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ORIGINAL PAPER

Frequency and genetic diversity of *Echinococcus granulosus* sensu stricto in sheep and cattle from the steppe region of Djelfa, Algeria

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Abstract

Cystic echinococcosis (CE) of humans and animals is caused by various species of *Echinococcus granulosus* sensu lato. Of these, *E. granulosus* sensu stricto has the widest geographical distribution and is the most important agent of human cystic echinococcosis. Previous molecular studies showed that *E. granulosus* s.s. isolates from the Middle East and western Asia exhibit higher intraspecific diversity than those from other parts of the world, which led to hypotheses on the origin of the species in that region. However, various high-endemicity regions have not been sufficiently covered by such studies, including northern Africa as a well-known focus of this parasite. Here, we report data on the mitochondrial cox1 gene (1609bp) sequence diversity of *E. granulosus* s.s. from Algerian livestock. An abattoir survey of 1278 animals from the Algerian steppe region (Djelfa) resulted in CE prevalence of 13.9% in cattle ($n = 266$), 5.7% in sheep ($n = 975$), and 0% in goats ($n = 37$). All of 125 molecularly examined cyst isolates belonged to *E. granulosus* s.s. In total, 73 haplotypes were found, only five of which have been previously reported (from the Middle East and Australia). One haplotype sequence (EgAlg01X) was found to contain an insertion of three bases at the end of the gene. To the best of our knowledge, this has not been reported before for *Echinococcus* spp. Diversity values of our panel of Algerian samples were in the range of those that have been previously reported from the Middle East and far higher than those from elsewhere. This, together with the low number of shared haplotypes, indicates a more complex biogeographical history of this parasite than hitherto assumed.

Keywords *Echinococcus granulosus* sensu stricto · Haplotype · cox1 · Genetic diversity · Steppe region · Algeria

Introduction

Cystic echinococcosis (CE) is a neglected zoonotic disease of worldwide occurrence. It is caused by metacestodes of five, possibly more, cryptic species within *Echinococcus granulosus* sensu lato (s.l.) (Nakao et al. 2013; Romig et al. 2017). Of these, *E. granulosus* sensu stricto (s.s.) that has the widest geographical distribution, is in most regions the most frequent species in animals, and has the highest global impact on public health with close to 90% of genotyped human CE cases (Alvarez Rojas et al. 2014). Some studies on the intraspecific diversity of mitochondrial marker genes suggest that the biogeographical origin of *E. granulosus* s.s. is the Middle East and western Asia, where domestication of sheep, the principal intermediate host, had initially occurred and where the highest level of gene-sequence polymorphism can still be detected (Yanagida et al. 2012; Romig et al. 2017). From there, the parasite has hypothetically spread, together with sheep, to Europe, Africa, and central/eastern Asia, where some of the ancient polymorphism were gradually lost due to bottleneck events, and where new diversification into unique variants occurred. During the European colonization of the Americas and Australia, stock populations of domestic animals (and their parasites) originated mainly from southern

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Abd Elkarim Laatamna and Dennis Ebi contributed equally to this work.

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Europe and North Africa (Alvarez Rojas et al. 2016, 2017). To shed further light on spread and accidental introductions of this zoonotic parasite, it is therefore of particular interest to investigate the identity and diversity of *E. granulosus* s.s. variants in the Mediterranean region.

There are numerous data on the high endemicity of CE in humans and animals in northern African countries as well as in the adjacent Middle East (reviewed in Sadjjadi 2006; Dakkak 2010; Deplazes et al. 2017); this includes extensive prevalence figures of unspecified CE in livestock in Algeria, where up to 78% of sheep, 91% of cattle, and 26% of camels were reportedly infected (Bardonnet et al. 2003; Hamrat et al. 2011a, b; Kouidri et al. 2012, 2013; Ouchene et al. 2014), and where dog infection with *Echinococcus* spp. ranged from 16 to 51% (Benchikh-Elfegoun et al. 2008; Bentounsi et al. 2009). Some of the more recent studies include molecular identification of the causative agents. These suggest that *E. granulosus* s.s. is the most common species in the sheep-raising areas from Morocco to Egypt. Confirmed hosts are humans, sheep, and camels in all countries, cattle in Morocco, Algeria, Tunisia, and Libya, goats and donkeys in Morocco and Tunisia, addax (*Addax nasomaculatus*) and wild boars (*Sus scrofa*) in Tunisia, domestic dogs in Tunisia and Libya, and wild canids in Tunisia. In contrast, *Echinococcus canadensis* G6/7 seems to be distributed in the more arid camel-raising regions of North Africa, where it is known from humans in Tunisia, Algeria by Zait et al. (2016), and Egypt, from camels in all countries except Morocco, from cattle in Libya and Egypt, and from sheep in Egypt; domestic pigs in Egypt where also found to be infected with this parasite. A third species, *Echinococcus equinus*, has been reported from donkeys in Tunisia and Egypt (reviewed by Deplazes et al. 2017).

Here, we report the results of a livestock survey for *Echinococcus* spp. in the steppe region of the central part of northern Algeria, demonstrate the genetic diversity of *E. granulosus* s.s., and discuss the implications of this diversity in the light of previous hypotheses about the biogeography of this parasite.

Materials and methods

Study area

The research was carried out in the province of Djelfa that is situated in the central part of northern Algeria (34° 11′ to 34° 54′ N; 3° 15′ to 3° 46′ E). The province is positioned in the central part of the steppe territory of Algeria, characterized by a semi-arid climate, cold in winter and warm and dry in summer. Breeding of small ruminants (3,364,460 sheep and 405,400 goats, data extracted from the direction of agricultural services of the province of Djelfa for the years 2014–2015) is economically most important in this region, while camel and cattle breeding is less frequent. The survey was done in the municipal slaughterhouse of Djelfa that has a daily slaughtering capacity of approximately 300 sheep, 15 cattle and 80 goats. The slaughtered animals originated, apparently, from within Djelfa province, but their exact origin could not be determined. It cannot be excluded, that some animals (mainly cattle) may have originated from neighboring provinces of central Algeria.

Sample collection and fertility assessment

From January to September 2016, a total of 1278 animals (975 sheep, 266 cattle, and 37 goats) underwent a postmortem inspection for cystic echinococcosis. Three to four visits per week were made to the slaughterhouse, and the carcass of each animal was examined for cystic lesions by observation, palpation, and incision of internal organs (the lung, liver, spleen, kidney, and heart). Fertility of isolated cysts was assessed by microscopic examination for presence of protoscoleces. Protoscoleces or small pieces of the germinal layer of each isolated cyst were placed into a sterile plastic tube with 70% ethanol, and stored at 4 °C until molecular analysis.

Sample processing, PCR amplification, and sequencing

One protoscolex or, in case of non-fertile cysts, a small piece of germinal layer of comparable size was lysed in 10 μl 0.02 M NaOH for 10 min as described by Nakao et al. (2003). Consecutively, a 1609bp-fragment of the mitochondrial cox1 (cytochrome C oxidase, subunit 1) was amplified in two nested PCRs with primers and PCR conditions as described in Alvarez Rojas et al. (2016). PCR products were electrophoresed in 1.5% agarose gels and visualized under ultraviolet light. Secondary PCR amplicons were purified with the high-pure PCR purification kit (Roche Diagnostics) and sequenced at GATC Biotech AG (Konstanz, Germany).

Sequence analysis and haplotype network

The sequences were processed and controlled for double peaks or other errors using GENtle 1.9.4 (© Magnus Manske, Cambridge, UK). Haplotype networks were created using TCS 1.2.1 (Clement et al. 2000) with 95% connection limit. Diversity and neutrality indices were calculated using DnaSP 5.10 (Librado and Rozas 2009).

To place our sample set in a wider context, additional sequences of isolates from regions worldwide (Middle East, Asia/Russia, Europe, Australia, and South America) were recovered from GenBank and inserted in Fig. 2. Twenty-four additional haplotypes were selected from eight publications (three per publication, Table 2). Additional haplotypes were chosen by priority when there was additional data on these haplotypes (e.g., findings in other regions) available in other publications. This was done to get the most data output for the additional network. The rest of the additional haplotypes were chosen randomly.

Results

Prevalence of *Echinococcus* spp.

Overall, 93 of 1278 animals were found infected with a total of 149 *Echinococcus* cysts in the liver, lungs, or both; no predilection for either organ was obvious in both livestock species. Prevalence, localization, and fertility status are listed in Table 1. Prevalence was highest in cattle (13.9%; 37/266), but most cysts (50/52) were sterile. Prevalence in sheep was 5.7% (56/975), where 42 of 97 cysts were fertile. No cysts were found in goats (0%; 0/37).

Molecular identification

For 125 of 149 collected cysts, the target fragment of 1609bp could be amplified and sequenced. All isolates belonged to *E. granulosus* s.s. and consisted of 73 different haplotypes (see ESM_1.pdf). Only five of these haplotypes were already known from different regions of the world. EG01 found in that study represents the most common haplotype which was described for the first time by Yanagida et al. (2012) in isolates from the Middle East, China, and Peru was also found in Russia (Konyaev et al. 2012, 2013: syn. EgRUS1 (AB688136)), in Mongolia (Ito et al. 2014: syn. EgMGL6 (AB893247)) and in Australia and Chile (Alvarez Rojas et al. 2016, 2017). Additionally, the haplotype EG40 was found which was also firstly published in Yanagida et al. (2012) from Chinese isolates. The last three haplotypes which were already in the databases are EgAus03 from Australia (Alvarez Rojas et al. 2016) and EgA01 and EgA16 from Armenia (Ebi, unpublished). The fact that the last four cox1 variants were also found now in Algeria shows that these haplotypes are maybe far wider distributed than since assumed. The remaining 68 haplotypes (EgAlg01–EgAlg67, EgAlg01X) were newly found in this study; sequences were deposited in GenBank under accession numbers (MG808282–MG808349). The sequence of haplotype EgAlg64 is identical to the corresponding sequence of “sample 1” from Tunisia (KY766885), whose near-complete mitochondrial genome was published by Kinkar et al. (2017). Sequence analysis of our isolates based on reference sequences of the 366bp cox1 region reported by Bowles et al. (1992), showed that 40 of our haplotypes are genotype G1, two are G3, and 31 are neither G1, G2, or G3 in the sense of that study (see Fig. 1 and ESM_1.pdf).

The new haplotype EgAlg01X is characterized by an insertion of three bases (TGC) after base 1592 of the cox1 fragment (see ESM_1.pdf). As this is a novelty for *Echinococcus*, amplification and sequencing underwent various repeats, one of which was carried out in an independent laboratory (Italian National Institute of Health, Rome), giving identical results.

Overall, the dataset consists of 87 different single nucleotide mutations at 87 variable sites (not taking the triplet insertion in EgAlg01X into account), of which 79 (91%) are transitions and only eight are of transversional character. Thirty-five out of 87 (40%) of these mutations lead to an alteration of the amino acid sequence.

Haplotype network and indices of diversity and neutrality

The haplotype network (Fig. 1) shows a high diversity and complex structure. The globally distributed haplotype EG01 is in the center of the network and most frequent among our panel of samples but, with 8% of the samples, does not predominate. Two secondary radiation centers (EG40 and

Table 1 Prevalence of cystic echinococcosis, organ localization, and fertility assessment of collected cysts

Animal species	No. of examined animals	No. of infected animals (%)	Organ localization			Number and fertility of obtained cysts			
			Liver	Lung	Both organs		Fertile	Sterile	Total
Cattle	266	37 (13.9)	13	17	7	Liver	0	21	21
						Lung	2	29	31
						Total	2	50	52
Sheep	975	56 (5.7)	20	16	20	Liver	23	31	54
						Lung	19	24	43
						Total	42	55	97
Goats	37	0 (0.0)	0	0	0	Liver	–	–	–
						Lung	–	–	–
						Total	–	–	–

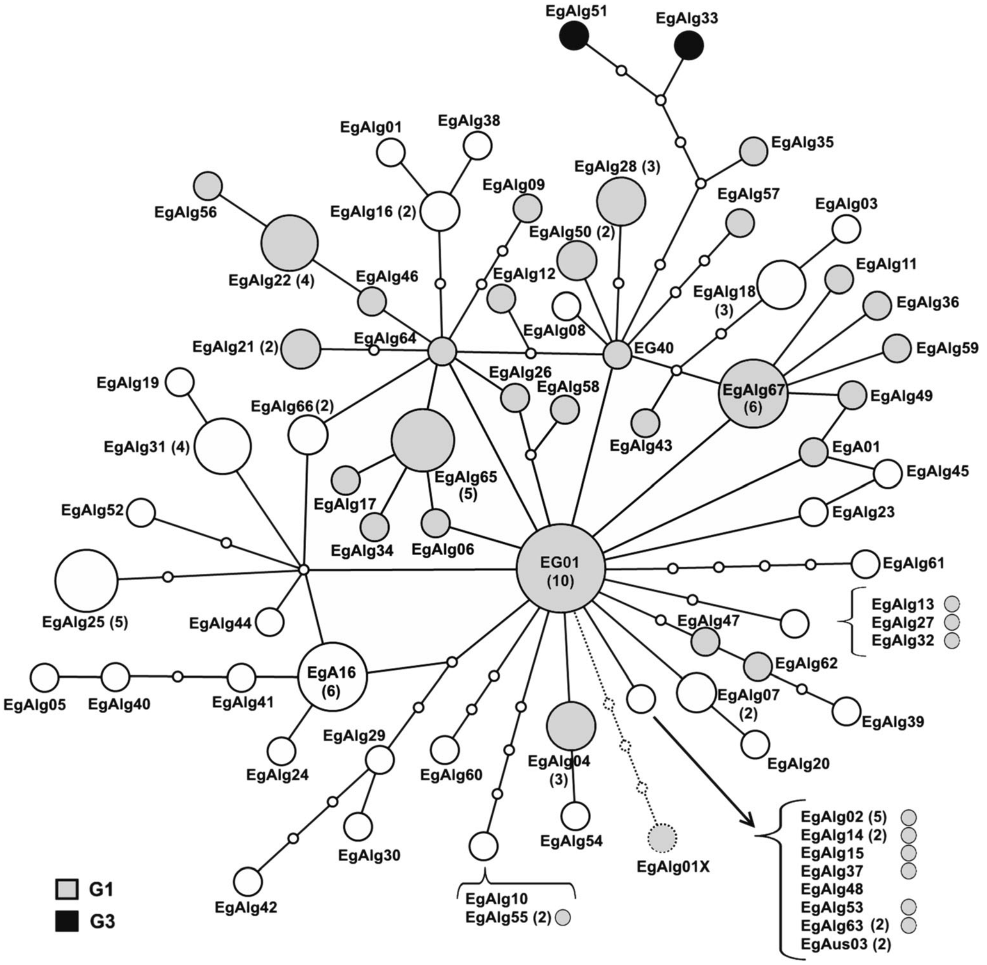

Fig. 1 Haplotype network calculated from the samples analyzed in this study. The circle's area corresponds to the frequency of the haplotypes in this sample set (number > 1 in brackets behind the name). Some haplotypes with the same topological information value are presented as one circle for better readability. The hypothetical position of the insertion-haplotype EgAlg01X is marked with a dashed line. White circles represent non-specific genotypes (neither G1, G2, or G3) of *E. granulosus* s.s

EgAlg64) add complexity to the network. To get more information about the connection to haplotypes found in other regions worldwide, an additional network (Fig. 2) was performed which shows the regional haplotypes reported in this study together with the position of 24 chosen haplotypes from eight publications (Table 2). Although few haplotypes from our panel of samples are shared with other regions worldwide, some of those that have been identified before are placed at central position of secondary radiation centers (EG01, EG40) (Fig. 2).

The high diversity among our isolates is also expressed by the high value of the diversity indices; values of the neutrality indices are negative, suggesting a bottleneck event in the past (Table 3). Haplotype EgAlg01X was omitted from all index calculations because of its sequence-length-dimorphism.

Discussion

Prevalence and species

This survey confirmed the predominance of *E. granulosus* s.s. as CE agent in northern Algeria, as had been indicated earlier by studies with much lower sample size (Bardonnet et al. 2003; Maillard et al. 2007). The prevalence of 5.7% in sheep and 13.9% in cattle is moderate compared to other high-endemicity regions of the world, and, although our results fit well into the range of published data from North Africa, even in some Algerian abattoir surveys far higher prevalence figures had been reported before (reviewed by Deplazes et al. 2017). We do not attempt to explain the very different CE prevalences published from Algerian livestock, which are certainly influenced by focal transmission, livestock age at slaughter, sample size and diagnostic procedure, and which are difficult to evaluate retrospectively. Our data on cyst fertility confirm the adaptation of *E. granulosus* s.s. to sheep as intermediate hosts, where cysts were of similar frequency in the liver and lungs and showed high fertility in either organ. In contrast, the more frequently infected cattle developed only very few fertile cysts; this is in agreement with findings from most world regions, although some studies are at variance with this (Cardona and Carmena 2013; Romig et al. 2017). No goats were found infected, which may be partly explained by the small sample size, but goats would also be expected to be a little affected by *E. granulosus* s.s. (Romig et al. 2017).

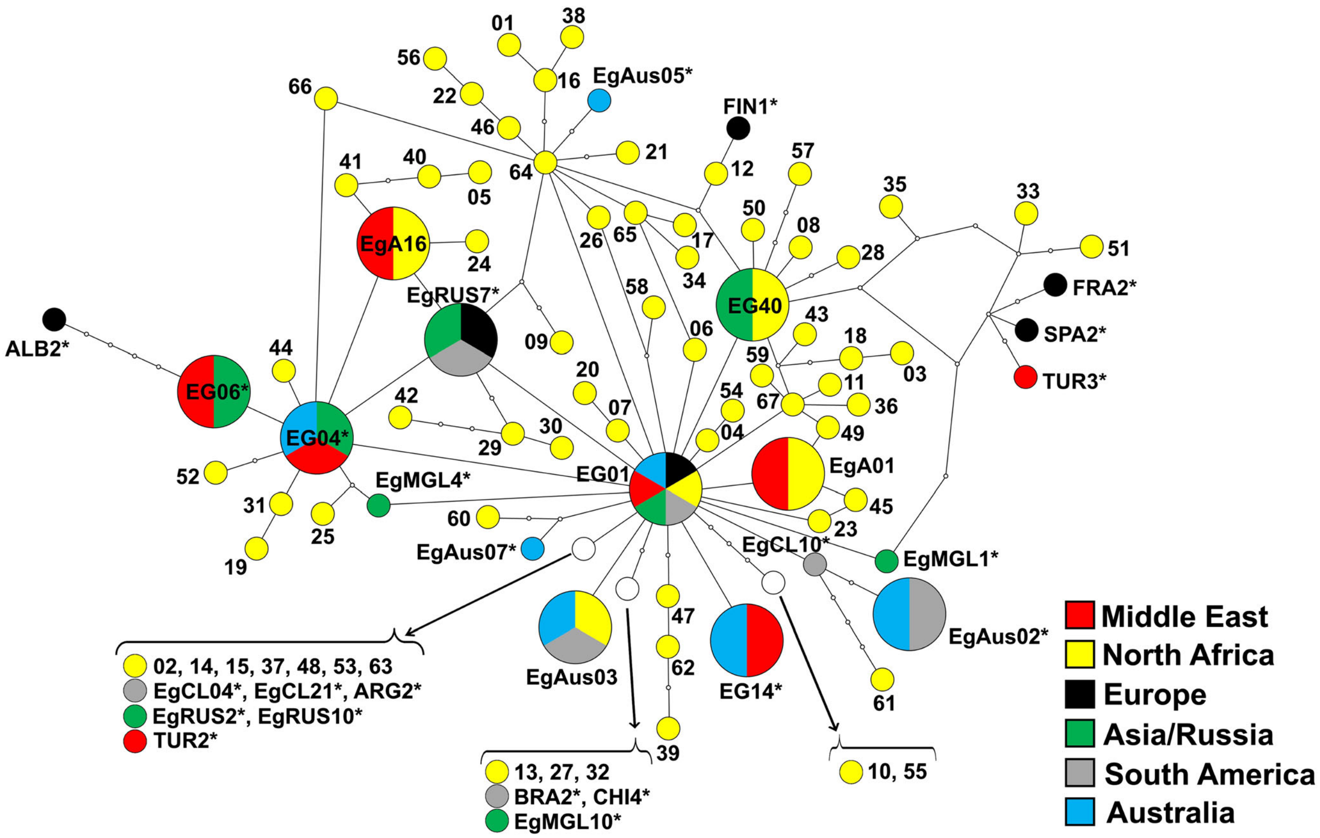

Fig. 2 Maximum parsimony network showing the haplotypes found in this study in combination with 24 chosen haplotypes and regional data from eight different publications. For a better visualization of the structure of the network, two adjustments were taken out: (1) Names of haplotypes newly found in this study (EgAlg...) were shortened to their numbers. (2) Some haplotypes with the same amount of topological information are shown as combined network knots with their regional information and names listed below. The circle sizes correspond to region information and not to frequency of findings. Haplotypes found in more than one region are shown with bigger circles

Sheep, therefore, are clearly the epidemiologically most important livestock host for the maintenance of CE transmission in the steppe region of Algeria.

Genetic variation in the dataset

Compared with previous studies on intraspecific genetic variation of *Echinococcus*, our sample set of 125 isolates from a geographically circumscribed area (Djelfa province in the central part of northern Algeria) is extensive. The genetic diversity observed in this study is at a comparable level with data from the Middle East and western Asia that are presently assumed to be the highest worldwide and resulted in the hypothesis of this parasite's origin and spread (Yanagida et al. 2012; Romig et al. 2017). Although this study was limited to a single province, the haplotype diversity of our Algerian isolates are considerably higher (ca. + 0.1) than those observed in country-wide sample sets from Australia and Chile (Alvarez Rojas et al. 2016, 2017). In addition to the diversity indices and the network structure that lacks a predominant haplotype, there are several radiation centers in the network, whose haplotypes, as far as known, are uniquely North African. This might indicate an evolutionary history of *E. granulosus* s.s. in North Africa that has been partly independent from the Middle East for a prolonged period. EG01 was the only cox1 variant which was found in all regions worldwide, as has been reported before (Alvarez Rojas et al. 2016; Romig et al. 2015). Sequencing the entire mitogenome, EG01 variant of cox1 could be further resolved in 22 haplotypes from all regions by Kinkar et al. (2016) and 13 haplotypes by Laurimäe et al. (2016) from South America. There are other cox1-haplotypes which are also found in more than one region but no other is coming even near the global distribution of EG01 (Fig. 2). The understanding of the genetic diversity and the phylogeographic history of *E. granulosus* s.s. based on cox 1 sequence data, is fully resolved using the high-resolution approach (Kinkar et al. 2016, 2018). Looking at the domestication and subsequent spread of sheep (*Ovis aries*), fossil data place the domestication event from wild sheep (*Ovis orientalis*) in the region of the Fertile Crescent in the Middle East, approximately 11,000 to 12,000 years ago (Groeneveld et al. 2010; Rannamäe et al. 2016). Archeological and genetic evidence indicates that sheep were introduced to northern Africa and the Nile valley already in the period of

Table 2 Haplotypes added to the network shown in Fig. 2

Haplotype	Accession number	Origin	Cox1-region identical to accession number
EG04$_{a}$	JQ250809	Iran	AB893246$_{c}$
EG06$_{a}$	JQ250811	Iran	AB777906$_{b}$, KU925358$_{f}$, KU925378$_{f}$, KU925404$_{f}$
EG14$_{a}$	AB688591	Jordan	
EgRUS2$_{b}$	AB688137	Russia	
EgRUS7$_{b}$	AB777904	Russia	KU925416$_{f}$
EgRUS10$_{b}$	AB777907	Russia	
EgMGL1$_{c}$	AB893242	Mongolia	
EgMGL4$_{c}$	AB893245	Mongolia	
EgMGL10$_{c}$	AB893251	Mongolia	
EgAus02$_{d}$	KT968703	Australia	
EgAus05$_{d}$	KT968706	Australia	
EgAus07$_{d}$	KT968708	Australia	
ARG2$_{e}$	KX039938	Argentina	
BRA2$_{e}$	KX039956	Brazil	
CHI4$_{e}$	KX039964	Chile	
ALB2$_{f}$	KU925433	Albania	KY766883$_{h}$
FIN1$_{f}$	KU925429	Finland	KY766884$_{h}$
TUR2$_{f}$	KU925352	Turkey	KU925388$_{f}$, KY766888$_{h}$
EgCL04$_{g}$	KX227119	Chile	KX039949$_{e}$, KY766882$_{h}$
EgCL10$_{g}$	KX227125	Chile	
EgCL21$_{g}$	KX227136	Chile	
FRA2$_{h}$	KY766892	France	
SPA2$_{h}$	KY766896	Spain	KY766900$_{h}$
TUR3$_{h}$	KY766898	Turkey	

[a] Yanagida et al. 2012
[b] Konyaev et al. 2013
[c] Ito et al. 2014
[d] Alvarez Rojas et al. 2016
[e] Laurimäe et al. 2016
[f] Kinkar et al. 2016
[g] Alvarez Rojas et al. 2017
[h] Kinkar et al. 2017

7500–7000 before present, and subsequently spread around the Saharan desert into western Africa around 3700 BP where the ancient breeds still exist (Muigai and Hanotte 2013). Only much later, fat-tailed types of sheep reached eastern Africa in a second introduction event from the Middle East during 4500–3500 years ago, who subsequently also replaced the older stock in North Africa (reviewed by Muigai and Hanotte 2013). These scenarios, augmented by additional introductions through maritime trade at later periods (Gifford-Gonzalez and Hanotte 2011; Muigai and Hanotte 2013) indicate a highly complex history of sheep and their parasites in northern Africa and would predict a higher genetic diversity of *E. granulosus* s.s. there than in any other parts of the African continent, which indeed seems to be the case (Ebi, unpublished). Conversely to introduction, North Africa has also been the origin of sheep for other world regions: during the European settlement of Australia, a part of the original stock was apparently shipped from northern Africa (Gemmell 2000). It is therefore of interest, that haplotype EgAus03 has so far only been detected in Algeria and Australia (Alvarez Rojas et al. 2016).

Table 3 Calculated indices of diversity and neutrality

Diversity						Neutrality	
n	Hn	Hd	± SD	π	± SD	*D*	Fs
124	72	0.982	± 0.004	0.00259	± 0.00014	− 2.366	− 95.900

Due to the difference in sequence length, all the indices were calculated without EgAlg01X

n number of sequences, *Hn* number of haplotypes, *Hd* haplotype diversity, *SD* standard deviation, *π* nucleotide diversity, *D* Tajima's D, *Fs* Fu's Fs

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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