sensu lato Genotypes in Different Hosts Worldwide: A Systematic Review

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Abstract

Introduction The aim of this study was to develop a synthesis of the evidence available regarding verified *E. granulosus sensu lato* (*s.l.*) genotypes in different species worldwide.

Material and Methods A systematic review was performed including studies concerning genotypes of *E. granulosus s.l.* without language or genotyped method restriction, published between 1990 and 2020. A systematic search was carried out in Trip Database, BIREME, SciELO, LILACS, IBECS, PAHO-WHO, EMBASE, PubMed, Scopus, and WoS. Variables of interest were year of publication, country, number of samples, and hosts; genotypes, molecular marker, haplotypes and molecular biology techniques used. Descriptive statistics were applied.

Results 2411 articles were analyzed, however 135 met the selection criteria, representing 8643 liver and lung samples. Of the samples selected 24% were human, the remaining samples pertained to non-human animal hosts; cattle and sheep prevailed with 28.6% and 26.6% of the studied samples, respectively. The reported evidence is mainly from Iran, Turkey, Argentina, China and Chile; with 50, 11, 6, 6 and 5 studies, respectively, published between 1992 and 2020 [most frequently during 2015–2020 (76/135 studies; 56.3%)]. The mitochondrial gene *cox1* was generally sequenced and informative (91.8%). Genotypes most frequently identified were *E. granulosus sensu stricto* (*s.s.*) (83.2%).

Conclusions Based on this overall evidence, it can be concluded that publications related to genotypes of *E. granulosus s.l.* are heterogeneous. *E. granulosus ss* accounts for the vast majority of the global burden of *E. granulosus s.l.* worldwide. Further studies including larger number of cases and adequate internal validity are required to specify the distribution of genotypes in various host species.

Trial registration: PROSPERO CRD42018099827.

Keywords Echinococcosis · *Echinococcus granulosus* · Genes · Genotype · Systematic review

Introduction

Cystic echinococcosis, caused by the cestode *Echinococcus granulosus sensu lato* (*s.l.*) is characterized by cystic lesions, most commonly in the liver and lungs, which can be fatal if left untreated. It can be found worldwide, and the World Health Organization considers it as one of the 17 neglected tropical diseases [1, 2]. The disease is the cause of substantial health and economic burdens, affecting especially low-income populations [2].

In the last decades, diverse research groups around the world have studied *E. granulosus s.l.*, used to be called strains. These, differ namely in protein profile includes, carbohydrate types, lipid repertoires, morphology of rostral hooks, metabolic characteristics, etc. [1, 3] Aspects observed

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are related to variations between the different genotypes and cyst fertility, specificity of intermediate hosts, and antigenicity. Furthermore, there is evidence suggesting that the identification of genotypes through sequencing mitochondrial DNA (mtDNA) of *E. granulosus s.l.*, can be helpful to identify differences in virulence [3], host specificity, pathogenicity, antigenicity, and transmission dynamics [4–6].

In the last decades, the development of the polymerase chain reaction (PCR) along with the Sanger sequencing process, allowed for the characterization of *E. granulosus s.l.* in diverse genotypes and development for a molecular classification sequencing mainly *cox1* and *nad1* genes in mtDNA. Until date, the genotype classification divided *E. granulosus* into *E. granulosus sensu stricto* (*s.s.*), *E. equinus*, *E. ortleppi*, *E. canadensis*, and *E. felidis* [6–8]. Some evidence exists which support that G2 is a subgroup of G1 (using *cox1* sequences) or G3 (using *nad1* sequences) [7], and there is controversy about the differentiation between G1 and G3 (using *rrnS* marker) in light of this issue, G1-G3 genotype is considered as a single species, *E. granulosus s.s*. On the other hand, G9 was reclassified as a microvariant of G7 as the initial classification was improved using mitochondrial DNA fragments instead of restriction fragment length polymorphisms. To date, the results obtained from similar areas are concordant with G7 genotype only, and G6–G10 is known as a single group, partially because the genotypes proposed are not able to be replicated or classic markers used were not enough to differentiate them as different genotypes [8].

Furthermore, a different specie named *E. felidis* was discovered in lions from Africa [9], and its confirmation as specie continue under scrutiny due to the low number of samples informed [10]. In 2016, a novel genotype (GOmo) related to *E. granulosus s.s*. was described in a 55-year-old male patient in South Omo, Ethiopia using whole mitochondrial sequences and nuclear genes elongation factor 1 alpha (ef1α) and ezrin-radixin-moesin (ERM)-like protein (elp) without exact *E. granulosus* or *E. felidis* classification [11].

Additionally, a different genetic classification remains questionable due to the low number of samples reported [10]. Globally, there are increasing numbers of reports of genotypes in diverse host species and isolates.

Furthermore, it should be noted that critical data with over 300 samples sequenced by Balbinotti's ($n = 638$), Nungari's ($n = 389$) and Khademvatan's ($n = 334$) research groups, were reported [12–14]. The aim of this study was to develop a synthesis of the evidence available regarding verified *E. granulosus s.l.* genotypes in different species worldwide.

Material and Methods

This systematic review (SR) was written following the guidelines of the PRISMA statement [15] and AMSTAR 2 (A Measurement Tool to Assess systematic Reviews) [16]; and registered as a protocol in PROSPERO (ID: CRD42018099827). Articles related to genotypes of *E. granulosus s.l.*, in human or non-human animal hosts, without language or genotyped method restriction, published between 1990 and 2020, were included. This study excludes cystic echinococcosis records with an ambiguous description of their genotype, studies contaminated with alveolar echinococcosis in which data were not ungrouped, as well as review articles and letters to the editor. Ten sources of information were consulted: Trip Database, BIREME-BVS, SciELO, LILACS, IBECS, PAHO-WHO, EMBASE, PubMed, Scopus, and WoS. In addition, a cross-reference search was performed manually.

The main search terms (MeSH and free terms) were: Echinococcus, "*Echinococcus granulosus*", "*Echinococcus granulosus sensu lato*", echinococcosis, "hydatid cyst", "hydatidosis", genotype, strain, species, sequence, molecular marker and gene; with Boolean operators AND and OR, in the period 1990–2020. Search for articles was closed on September 31, 2020. Searches were adapted to each database and its corresponding language. For instance, the generic syntax for the PubMed database was as follow: ("Echinococcosis" OR "*Echinococcus granulosus*") ("Genotype" OR "Haplotypes" OR "Molecular Epidemiology").

Eligibility assessment was performed independently in an unblinded standardized manner by two groups of two reviewers each (CM-CR and ATS-NG). Disagreements between reviewers were resolved by consensus. Studies which accomplished the criteria above were included in a data extraction form in an Excel sheet by two investigators (CM, ATS), and the other three checked the extracted data (NG, AR and CR). Disagreements were resolved by consensus between the two review authors.

The following information was extracted from each included study: (1) characteristics of studies participants (year of publication, country and region, number of samples, host and organ of origin of the samples, and type of primary study design); (2) type of intervention (molecular techniques used, gene, and number of base pairs used); (3) type of outcome measure (genotype and haplotype identified).

Summary measures were descriptive statistics (percentages and average calculation). The risk of potential missing studies was avoided applying cross reference search. Study design of each article was determined. Additionally, judgments about overall risk of bias for each study was done using the AMSTAR checklist (www.amstar.ca), categorizing

as low, moderate, high, or unknown risk of bias [16]. The documents identified in each information source were filtered by duplication between bases. Subsequently, titles and abstracts were examined by applying selection criteria. Finally, an in-depth analysis of each of the selected primary articles was carried out, applying reading guides. This allowed for better organization of information synthesis. Potential missing studies were obtained applying cross-reference. The articles included in this study agree the ethical guidelines for research in humans and animals.

In addition, sequences of the *cox1* gene and complete mitochondrial genome sequences were searched from GenBank database (https://www.ncbi.nlm.nih.gov/pmc/articles/PMC4702903) and literature as of April 2020 (include the isolates of this study). Nucleotide sequences were separated between short and full length. Phylogenetic trees were made using 500 bootstrap and the "neighbor-joining model". The haplotype networks were performed using the PopArt software (https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12410).

Results

The systematic search within the information sources allowed 2411 records to be recovered. It was verified that 291 articles were duplicated between different databases consulted. Analysis of titles and abstracts allowed deleting 1567 records. In-depth analysis of the 553 selected studies; and the detailed reading of these, allowed exclusion of 437 articles for not meeting inclusion and exclusion criteria. To the 116 selected studies, 19 obtained from cross-reference search were added, to obtain a final number of 135 studies corresponding to this SR [4, 5, 7, 12–14, 17–145] (Fig. 1).

General Characteristics of Studies Informing Genotypes

All studies finally selected for the SR were case series. They represent 8643 samples, being cattle (28.6%), sheep (26.6%) and human (24.0%) the majoritarian hosts (Table 1). The existing evidence mainly comes from Iran, Turkey, Argentina, China and Chile; with 50, 11, 6, 5 and 5 studies, respectively (Table 2), but there are samples representing 48

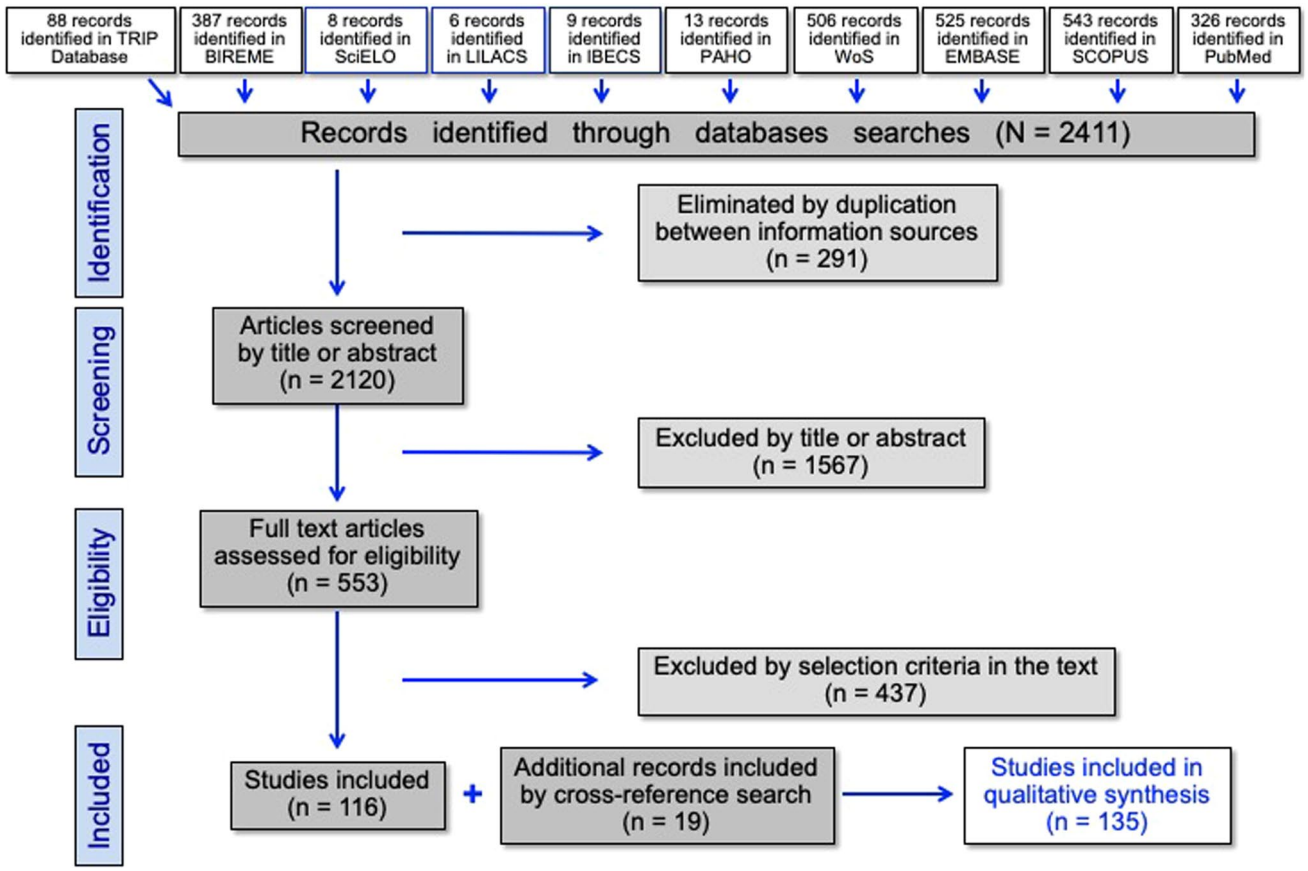

Fig. 1 Flowchart of the participating studies (according to PRISMA statement [15])

Table 1 *Echinococcus granulosus sensu lato* hosts

Species	No. samples	%	No. studies**	%
Cattle	2472	28.6	62	45.9
Sheep	2296	26.6	74	54.8
Human	2073	24.0	77	57.0
Goat	588	6.8	41	30.4
Camel	531	6.1	27	20.0
Dog	141	1.6	19	14.1
Pig	138	1.6	20	14.8
Buffalo	111	1.3	10	7.4
Yak	110	1.3	3	2.2
Horse	46	0.5	5	3.7
Wild boar	44	0.5	4	3.0
Dromedary	23	0.3	3	2.2
Wild pika	22	0.2	1	0.7
Others*	48	0.6	17	12.6
Total	8643	100		

*Donkey 16 samples; alpaca and reindeer 4 samples each; kangaroo and rabbit 3 samples each; moose, lemur, jackal, dingo, water buffalo, huemul, crested porcupine, zebra and cat, 2 samples each

**90 articles considered in this SR, studied more than one specie samples

Table 3 Publication period of primary studies used in this systematic review

Period	No. studies	%
2020–2015	76	56.3
2014–2010	38	28.1
2009–2005	7	5.2
2004–2000	8	5.9
1999–1995	4	3.0
1994–1990	2	1.5
Total	135	100

Table 4 Molecular biology techniques utilized for sequencing, reported in the primary studies used in this systematic review

Techniques	No. studies	%
PCR + SS	98	72.5
PCR + RFLP	17	12.6
PCR + RFLP + SS	16	11.9
PCR + RFLP + HRM + SS	4	3.0
Total	135	100

PCR polymerase chain reaction, *SS* Sanger sequencing, *RFLP* restriction fragment length polymorphism, *HRM* high-resolution melting

different countries. The time period with the greater number of articles related was the quinquennium 2015–2020 (76 studies, 56.3%), and the first report of this group of articles was published in 1992 [4] (Table 3).

Information Related Directly with Genotypes

DNA sequences were obtained using Sanger sequencing in 98 studies (72.5%), see Table 4. In most of the studies, the mitochondrial genes *cox1* (91.8%) and *nad1* (40.0%) were sequenced, simultaneous in some cases (Table 5).

Geographical distribution of the number of samples considered in this SR, can be verified in Fig. 2, highlighting Iran, Turkey, Argentina, Chile, Brazil and China.

On the other hand, genotypes most frequently identified were G1, complex G1–G3 and G6 (45.3%, 33.0%, and 5.7% of the studied samples, respectively) (see Table 6).

Additionally, 50 studies were identified where the haplotype analysis was carried out, this information is included

Table 2 Country of origin of primary studies used in this systematic review

Countries	No. studies	%
Iran	50	37.0
Turkey	11	8.1
Argentina	6	4.4
China	5	3.7
Chile	5	3.7
Kenya	4	3.0
Mexico	4	3.0
Peru	4	3.0
Others*	46	34.1
Total	135	100

Finally, three studies report samples coming from different countries without differentiation in the sampling (Australia, China, Holland, India, Ireland, Italy, Jordan, Kenya, Lebanon, Poland, Somalia, Spain, Sudan, Tasmania, Turkey, UK, USA, and Uruguay)

*Pakistan and Spain (three studies each), Algeria, Brazil, Egypt, Greece, India, Italy, Sudan, Russia, and Tunisia (two studies each); Australia, Azerbaijan, Bolivia, Bulgaria, Ethiopia, Finland, France, Iraq, Libya, Moldova, Mongolia, Oman, Poland, Romania, Saudi Arabia, Slovenia, Serbia, Slovakia, and Tibet (one study each)

Table 5 Genetic marker sequenced reported in primary studies used in this systematic review

Marker	No. studies*	%
cox1	123	91.8
nad1	54	40.0
ITS1	22	16.3
rrnS	13	9.6
atp6	5	3.7
ef1a	4	2.9
actII	3	2.2
rrnL	2	1.4
hbx2	1	0.7
nd2	1	0.7
nd4	1	0.7

*Several studies used more than one gene for genotyping

in Table 7. In most of the studies found in the literature, various phylogenetic analyzes or haplotype networks have been carried out from the use of partial sequences of the *cox1* and *nad1* genes, and on some occasion's complete mitochondrial genomes or lesser informative mitochondrial genes have been sequenced (interspaced regions, or nuclear gene sequences). A phylogenetic tree was carried out using the sequences obtained from GenBank. The results indicate that there was a concordance between the identified genotype in the articles and the proximity of the branches in the phylogenetic tree for the *cox1* gene (*E. granulosus s.s.*, *E. equinus, E. ortleppi*, *E. canadensis*; Fig. 3). The same information was obtained by means of haplotype networks, finding similar results in the grouping of the sequences, finding a great dispersion of the samples obtained for the American continent (Fig. 4).

In the haplotype networks, the results are grouped in a similar way to those as previously described in the literature, *E. granulosus s.s.* being more frequent worldwide with *E. canadensis* in second place in the American and European continents. *E. granulosus s.s.* are most common in Africa, while *E. granulosus s.s.* prevail highest in Asia, with low numbers of *E. canadensis* samples reported.

Risk of Bias

All studies are either case reports ($n < 10 = 20$ articles) or case series ($n = 115$ articles). Therefore, the overall risk of bias was: high $n = 109$ (80.1%), and moderate $n = 26$ (19.9%) [16]. Even though we requested additional information from several authors to expand and/or verify some study data, no replies were received; missing data may therefore contribute to bias in this review.

There may be a publication bias, given the scarcity of studies from certain geographic areas and countries, which could represent variants not verified in this review. This SR collects gathered and included genotypic evidence of cystic echinococcosis informed worldwide.

All potential hosts (humans, animals, intermediate and definitive) based on 135 articles as a primary source, with 8643 samples sequenced mainly through analysis of mitochondrial *cox1* and *nad1* genes were considered. In some cases, nuclear genes have also been included. Additionally, collected data of haplotypes included, are reported and analyzed via different approaches such as haplotype networks and phylogenetic trees. Genotype classification is informed commonly in the literature using the "G-system", which leads to a classification bias due to recent reconsideration about this classification and lack of replication for some genotypes proposed, and low sample size for the new genotypes informed, and in some cases the molecular technique as qualitative techniques such as RFLP alone instead of Sanger sequencing.

Discussion

Globally, and over the past 20 years identification of *E. granulosus s.l.* genotypes have been increasing in various studies. However, there are 5 SRs in which results of *E. granulosus s.l.* genotyping is reported with a significant sample size. In one of these, the results of 1534 samples in humans and animals from South America are analyzed [3]. The second study from Southern Africa, included studies from only 2 databases, between December 2017 and June 2019 (48 studies), and is oriented principally to the prevalence of the infection [8]. In the third study from Iran, the country with the most information gathered, only 559 human samples were reported [146]. In another study carried out in Iran, results of 340 samples from human and animal hosts were included [147], most of the studies where genotyping including intermediate hosts such as cattle, sheep and pig livestock samples; noted for their great economic impact, and in lesser numbers,

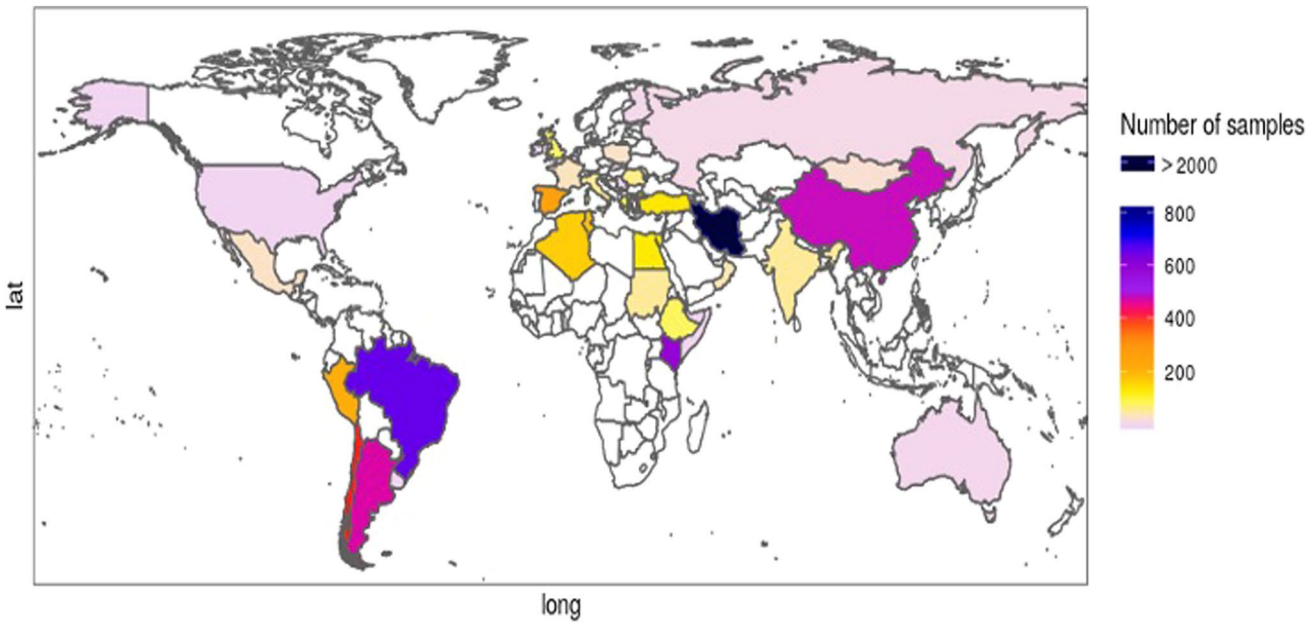

Fig. 2 Geographical distribution of samples considered in this systematic review

Table 6 Isolated genotypes reported in primary studies used in this systematic review ($n = 8643$ samples)

Genotypes	No. studies*	No. sequences	%
E. granulosus sensu stricto	187	7190	83.2
G1**	95	3921	45.3
G2**	12	48	0.6
G3**	42	369	4.3
G1-G3**	38	2852	33.0
E. equinus	8	76	0.9
E. ortleppi	15	430	5.0
E. canadensis	177	947	10.9
G6**	41	499	5.7
G7**	21	204	2.4
G6-G7**	11	214	2.5
G8**	1	1	0.01
G9**	1	17	0.2
G10**	1	5	0.06
G6-G10**	2	7	0.08
Total		8643	100

*In several studies more than one genotype was identified

**This was the way it was reported in primary studies (using G-system in the majority of studies)

human samples have been genotyped as a means of preventive community health epidemiological studies. And other, carried out only in human samples worldwide ($n = 1511$), obtained from primary studies from 1994 to 2019 [148].

To obtain larger numbers of DNA sequences, most studies have combined sequences of different intermediate hosts of the same area, including human beings.

During the last 10 years, there has been greater interest in the study of molecular epidemiology of *E. granulosus s.l.* in Iran, Turkey and China in Asia, as well as in Argentina and Chile, where research focused on highlighting the relevance of this disease. Slightly more than 84% of the studies analyzed in this systematic review were published in the last decade, and it is quite possible that the number of analyzed samples, intermediate hosts, and published articles will continue to increase.

Regarding the molecular biology techniques used, in a first approximation in the 90s qualitative studies began by means of restriction analysis fragment length polymorphisms (RFLPs) of specific markers in mitochondria such as *ITS1*, which became controversial, since it is considered in certain cases, that results cannot be properly replicated. Therefore, samples were subsequently sequenced using the Sanger technique, which nowadays is a feasible option to

Table 7 *Echinococcus granulosus s.l.* haplotypes informed in the literature ($n = 50$ studies)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Ali [21]	Eg01 (JQ250806), EgCL03 (KX227118), EgBol1-EgBol7 (MT072973-MT072979), Eo12 (KU743926), EcPer1 (AB777924)	Cattle (25), sheep (7), and pig (3)	*cox1*	PCR and Sanger sequencing	Bolivia
Alvarez-Rojas [22]	EG01 (JQ250806); EGp1 (AB522646); EgAus03 (KT968704); EgAus02 (KT968703); EgRUS7 (AB777904); EgCL1-EgCl21 (KX227116-KX227136)	Cattle (43), human (13), dog (7), sheep (5), and goat (1)	*cox1*	PCR and Sanger sequencing	Chile
Alvi [23]	MN886252-MN886293	Cattle (40) and buffalo (20)	*cox1*, *nad1*	PCR and Sanger sequencing	Pakistan
Andresiuk [24]	C1-C7; N1-N3 (KC579441–KC579451)	Cattle (42) and sheep (34)	*cox1*, *nad1*	PCR, Sanger sequencing	Argentina
Barazesh [29]	H1 (MF544127); H2 (MG672258); H3 (MH542404); H4 and H5 (MH542399, MH542406, and MH542395)	Sheep (25) and cattle (24)	*cox1, nad1*	PCR and Sanger sequencing	Turkey and Iran
Bold [30]	H1 (EcMGL2); H2 (no registered); H3 (EcMGL15); H4 (no registered)	Camel (19) and goat (1)	*cox1*	PCR and Sanger sequencing	Mongolia
Bonelli [31]	SAR1 MK780826, SAR2 MK780827, SAR3 MK780828, SAR4 MK780829, SAR5 MK780830, SAR6 MK780831, SAR7 MK780832, SAR8 MK780833 SAR9 MK780834, SAR10 MK780835, SAR11 MK780836, SAR12 MK780837, SAR13 MK780838, SAR14 MK780839, SAR15 MK780840, SAR16 MK780841, SAR17 MK780842, SAR18 MK780843, SAR19 MK780844, SAR20 MK780845, SAR21 MK780846, SAR22 MK780847, SAR23 MK780848, SAR24 MK780849, SAR25 MK780850, SAR26 MK780851, SAR27 MK780852, SAR28 MK780853, SAR29 MK780854, SAR30 MK780855	Sheep (52), cattle (16), goat (2), pig (4), wild boar (3), domestic cat (1), and human (5)	*cox1*	PCR and Sanger sequencing	
Boufana [33]	EGUK01-EGUK03 (AF346403; AB786665; AF346403)	Horse (31), dog (26), sheep (10), human (4), cattle (2), lemur (2), and zebra (1)	*cox1*	PCR and Sanger sequencing	UK
Boufana [34]	EgTu01–EgTu39 (KM014606–KM014644)	Sheep (33), human (22), dog (20), cattle (16), goat (14), wild boar (13), donkey (10), camel (7), and jackal (2)	*cox1*	PCR and Sanger sequencing	Tunisia
Cengiz [37]	ANK1, ANK2, ANK3, ANK4, ANK5, ANK6, ANK7, ANK8, ANK9, ANK10,ANK11, ANK12,ANK13, ORD1, ORD2, ORD3, ORD4, ORD5, ORD6, ORD7, ORD11, ORD12, ORD13, ORD14, ORD15, ORD16, ORD17, ORD18, ORD19, ORD20, ORD21, ORD22,ORD23,ORD24, ORD25, ORD26,ORD27, MER1, MER2, MER3, ADN1,ADN2, ADN3,ADN4, ADN5, ADN6, ADN7	Sheep (39) and cattle (10)	*cox1*	PCR and Sanger sequencing	Tiurquia
Correa [38]	H1-H11 (MF421702-MF421712)	Cattle (284)	*cox1*	PCR–RFLP,Sanger sequencing	Chile
De la Rue [43]	H1 (M84661); H2 (AF458872); H3 (EF367289); H4 (no registered)	Dog (12) and human (6)	*cox1*	PCR and Sanger sequencing	Brazil

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Farhadi [49]	EGH1-EGH13 (KP859559–KP859571)	sheep (49), cattle (28), and human (9)	*cox1*	PCR sanger squencing	Iran
Gorgani-Firouzjae [52]	H1 ([EgS2] MF346705; [EgB2] MF625021); H2 ([EgS1] MF625022); H3 ([EgS12] MF625020); H4 ([EgB6] MF449137); H5 ([EgB1] MF346706); H6 ([EgHum5] MG099696); H7 ([EgHum4] MG099695); H8 ([EgS11] MF625018); H9 ([EgS6] MF449131); H10 ([EgB3] MF625019)	Sheep (28), cattle (9), and human (5)	*cox1*	PCR–RFLP, Sanger sequencing	Iran
Guo [54]	H1-H15 (MH211191-MH211205)	Sheep (44), cattle (31), and human (26)	*cox1*	PCR and Sanger sequencing	China
Hajialilo [55]	H1 ([IRCO1] HM563001, HM563009–11; [IRND1] HM563023–26); H2 ([IRCO1] HM563011, [IRND2] HM563027); H3 ([IRCO1] HM563011, [IRND3] HM563028), H4 ([IRCO1] HM563010, [IRND4] HM563029); H5 ([IRCO1] HM563010, [IRND6] HM563031); H6 ([IRCO2] HM563012, HM563013, [IRND1] HM563023, HM563026); H7 ([IRCO2] HM563012, [IRND3] HM563028); H8 ([IRCO3] HM563014, [IRND5] HM563030); H9 ([IRCO4] HM563016, [IRND7] HM563032); H10 ([IRCO4] HM563017, [IRND8] HM563033); H11 ([IRCO4] HM563015, [IRND9] HM563034); H12 ([IRCO5] HM563018, HM563019, [IRND10] HM563035, HM563036); H13 ([IRCO6] HM563020, [IRND11] HM563037)	Sheep (15), cattle (10), camel (9), goat (3), and human (1)	*cox1*, *nad1*	PCR and Sanger sequencing	Iran
Hammad [56]	Hap_5; Hap_6; Hap_7; Hap_8; Hap_9 (no registered)	Cattle (20), sheep (17), human (3), buffalo 2, and goat (1)	*cox1*	PCR and Sanger sequencing	Irak
Han [57]	EgQH1 (MG674403); EgQH2 (MG674404); EgQH3 (MG674405); EgQH4 (MG674406); EgQH5 (MG674407); EgQH6 (MG674408); EgQH7 (MG674409); EgQH8 (MG674410); EgQH9 (MG674411); EgQH10 (MG674412); EgQH11 (MG674413); EgQH12 (MG674414); EgQH13 (MG674415); EgQH14 (MG674416); EgQH15 (MG674417); EgQH16 (MG674418); EmQH1 (MG674419); EsQH1 (MG674420);	Human (93), yak (91), sheep (38), and wild pika (22)	*cox1*	PCR and Sanger sequencing	Tibet (China)
Hidalgo [64]	Haplotype Eg01 (JQ250806), EGp1 (AB522646), EgAus03 (KT968704), EgCL01 (KX227116), EgCL02 (KX227117), EgCL20 (KX227135), EgCL22 (MK139300), EgCL23 (MK139301), EgCL25 (MK139305), EgCL26 (MK139303), EgCL28 (MK399399), EgCL29 (MK399400), EgCL30 (MK401902), EgCL31 (MK399401), EgCL32 (MK399402), EgCL33 (MK399403)	Cattle (7) and sheep (3)	*cox1*	PCR and Sanger sequencing	Chile

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Jafari [67]	IfnN1 (KX186691.1); IfnC1 (KU360325.1); IfnN2 (KU925412.1); IfnC2 (KT254124.1); IfnN3 (KY495928.1); IfnC3 (EF367259.1); IfnN4 (HM853647.1); IfnC4 (KU360316.1); IfnN5 (KX298249.1); IfnC5 (KX269858.1); IfnN6 (KF437795.1); IfnC6 (KU360299.1); IfnN7 (GQ168810.1), IfnC7 (DQ269944.1); IfnN8 (KX010894.1); IfnC8 (KX010872.1); IfnN9 (KP751440.1)	Human (50)	*cox1*, *nad1*	PCR, Sanger sequencing	Iran
Khan [71]	MG958694-PK1	Human (1)	*cox1*	PCR and Sanger sequencing	Pakistan
Kinkar [74]	SPA5 (KY766886); SPA1 (KY766900); SPA2 (KY766896); SPA4 (KY766897); SPA3 (KY766903)	Sheep (5)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Spain
Kinkar [74]	FIN1- (KY766884)	Human (1)	WMG, *cal, ef1, tgf*	PCR. and Sanger sequencing	Algeria (patient detected in Finland)
Kinkar [74]	TUN1 (KY766885)	Sheep (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Tunez
Kinkar [74]	ARG1 (KY766882)	Cattle (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Argentina
Kinkar [74]	IND2 (KY766891); IND1 (KY766902)	Buffalo (2)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	India
Kinkar [74]	CHI1 (KY766890)	Cattle (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Chile
Kinkar [74]	TUR4 (KY766888); TUR1 (KY766901); TUR2 (KY766904); TUR3 (KY766898)	Sheep (3) and cattle (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Turkey
Kinkar [74]	FRA3 (KY766889); FRA1 (KY766893); FRA2 (KY766892)	Sheep (2) and cattle (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	France
Kinkar [74]	ALB1 (KY766883)	Sheep (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Albania
Kinkar [74]	IRA4 (KY766887); IRA3 (KY766899); IRA1 (KY766894); IRA2 (KY766895)	Camel (3) and sheep (1)	WMG, *cal, ef1, tgf*	PCR and Sanger sequencing	Iran
Karamian [69]	Cox1-EIran-1 (KP751430); Cox1-EIran-2 (KP751426)	Human (9), camel (5), and sheep (3)	*cox1*	PCR and Sanger sequencing	
Konyaev [75]	EgRUS7 (AB777904); EgRUS10 (AB777907); EgRUS11 (AB777908); EgRUS8 (AB777905); EgRUS9 (AB777906); EcRUS7 (AB777914)	Sheep (4) and human (3)	*cox1*	PCR and Sanger sequencing	Russia

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Laatamna [77]	EG01 (JQ250806); EG40 (AB688617); EgA01 (KX020323); EgA16 (KX020337); EgAus03 (KT968704); EgAlg01 (MG808282); EgAlg02 (MG808283); EgAlg03 (MG808284); EgAlg04 (MG808285); EgAlg05 (MG808286); EgAlg06 (MG808287); EgAlg07 (MG808288); EgAlg08 (MG808289); EgAlg09 (MG808290); EgAlg10 (MG808291); EgAlg11 (MG808292); EgAlg12 (MG808293); EgAlg13 (MG808294); EgAlg14 (MG808295); EgAlg15 (MG808296); EgAlg16 (MG808297); EgAlg17 (MG808298); EgAlg18 (MG808299); EgAlg19 (MG808300); EgAlg20 (MG808301); EgAlg21 (MG808302); EgAlg22 (MG808303); EgAlg23 (MG808304); EgAlg24 (MG808305); EgAlg25 (MG808306); EgAlg26 (MG808307); EgAlg27 (MG808308); EgAlg28 (MG808309); EgAlg29 (MG808310); EgAlg30 (MG808311); EgAlg31 (MG808312); EgAlg32 (MG808313); EgAlg33 (MG808314); EgAlg34 (MG808315); EgAlg35 (MG808316); EgAlg36 (MG808317); EgAlg37 (MG808318); EgAlg38 (MG808319); EgAlg39 (MG808320); EgAlg40 (MG808321); EgAlg41 (MG808322); EgAlg42 (MG808323); EgAlg43 (MG808324); EgAlg44 (MG808325); EgAlg45 (MG808326); EgAlg46 (MG808327); EgAlg47 (MG808328); EgAlg48 (MG808329); EgAlg49 (MG808330); EgAlg50 (MG808331); EgAlg51 (MG808332); EgAlg52 (MG808333); EgAlg53 (MG808334); EgAlg54 (MG808335); EgAlg55 (MG808336); EgAlg56 (MG808337); EgAlg57 (MG808338); EgAlg58 (MG808339); EgAlg59 (MG808340); EgAlg60 (MG808341); EgAlg61 (MG808342); EgAlg62 (MG808343); EgAg63 (MG808344); EgAlg64 (MG808345); EgAlg65 (MG808346); EgAlg66 (MG808347); EgAlg67 (MG808348); EgAlg01X (MG808349)	Sheep (56) and cattle (37)	*cox1*	PCR and Sanger sequencing	Algeria
Laurimäe [79]	IRA3 (MH300931); IRA4 (MH300932)	Camel (4)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Iran

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Laurimäe [79]	ARG4 (MH300955); ARG5 (MH300956); ARG5 (MH300957); ARG5 (MH300958); ARG5 (MH300960); ARG7 (MH300962); ARG7 (MH300963); ARG8 (MH300964); ARG9 (MH300965); ARG10 (MH300966); ARG11 (MH300967); ARG12 (MH300968); ARG12 (MH300970)	Pig (16) and goat (3)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Argentina
Laurimäe [79]	KEN2 (MH300937); KEN3 (MH300938)	Human (3)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Kenya
Laurimäe [79]	SUD1 (MH300939); SUD1 (MH300942); SUD1 (MH300943); SUD1 (MH300944); SUD1 (MH300945); SUD1 (MH300946); SUD1 (MH300947); SUD1 (MH300948); SUD1 (MH300949); SUD2 (MH300950); SUD2 (MH300951); SUD3 (MH300952);	Sheep (6), cattle (3), goat (3), and camel (2)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Sudan
Laurimäe [79]	MAU1 (MH300953); MAU2 (MH300954)	Camel (2)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Mauritana
Laurimäe [79]	Gmon (MH300971)	Human (1)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Mongolia
Laurimäe [79]	MEX1 (MH300972); MEX2 (MH300973); MEX3 (MH300974); MEX4 (MH300975); MEX5 (MH300976); MEX5 (MH300977); MEX6 (MH300978); MEX7 (MH300979); MEX8 (MH300980); MEX9 (MH300981)	Pig (10)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Mexico
Laurimäe [79]	FRA2 (MH300987); FRA3 (MH300988); FRA4 (MH300989); FRA4 (MH300990); FRA4 (MH300991); FRA5 (MH300992); FRA5 (MH300993); FRA5 (MH300994); FRA6 (MH300995); FRA6 (MH300997); FRA6 (MH300998); FRA6 (MH301000); FRA7 (MH301001); FRA8 (MH301002); FRA10 (MH301010); FRA10 (MH301011); FRA10 (MH301012); FRA12 (MH301015); FRA13 (MH301016); FRA14 (MH301017)	Pig (27)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	France
Laurimäe [79]	POL1 (MH301003); POL2 (MH301004); POL3 (MH301005); POL4 (MH301006); POL5 (MH301007)	Human (3) and pig (2)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Poland
Laurimäe [79]	LIT1 (MH301020)	Pig (1)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Lithuania
Laurimäe [79]	UKR1 MH301021); UKR1 (MH301022)	Pig (2)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Ukraine
Laurimäe [79]	SER1 (MH300984)	Pig (1)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Serbia
Laurimäe [79]	ROM2 (MH300983)	Sheep (2)	*ef1, cal, tgf, elp, pepck, pold*	PCR and Sanger sequencing	Romania

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Marinova [84]	H1 ([C1] KR070964, [N1] KR070984, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H2 ([C1] KR070964, [N3] KR070986, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H3 ([C1] KR070964, [N5] KR070988, [S1] KR070969, [L2] KR070974, [ATP1] KR070978); H4 ([C1] KR070964, [N2] KR070985, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H5 ([C1] KR070964, [N6] KR070989, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H6 ([C1] KR070964, [N4] KR070987, [S1] KR070969, [L1] KR070973, [ATP2] KR070979); H7 ([C2] KR070965, [N1] KR070984, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H8 ([C1] KR070964, [N8] KR070991, [S1] KR070969, [L1] KR070973, [ATP1] KR070978); H9 ([C3] KR070966, [N7] KR070990, [S2] KR070970, [L4] KR070976, [ATP4] KR070981); H10 ([C3] KR070966, [N7] KR070990, [S2] KR070970, [L3] KR070975, [ATP3] KR070980); H11 ([C3] KR070966, [N7] KR070990, [S3] KR070971, [L3] KR070975, [ATP3] KR070980); H12 ([C3] KR070966, [N7] KR070990, [S2] KR070970, [L3] KR070975, [ATP5] KR070982); H13 ([C4] KR070967, [N7] KR070990, [S2] KR070970, [L3] KR070975, [ATP3] KR070980); H14 ([C5] KR070968, [N9] KR070992, [S4] KR070972, [L5] KR070977, [ATP6] KR070983)	Human (30)	*cox1, nad1, rrnS, rrnL, atp6*	PCR-Sanger sequencing	Bulgaria
Matini [86]	Hamc1 (MG792551); Hamc2 (MG792552); Hamc3 (MG792553); Hamc4 (MG792554); Hamc5 (MG792555); Hamc6 (MG792556); Hamc7 (MG792557); Hamc8 (MG792558); Hamc9 (MG792559); Hamc10 (MG792560); Hamc11 (MG792561); Hamc12 (MG792562); Hamc13 (MG792563)	Sheep (32), human (10), cattle (5), and goat (3)	*cox1*	PCR and Sanger sequencing	Iran
Mehmood [88]	PKH1, PKH2, PKH3, PKH4, PKH5, PKH6, PKH7, PKH8, PKH9	Sheep (35), goat (26), cattle (30), and buffalo (30)	*cox1*	PCR and Sanger sequencing	Pakistan
Metwally [89]	Echs1-Echs12 (no registered); Echc1 (no registered); Echc2 (no registered)	Sheep (16) and camel (2)	*cox1*	PCR and Sanger sequencing	Saudi Arabia
Mirahmadi [90]	EgC1 MT786857,EgC2 MT786852, EgC3 MT786855, EgC4 MT786853, EgC5 MT786856, EgC5 MT786856, EgC6 MT786854, EgC7 MT800786, EgC8 MT786858, EgN1 MT793713, EgN2 MT799804, EgN3 MT793715, EgN4 MT793714, EgN5 MT793711, EgN6 MT79712	Human (44)	*cox1*, *nad1*	PCR and Sanger sequencing	Iran

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Moro [92]	Egra-A (AB458672); Egra-B (AB458673); Egra-C (AB458674); Egra-D (AB458675); Egra-E (AB470527); Ecan-A (AB458676); Ecan-B (AB458677); Ecan-C (AB458678)	Sheep (32), cattle (16), pig (12), goat (6), and human (5)	*cox1*	PCR and Sanger sequencing	Peru
Muqaddas [94]	PK-H1c, PK-H2c KP859560, PK-H3c KP859565, PK-H4c MG672235, PK-H5c HM563014, PK-H6c MN640735, PK-H7c KC422644, PK-H8c AB677807, PK-H9c AB677814, PK-H10c JX854025, PK-H11c MN640733, PK-H12c MN640731, PK-H13c DQ104331, PK-H14c MK310277	Human (94)	*cox1*	PCR and Sanger sequencing	Pakistan
Nikmanesh [98]	H1 (KF612381, KF612357); H2 (KF612356); H3 (KF612390, KF612360); H4 (KF612380, KF612358); H5 (KF612376, KF612349); H6 (KF612395, KF612350); H7 (KF612396, KF612355); H8 (KF612394), KF612343); H9 (KF612386, KF612351); H10 (KF612397, KF612369); H11 (KF612400, KF612372)	Human (30)	*cox1*, *nad1*	PCR and Sanger sequencing	Iran
Ohiolei [101]	NIG1-NIG7; MT166284-MT166290	Camel and cattle (NDF)	WMG	PCR and Sanger sequencing	Nigeria
Orsten [104]	TUK01-TUK28 (no registered)	Human (46)	*cox1*	PCR and Sanger sequencing	Turkey
Parsa [105]	H1 ([Lorc1] JN604097, [Lorn2] JN604107); H2 ([Lorc1] JN604097), [Lorn3] JN604108); H3 ([Lorc1] JN604097), [Lorn4] JN604109); H4 ([Lorc1] JN604097), [Lorn5] JN604110); H5 ([Lorc1] JN604097), [Lorn6] JN604111); H6 ([Lorc2] JN604098), [Lorn2] JN604107); H7 ([Lorc3] JN604099), [Lorn1] JN604106); H8 ([Lorc4] JN604100), [Lorn5] JN604110); H9 ([Lorc5] JN604101), [Lorn2] JN604107); H10 ([Lorc6] JN604102), [Lorn2] JN604107); H11 ([Lorc7] JN604103), [Lorn7] JN604112); H12 ([Lorc8] JN604104), [Lorn7] JN604112); H13 ([Lorc9] JN604105), [Lorn7] JN604112)	Dogs (20)	*cox1, nad1*	PCR and Sanger sequencing	Iran

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Pezeshki [107]	H1(AB677806 + AB677815); H2(AB677806 + AB677816); H3(AB677806 + AB677817); H4(AB677806 + AB677819); H5(AB677807 + AB677815); H6(AB677808 + AB677815); H7(AB677809 + AB677818); H8(AB677810 + AB677815); H9(AB677811 + AB677815); H10(AB677811 + AB677821); H11(AB677812 + AB677815); H12(AB677813 + AB677815)	Cattle (19), sheep (19), human (9), and goat (3)	*cox1, nad1*	PCR and Sanger sequencing	Iran
Pour [109]	G1α (HM130574, HM130575, HM130576, HM130577, HM130578); G1β (HM130579, HM130580, HM130581, HM130582, HM130583, HM130584 and HM130585); G1γ (HM130586, HM130587, HM130588, HM130589, HM130590, HM130591); G1δ (HM130593, HM130594, HM130595, HM130596)	Buffalo (25)	*cox1*	PCR and Sanger sequencing	Iran
Rodriguez-Prado [111]	KF734649-KF734660	Pig (9), and dog (3)	*cox1*	PCR and Sanger sequencing	Mexico
Roinioti [112]	KT285513; KT285514; KT285515; KT285516; KT285517; KT285518; KT285519; KM245580; KM521206; KT184863; KT184864; KT184865; KT184866; KT285520	Sheep (75), goat (6), and cattle (1)	*12S-rRNA, cox1*	PCR and Sanger sequencing	Greece

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Rostami [114]	IREG1 (KF443137); IREG2 (KF443138); IREG3 (KF443139); IREG4 (KF443140); IREG5 (KF443141); IREG6 (KF443142); IREG7 (KF443143); IREG8 (KF443144); IREG9 (KF443145); IREG10 (KF443146); IREG11 (KF443147); IREG12 (KF443148); IREG13 (KF443149); IREG14 (KF443150); IREG15 (KF443151); IREG16 (KF443152); IREG17 (KF443153); IREG18 (KF443154); IREG19 (KF443155); IREG20 (KF443156); IREG21 (KF443157); IREG22 (KF443158); IREG23 (KF443159); IREG24 (KF443160); IREG25 (KF443161); IREG26 (KF443162); IREG27 (KF443163); IREG28 (KF443164); IREG29 (KF443165); IREG30 (KF443166); IREG31 (KF443167); IREG32 (KF443168); IREG33 (KF443169); IREG34 (KF443170); IREG35 (KF443171); IREG36 (KF443172); IREG37 (KF443173); IREG38 (KF443174); IREG39 (KF443175); IREG40 (KF443176); IREG41 (KF443177); IREG42 (KF443178); IREG43 (KF443179); IREG44 (KF443180); IREG45 (KF443181); IREG46 (KF443182); IREG47 (KF443183); IREG48 (KF443184); IREG49 (KF443185); IREG50 (KF443186); IREG51 (KF443187); IREG52 (KF443188); IREG53 (KF443189); IREG54 (KF443190); IREG55 (KF443191); IREG56 (KF443192); IREG57 (KF443193); IREG58 (KF443194); IREG59 (KF443195); IREG60 (KF443196); IREG61 (KF443197); IREG62 (KF443198)	Sheep (75), goat (6), and cattle (1)	*cox1*	PCR–RFLP and Sanger sequencing	Iran
Shang [126]	G1-G34 (KX685889–KX685927)	Human (109)	*cox1*	PCR and Sanger sequencing	China

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Sharbatkhori [127]	H1 ([Golc1] KM513626, [Golc1-1] KT074941, [Goc1-2] KT074942, [Goln1] KM513634, [Goln1-1] KT074936, [Goln1-3] KT074938); H2 ([Golc1] KM513626, [Goln3] KM513636); H3 ([Golc1-1] KT074941, [Golc1-2] KT074942, [Golc1-3] KT074943, [Goln4] KM513637, [Goln4-1] KT074939, [Goln4-2] KT074940); H4 ([Golc2] KM513627), [Golc2-1] KT074944, [Golc2-2] KT074945, [Goln1] KM513634, [Goln1-1] KT074936, [Goln1-3] KT074938); H5 (Golc2-2] KT074945, [Goln2] KM513635); H6 ([Golc2-2] KT074945, [Golc2-3] KT074946, [Goln4-1] KT074939, [Goln4-2] KT074940); H7 ([Golc3]KM513628, [Golc3-1] KT074947, [Goln4-1] KT074939, [Goln4-2] KT074940); H8 ([Golc4] KM513629, [Goln1-2] KT074937); H9 ([Golc4-1] KT074948, [Goln4-1] KT074939); H10 ([Golc5] KM513630, [Goln4-1] KT074939); H11 ([Golc6] KM513631, [Goln1-3] KT074938); H12 ([Golc6] KM513631, [Golc6-1] KT074949, [Goln4-1] KT074939, [Goln4-2] KT074940); H13 ([Golc7] KM513632, [Goln1-3] KT074938); H14 ([Golc7] KM513632, [Goln4-1] KT074939); H15 ([Golc8] KM513633, [Goln5] KM513638)	Cattle (40), sheep (18), camel (9), human (4), buffalo (2), and goat (1)	*cox1*, *nad1*	PCR and Sanger sequencing	Iran
Shariatzadeh [128]	AZE03 (KP723338); AZE11 (KT154000); AZE01 (KT153999); AZE02 (KT153998); AZE04 (KT153997); AZE05 (KT153996); AZE10 (KT153995)	Dog (16)	*cox1*	PCR and Sanger sequencing	Iran
Sharifiyazdi [129]	Camel A CO1 (HM626405), Camel B CO1 (HM626406),Camel A ND1 (HQ585933), Camel B ND1 (HQ585934), Microvariant (HM626405)	Camel (15)	*cox1, nad1, its1*	PCR and Sanger sequencing	Iran
Soriano [132]	G1nqnA; G1nqnB; G1nqnC; G6nqn; (GU980906-14)	Goat (23), pig (18), sheep (16), and dog (10)	*cox1*	PCR and Sanger sequencing	Argentina
Spotin [133]	IR2; IR3; IR5; IR6; IR7; IR8; IR10; IR12; IR13; IR14; IR17;IR18; IR19; IR22; IR34; IR35; IR36; IR38; IR39; IR43; IR44; IR47; IR48; IR49	Human (41), dog (22), camel (21), goat (15), sheep (12), and cattle (4)	*cox1*	PCR and Sanger sequencing	Iran
Yan [141]	YLN1; YLY1; YLY2; YLY3; YLY4; YLY5; YLY16; YLY17; CJ128; CJ328; CJ429; CJ529; CJ618; CJ719; CJ23; CJ51; CJ75; YL1; YL2; YL5	Sheep (45) and cattle (10)	*cox1*	PCR and Sanger sequencing	China

Table 7 (continued)

References	Haplotypes informed in literature	Molecular technique	Markers	Molecular Technique	Country
Zait [143]	HL1 (C1, N1); H2 (C6, N1); H3 (C1, N6); H4 (C12, N1); H5 (C13, N7); L6 (C8, N1); H7 (C1, N2); L8 (C7,N8); H9 (C1, N5); H10 (C3, N1); H11 (C1, N13); H12 (C2, N3); H13 (C2, N1); H14 (C5, N1); H15 (C4, N4); H16 (C10, N10); H17 (C9, N9); H18 (C10, N9); H18 (C10, N9); HL19 (C11, N11); HL19 (C11, N11); L20 (C11, N12); (AKR349027-KR349036, KR349038-KR349047, KR381826, KT316341-KT316343, KR349037, KR349048)	Human (54), sheep (7), cattle (4), goat (3) and dromedary (2)	*cox1*, *nad1*	PCR and Sanger sequencing	Algeria

WMG whole mitochondrial genome

*The table includes the access number to GenBank when it was available (adapted from Totomoch *et al.* [154])

study genotypes. At the present time, 72.1% of the studies found in the literature used Sanger sequencing, and in some cases this was combined with High-Resolution Melting (HRM) and multiplex PCR to have a pool of techniques that improve screening and specific genotypes identification.

In recent years, the number of genome sequences reported in the literature has increased and is expected to continue to do so due to the emergence of the second and third generation sequencing with improved performance and relatively low cost. As an example, is the identification of a 4.4 kb region in tandem obtained using PacBio Single Molecule Real-Time in a G1 sample obtaining a 4.4 kb tandem repeat region from a sheep [149], which could help to include in the future a new set of markers for a better genotyping classification using of microsatellites as a viable method for genotyping *E. granulosus s.s.* [150, 151].

Additionally, it has been detected that there is an under representation of genotypes in South America [148], North America and Africa. Furthermore, there are wild species not commonly studied in the different continents such as wild-pika, alpaca, huemul, kangaroo and others. Pilot studies in natural reserves in Australia found a number of infected wildlife species [152].

E. granulosus s.s. and *E. canadensis* show a notable difference in the number and distribution of cases since studies show significant differences regarding the relevance of the information available. Such data help to clarify the information in as far as the dynamic of the parasite in South America. Nevertheless, in North America there are still under reported registers of the disease [153]. According to the information obtained and analyzed in the various phylogenies and the haplotype network, it can be inferred that the occurrence is higher in the American continent. A single *E. granulosus s.s.* group exists in the genotype classification and the number of mutations between *E. canadensis* (G6/G7), are not significant to consider a division between the two genotypes because there is a very limited gene flow between these genotypic groups [74, 79]. Additionally, is has been established that the GOmo is based on the *E. granulosus s.s.* genotype, concluding that the various mutation changes depend on the adaptive structure of each genotype, local changes leading to a unique population structure as the one presented in this manuscript.

The evidence obtained is sufficiently robust to determine that *E. granulosus s.s.*, are responsible for a great part of cystic echinococcosis worldwide, followed by *E. canadensis*. There is scarce evidence of infection by *E. equinus*, GOmo and *E. felidis* and there is low information of human samples with *E. ortleppi* (in this systematic review, it was reported in 15 of 135 studies, representing only the 5% of studied samples).

In this analysis, it was found that Iran has the largest number of publications and sequenced samples. This does not necessarily render that particular area more endemic than

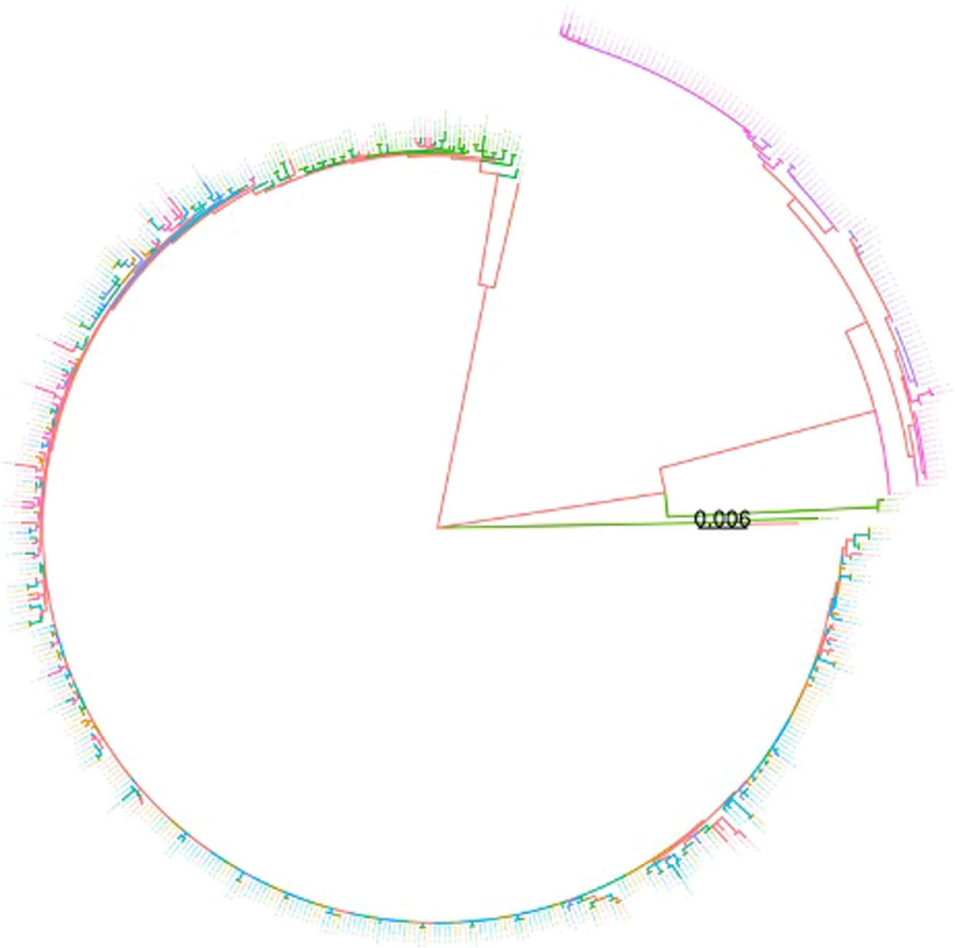

Fig. 3 A phylogenetic tree of *E. granulosus s.l.* based on *cox1* mitochondrial DNA sequences

other locations. Undoubtedly, this situation is underreported in other latitudes [148, 154].

Limitations of the Study

Regarding the limitations of this study, we can point out that primary studies are heterogeneous (using different methodologies) and are of low methodological quality (risk of bias high or moderate), since these are isolated case reports and case series (12 are unique case reports, 70 case series between 2 and 50 samples, 45 series between 51 and 200 cases, and only 8 series over 200 cases).

Additionally, data collection was hindered by the fact that authors of many of the publications reviewed, began their work with a determinate number of samples. These figures, however, did not coincide with the final number of sequenced samples; in some cases, the difference was significant, and the number of genotyped samples varied substantially.

On the other hand, concerning Sanger sequencing of mitochondrial genes, there is evidence which supports that the use of the short *cox1* fragments [4]; and even the use of the short *nad1* sequence [155] may not clearly discriminate a genotype of *E. granulosus s.s.* [74], and of *E. canadensis* [78]. Thus, the use of the genotypes reported by the authors should at least be discussed as it can lead to wrong genotype identification.

Finally, it is possible that there may be a reporting and publication biases, because there is a lot of unpublished experience, some studies published in poor visible journals, and studies that are not captured by search strategies.

Conclusions

These findings improve our understanding of the genetic diversity of *E. granulosus s.l.* Nonetheless, further in-depth studies are needed to better knowledge and understanding of the morpho-quantitative characterization of the genomic profile in the various hosts. This may be achieved through the application of the sequencing of whole genomes and transcriptomes, using second and third generation sequencing techniques for a better classification of genotypes and to identify new diagnostic candidates. In turn, these data

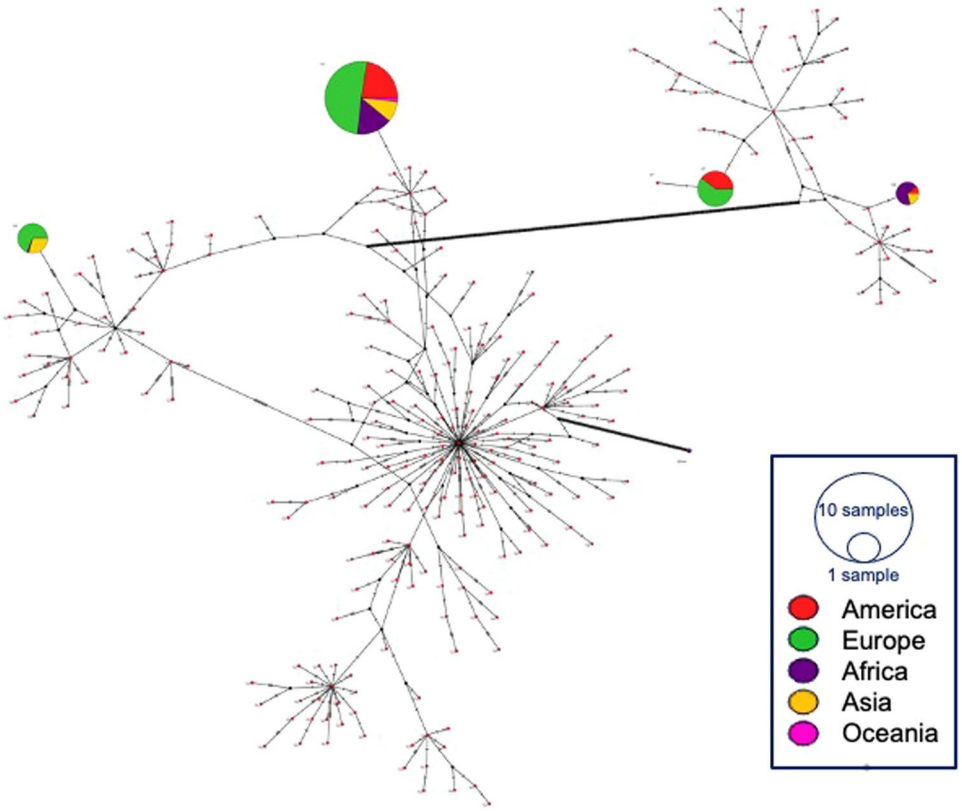

Fig. 4 Global Haplotype Network of *E. granulosus s.l.* based in whole mitochondrial genomes from GenBank databases by continents and number of study samples

may help to identify potential targets to develop vaccines or treatments. These may also aid in the development and standardization of molecular biology techniques for the identification of regions in the genome, or proteins for the selective and sensitive diagnosis of cystic echinococcosis infection. Finally, since *E. granulosus s.s.* are most prevalent in humans, cystic echinococcosis control initiatives should be directly aimed at the definitive host of this cycle (dogs other canines) and their intermediate hosts (cattle, sheep and goat).

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Declarations

Conflict of interest The authors have no conflict of interest.

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