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ORIGINAL PAPER

Genetic variability of *Taenia saginata* inferred from mitochondrial DNA sequences

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Abstract *Taenia saginata* is an important tapeworm, infecting humans in many parts of the world. The present study was undertaken to identify inter- and intraspecific variation of *T. saginata* isolated from cattle in different parts of Iran using two mitochondrial CO1 and 12S rRNA genes. Up to 105 bovine specimens of *T. saginata* were collected from 20 slaughterhouses in three provinces of Iran. DNA were extracted from the metacestode *Cysticercus bovis*. After PCR amplification, sequencing of CO1 and 12S rRNA genes were carried out and two phylogenetic analyses of the sequence data were generated by Bayesian inference on CO1 and 12S rRNA sequences. Sequence analyses of CO1 and 12S rRNA genes showed 11 and 29 representative profiles respectively. The level of pairwise nucleotide variation between individual haplotypes of CO1 gene was 0.3–2.4 % while the overall nucleotide variation among all 11 haplotypes was 4.6 %. For 12S rRNA sequence data, level of pairwise nucleotide variation was 0.2–2.5 % and the overall nucleotide variation was determined as 5.8 % among 29 haplotypes of 12S rRNA gene. Considerable genetic diversity was found in both mitochondrial genes particularly in 12S rRNA gene.

Keywords *Taenia saginata* · Mitochondrial cox1 · 12S rRNA · Iran

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Introduction

The beef tapeworm, *Taenia saginata* is an important taeniid species infecting humans in many parts of the globe. Taeniasis/cysticercosis are recognized by the World Health Organization (WHO) as neglected tropical diseases. Taeniasis caused by *T. saginata* is a cyclozoonosis in which the tapeworm uses human and cattle as definitive and intermediate hosts, respectively. The prevalence of *T. saginata*/*Taenia solium* infection in man ranged from 0.3 to 64.2 %. Forty five to 77 million people have been estimated to be infected with *T. saginata* in the world (Abunna et al. 2008; Megersa et al. 2010; Roberts et al. 1994). In Iran, recent information indicates 0.5 % prevalence of *T. saginata* in northern province of Mazandaran (Kia et al. 2005). Prevalence of taeniasis depends on the level of sanitation and food habits like consuming raw or undercooked infected beef. Low prevalence rates have been observed in developed countries and higher rates of infection occur in less-developed countries especially in African states (Cabaret et al. 2002). Furthermore, bovine cysticercosis causes considerable economic losses mainly due to the condemnation of infected organs and/or carcasses. Results of several studies in different parts of the

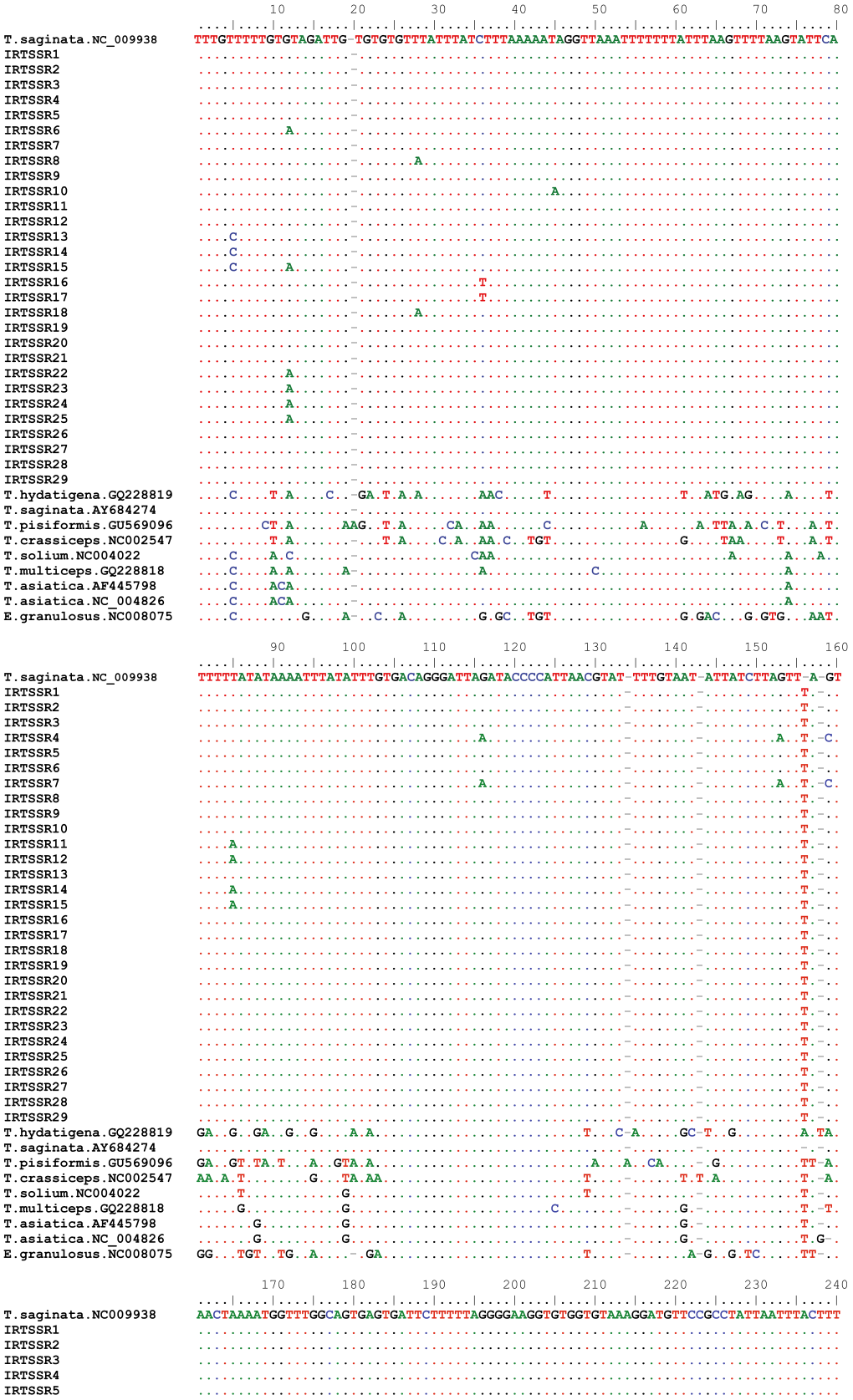
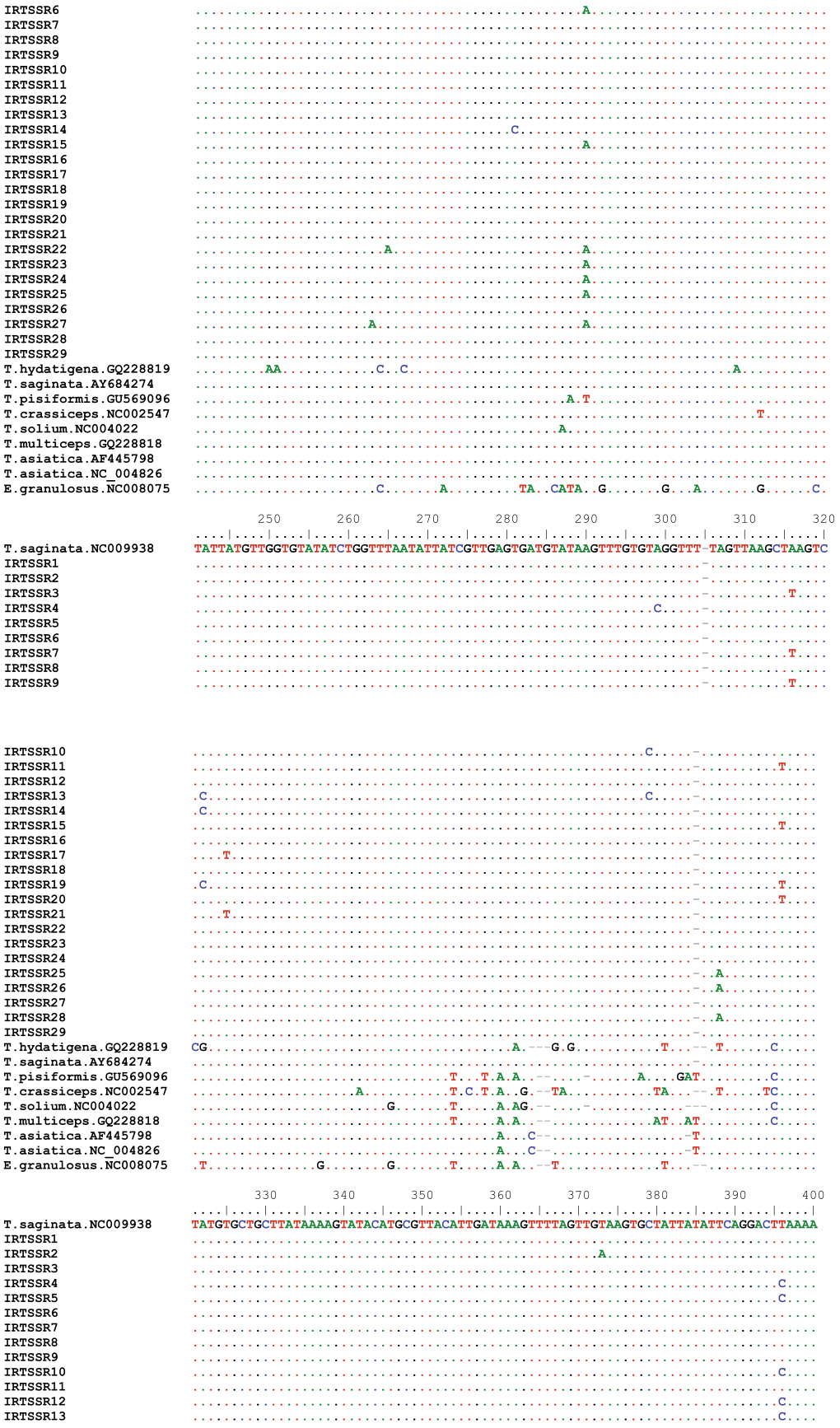


Fig. 1 Alignments of the 11 representative profiles of CO1 sequences and 29 representative profiles of 12S rRNA sequences, among *Taenia saginata* isolates from Iran with key reference sequences (for other taeniid species) from previous studies. *Echinococcus granulosus* sensu stricto was used as outgroup



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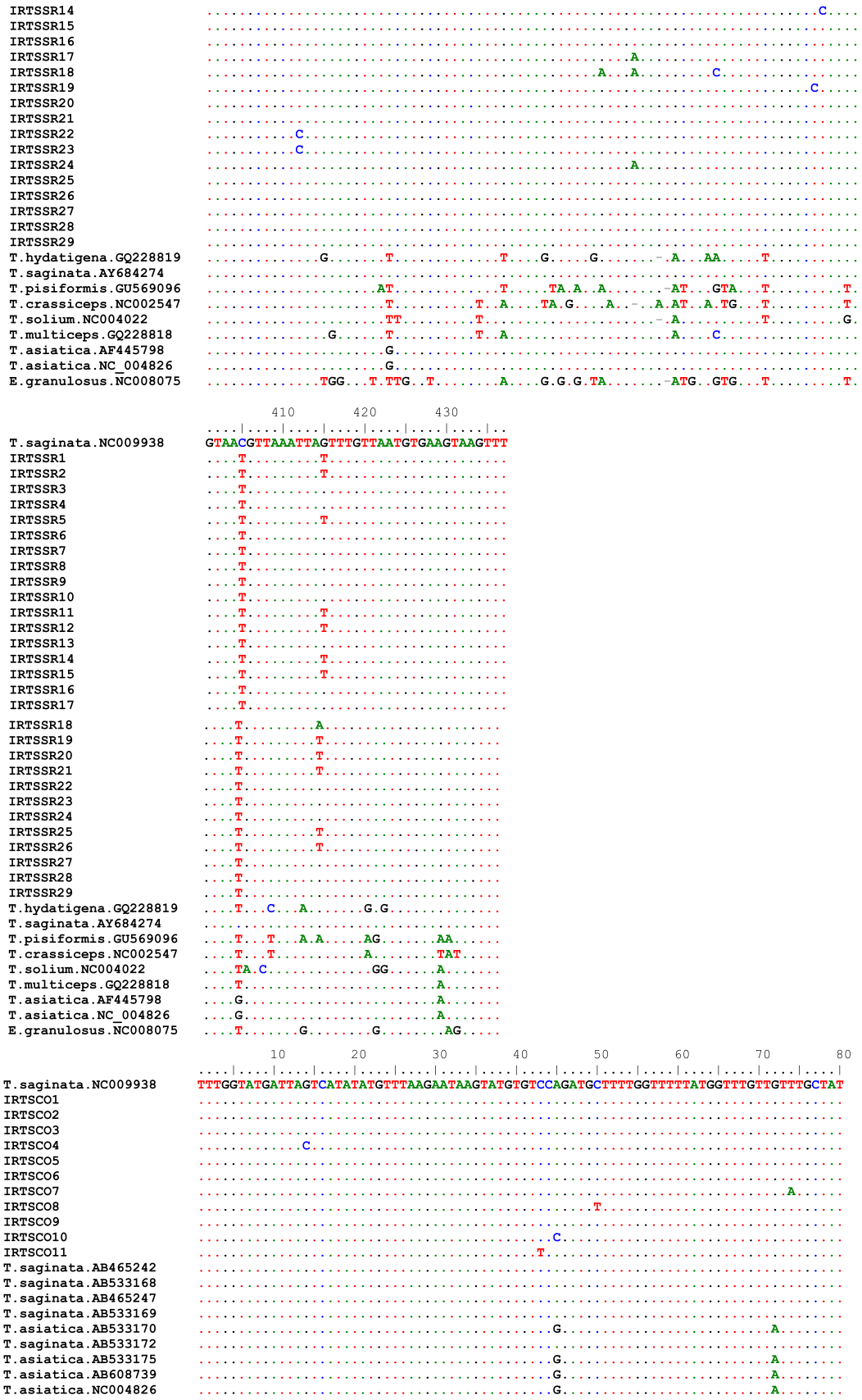

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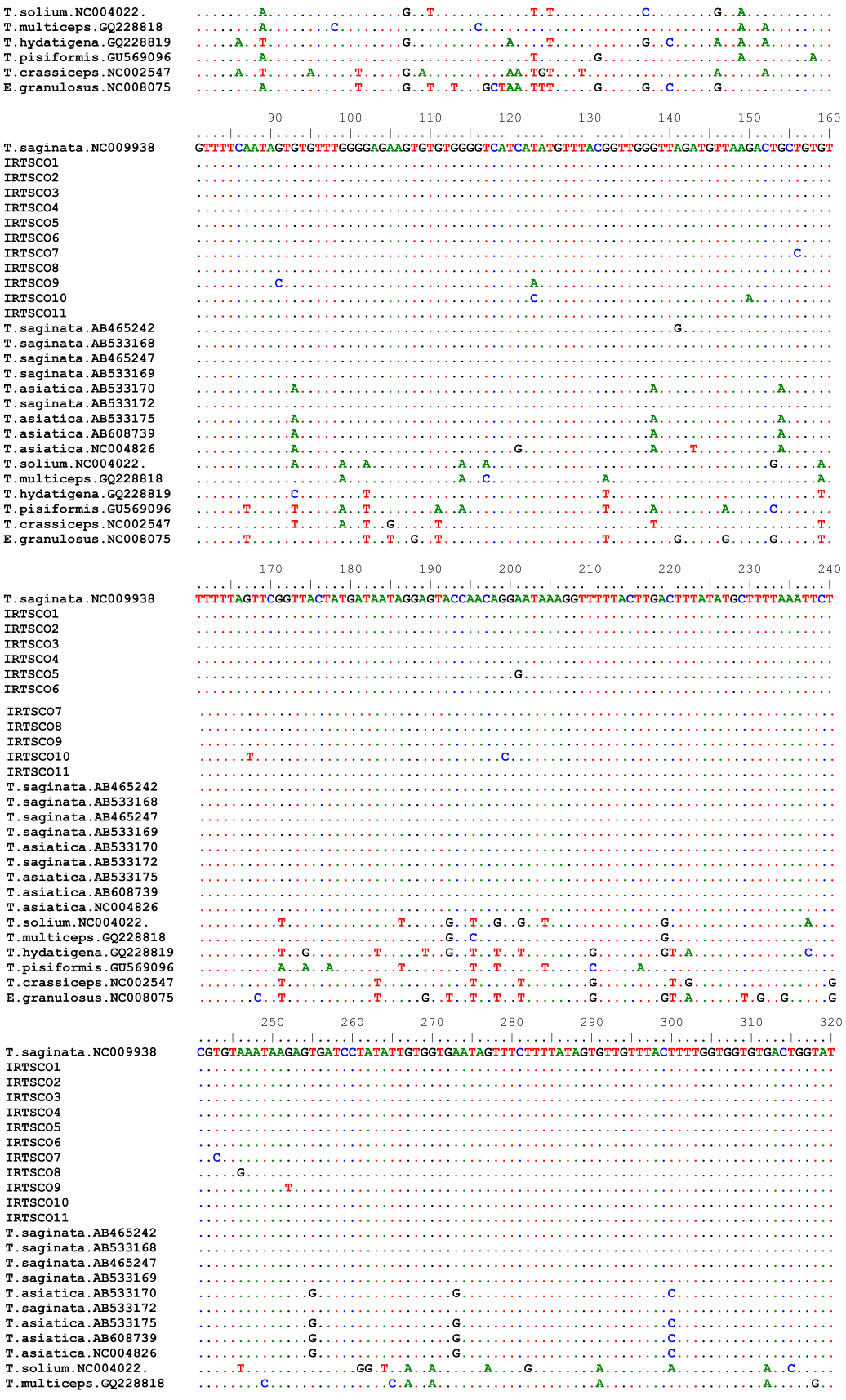

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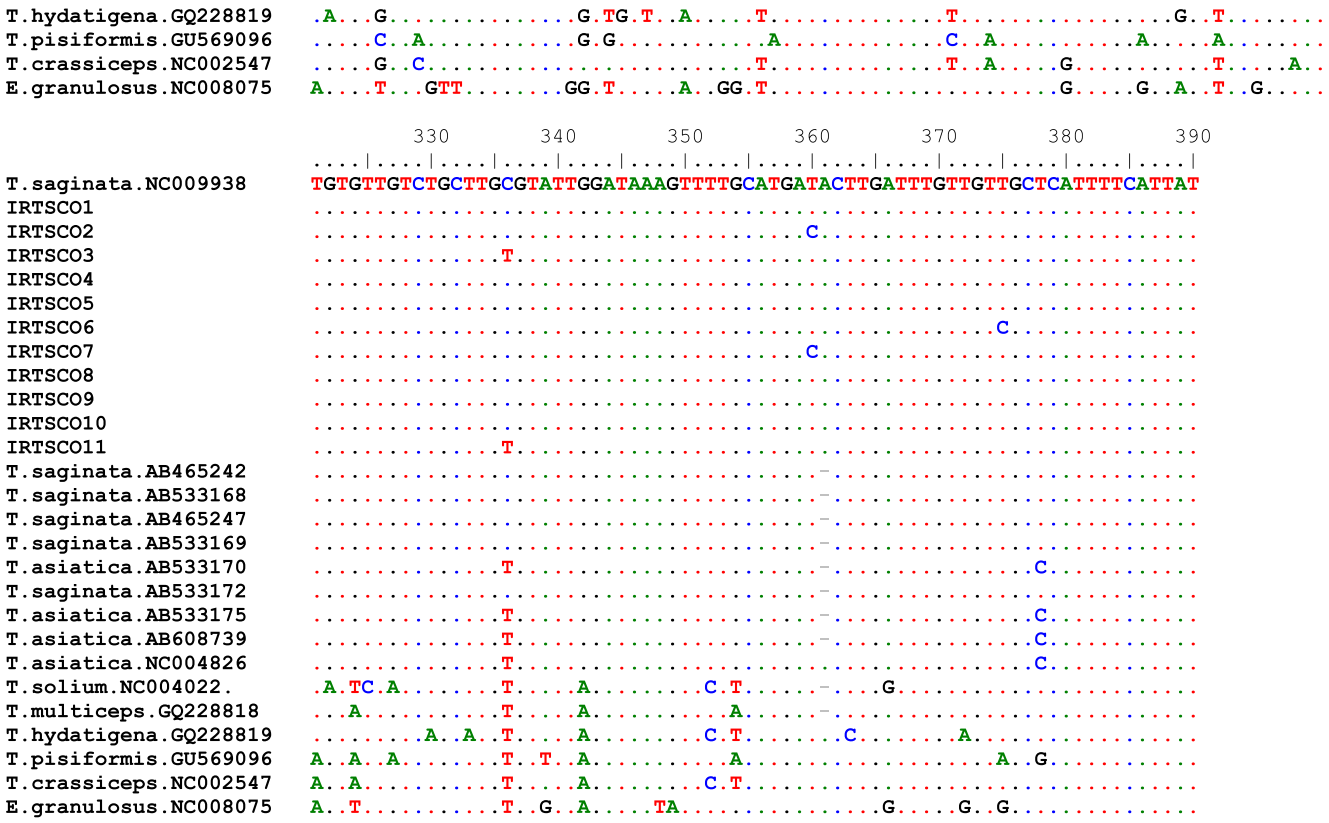

Fig. 1 (continued)

world indicate 0.007–26.3 % of cattle infected with *Cysticercus bovis* (Abunna et al. 2008; Dorny and Praet 2007). Annual monetary cost of human taeniasis is estimated at US$ 263,000 in the USA mainly due to medical costs and wage losses. In England, annual losses due to bovine cysticercosis are estimated about £4 million (Roberts et al. 1994; Silva and Costa-Cruz 2010). Understanding the genetic identity of the parasite as well as the extent of genetic variation within *T. saginata* is essential for diagnosis and control of taeniasis.

Several studies have investigated genetic variation of human taeniid tapeworms, however, most of the research activity has been focused on *T. solium* and human cysticercosis. Relatively limited information is available on genetic variation within *T. saginata* from different parts of the world. The complete mitochondrial genome of *T. saginata* has been determined in 2007 (Jeon et al. 2007). Genetic characterization of *T. saginata* has been carried out in Ethiopia, Indonesia, and Thailand (Hailemariam et al. 2013; Okamoto et al. 2010). Molecular characterization in Iranian isolates of *T. saginata* has not been demonstrated so far. Comprehensive molecular studies in this area are required to increase our knowledge on the genetic diversity of this species and to provide effective vaccine against the parasite. Mitochondrial genes especially cytochrome *c* oxidase subunit 1 (CO1) are universally accepted markers for molecular identification of helminth parasites (Gasser et al. 1999). The purpose of the present study was to identify inter- and intraspecific variation of *T. saginata* in a large number of cattle isolates from different parts of Iran using PCR sequencing of two mitochondrial genes, i.e., CO1 and 12S rRNA.

Materials and methods

One hundred and five specimens of *T. saginata* metacestode were collected from cattle in 20 slaughterhouses from Tehran, Alborz, and Kerman provinces of Iran from August 2010 to July 2011. The scolex was detached from the infected organs and each isolate was transferred to the Parasitology Lab of the School of Medicine, Kerman University of Medical Sciences. After three times rinsing with normal saline, the specimens were stored at −20 °C until used.

Genomic DNA of the isolates was extracted from each scolex by using High Pure PCR Template Preparation Kit (Roche, Mannheim, Germany) as described elsewhere (Rostami et al. 2013). The DNA was used for PCR amplification of cytochrome *c* oxidase subunit I (CO1) and 12S ribosomal DNA (12S rRNA) genes. A 400-bp fragment of CO1 was amplified by PCR with the forward JB3 (5′-TTTTTTGGGCATCCTGAGGTTTAT-3′) and reverse

Table 1 Frequency distribution of *Taenia saginata* haplotypes from Iranian cattle for two mitochondrial CO1 and 12S rRNA genes with the corresponding GenBank accession numbers

CO1	No. of isolates	Accession no.	12S rRNA	No. of isolates	Accession no.
IRTSCO1	70	JQ756969	IRTSSR1	56	KF362126
IRTSCO2	16	JQ756970	IRTSSR2	10	KC344674
IRTSCO3	8	JQ756971	IRTSSR3	6	KC344676
IRTSCO4	2	JQ756972	IRTSSR4	3	KC344677
Other haplotypes	9	JQ756973–JQ756979	Other haplotypes	30	KC344678–KC344701

JB4.5 (5′-TAAAGAAAGAACATAATGAAAATG-3′) primer (Bowles et al. 1992).

Polymerase chain reactions (50 μL) were performed using 3.5 mM $MgCl_2$, 250 mM each of dNTPs, 25 pmol of each primer and 2 U Taq polymerase, and 4 μl (50–100 ng/ml) of DNA template, under the following thermal profile: 5 min at 94 °C as an initial denaturation step, followed by 35 cycles of 30 s at 94 °C, 45 s at 50 °C, 35 s at 72 °C, and a final extension step of 10 min at 72 °C.

A taeniid-specific primer pair was designed for amplification of 12S rRNA gene using Primer-BLAST (http://www.ncbi.nlm.nih.gov/tools/primer-blast/). PCR was carried out using 12SRF (5′-AGGGGATAGGAC ACAGTGCCAGC-3′) as the forward and 12SRR (5′-

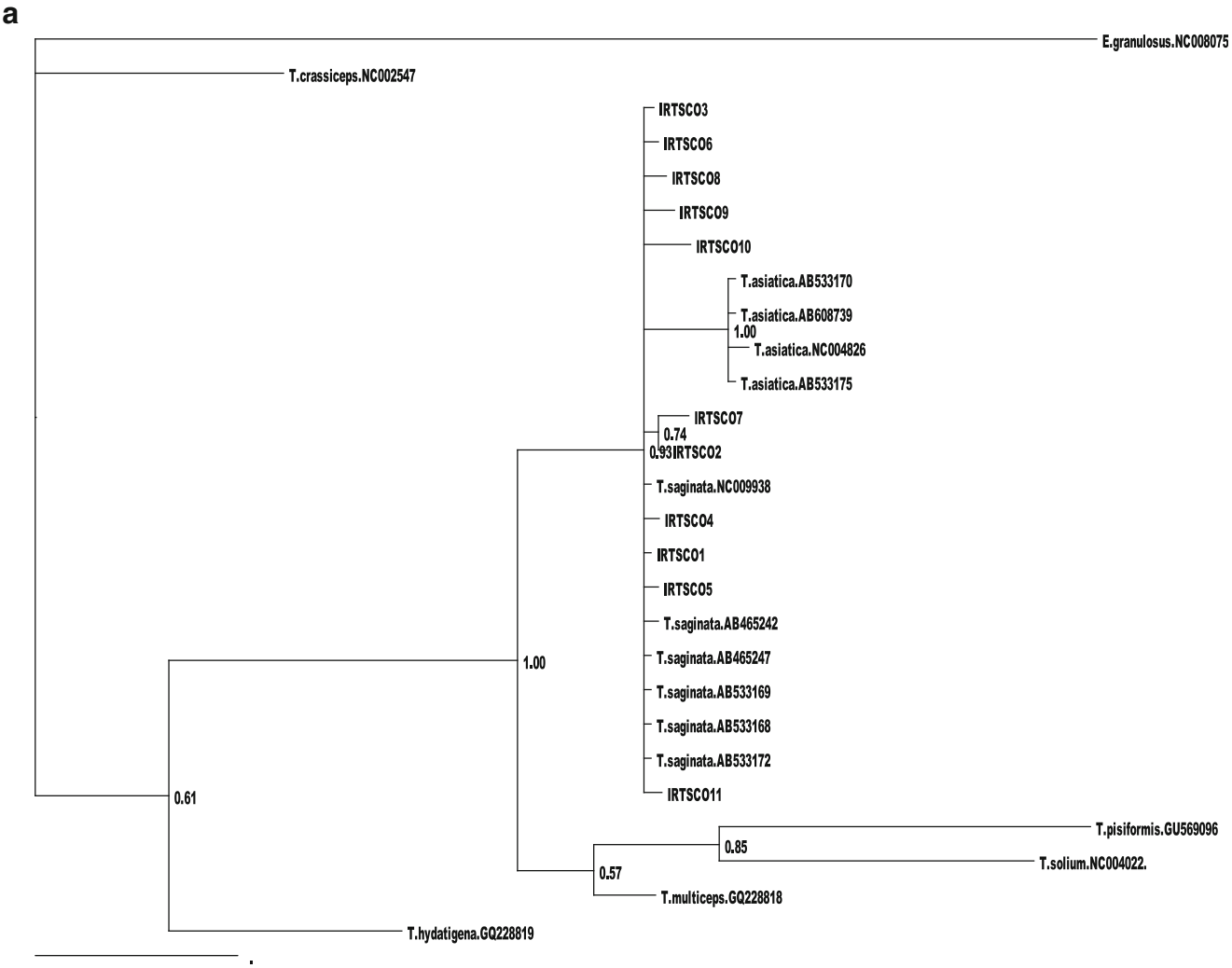

Fig. 2 Genetic relationships of *T. saginata* isolated from cattle and other published for taeniid and *E. granulosus* as outgroup. The relationships were inferred based on phylogenetic analysis of cox1 and 12S rRNA data using Bayesian inference. The accession numbers and sources of sequences are shown in Table 1. Nodal support is given as a pp value

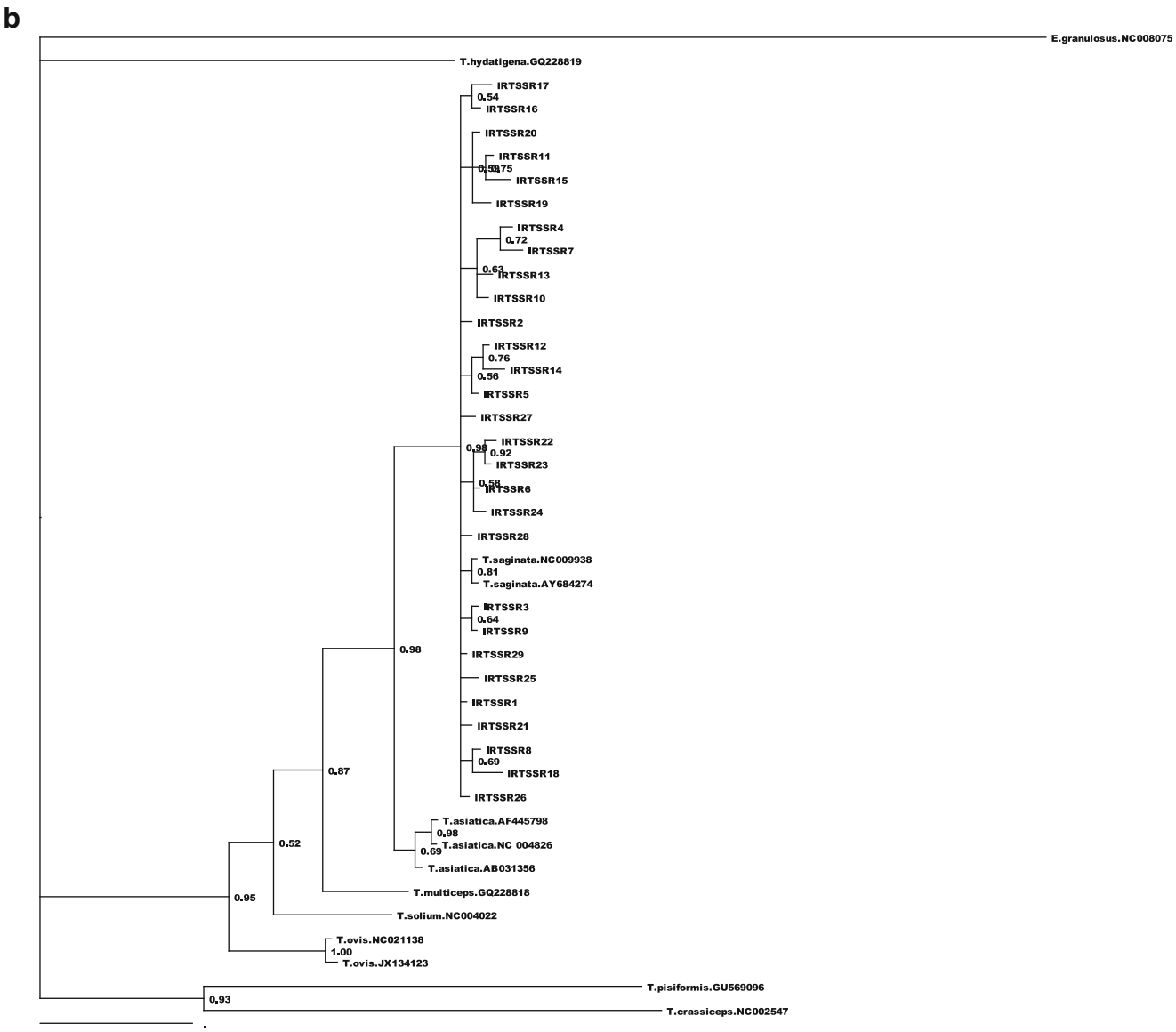

Fig. 2 (continued)

CGGTGTGTACAT GAGCTAAAC-3′) as reverse primers under the following thermal conditions: 5 min at 94 °C as a primary denaturation step, followed by 35 cycles of 30s at 94 °C, 45 s at 57 °C, 35 s at 72 °C, and a final extension of 10 min at 72 °C. The primers amplified an approximately 450-bp fragment of 12S rRNA gene. Negative control (no DNA) was included in each experiment. The PCR products were electrophoresed on 1 % (*w*/*v*) agarose gel containing ethidium bromide.

All amplicons were sequenced by an ABI-3730XL capillary machine (Macrogen Inc., South Korea). Sequence data were analyzed with Blast program while alignments were conducted using the softwares ClustalX and Bioedit (Fig. 1). CO1 and 12S rRNA nucleotide sequences of the representative isolates were submitted to NCBI GenBank (Table 1). Two phylogenetic analyses of the sequence data were inferred by Bayesian inference on CO1 and 12S rDNA sequences (Fig. 2) using the program MrBayes v.3.1.2 (http://mrbayes.csit.fsu.edu/index.php). Posterior probabilities (pp) were designed for 2,000,000 generations (ngen: 2,000,000). The TreeviewX v.0.5.0 program (Page 1996) was used to depict the resulting trees. Two dendrograms were drawn by using the sequences obtained in this study as well as reference sequences available for *T. saginata* and representative *Taenia* species in GenBank. *Echinococcus granulosus* sensu stricto G1 genotype (Accession No. NC008075) was applied in the model as outgroup. Pairwise comparisons were made for the two mitochondrial gene sequences of *T. saginata* isolates of the present study as well as the other published studies.

Table 2 Pairwise comparison of nucleotide sequence differences (%) in CO1 gene among *T. saginata* isolates and some other taeniids

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1. *T. saginata*.NC009938																											
2. IRTSC01	0.000																										
3. IRTSC02	0.003	0.003																									
4. IRTSC03	0.003	0.003	0.005																								
5. IRTSC04	0.003	0.003	0.005	0.005																							
6. IRTSC05	0.003	0.003	0.005	0.005	0.005																						
7. IRTSC06	0.003	0.003	0.005	0.005	0.005	0.005																					
8. IRTSC07	0.010	0.010	0.008	0.013	0.013	0.013	0.013																				
9. IRTSC08	0.005	0.005	0.008	0.008	0.008	0.008	0.008	0.016																			
10. IRTSC09	0.008	0.008	0.010	0.010	0.010	0.010	0.010	0.018	0.013																		
11. IRTSC010	0.013	0.013	0.016	0.016	0.016	0.016	0.016	0.024	0.018	0.018																	
12. IRTSC011	0.005	0.005	0.008	0.003	0.008	0.008	0.008	0.016	0.010	0.013	0.018																
13. *T. saginata*.AB465242	0.003	0.003	0.005	0.005	0.005	0.005	0.005	0.013	0.008	0.010	0.016	0.008															
14. *T. saginata*.AB533168	0.000	0.000	0.003	0.003	0.003	0.003	0.003	0.010	0.005	0.008	0.013	0.005	0.003														
15. *T. saginata*.AB465247	0.000	0.000	0.003	0.003	0.003	0.003	0.003	0.010	0.005	0.008	0.013	0.005	0.003	0.000													
16. *T. saginata*.AB533169	0.000	0.000	0.003	0.003	0.003	0.003	0.003	0.010	0.005	0.008	0.013	0.005	0.003	0.000	0.000												
17. *T. saginata*.AB533170	0.026	0.026	0.029	0.024	0.029	0.029	0.029	0.037	0.032	0.034	0.037	0.026	0.029	0.026	0.026	0.026											
18. *T. saginata*.AB533172	0.000	0.000	0.003	0.003	0.003	0.003	0.003	0.010	0.005	0.008	0.013	0.005	0.003	0.000	0.000	0.000	0.026										
19. *T. saginata*.AB533175	0.026	0.026	0.029	0.024	0.029	0.029	0.029	0.037	0.032	0.034	0.037	0.026	0.029	0.026	0.026	0.026	0.000	0.026									
20. *T. asiatica*.AB608739	0.026	0.026	0.029	0.024	0.029	0.029	0.029	0.037	0.032	0.034	0.037	0.026	0.029	0.026	0.026	0.006	0.000	0.026	0.000								
21. *T. asiatica*.NC004826	0.032	0.032	0.034	0.029	0.034	0.034	0.034	0.043	0.037	0.040	0.042	0.032	0.034	0.032	0.032	0.032	0.005	0.032	0.005	0.005							
22. *T. solium*.NC004022	0.127	0.127	0.130	0.124	0.130	0.124	0.130	0.139	0.130	0.136	0.139	0.120	0.130	0.127	0.127	0.127	0.139	0.127	0.139	0.139	0.145						
23. *T. multiceps*.GQ228818	0.066	0.066	0.068	0.063	0.068	0.068	0.068	0.077	0.071	0.074	0.080	0.066	0.068	0.066	0.066	0.066	0.083	0.066	0.083	0.083	0.089	0.108					
24. *T. hydatigena*.GQ228819	0.129	0.129	0.132	0.126	0.132	0.129	0.0132	0.141	0.129	0.138	0.141	0.129	0.132	0.129	0.129	0.129	0.141	0.129	0.141	0.141	0.147	0.141	0.132				
25. *T. pisiformis*.GU569096	0.117	0.117	0.120	0.114	0.120	0.120	0.117	0.129	0.120	0.126	0.132	0.111	0.120	0.117	0.117	0.117	0.129	0.117	0.129	0.129	0.135	0.138	0.123	0.179			
26. *T. crassiceps*.NC002547	0.120	0.120	0.123	0.117	0.123	0.120	0.123	0.132	0.120	0.129	0.132	0.114	0.123	0.120	0.120	0.120	0.126	0.120	0.126	0.126	0.132	0.163	0.135	0.114	0.157		
27. *E. granulosus*.NC008075	0.206	0.206	0.209	0.202	0.209	0.206	0.206	2.220	0.209	0.209	0.220	0.199	0.202	0.206	0.206	0.206	0.220	0.206	0.220	0.220	0.226	0.199	0.234	0.176	0.227	0.179	

T. saginata: NC009938, AB465242, AB533168, AB465247, AB533169, AB533170, AB533172, *T. multiceps*: GQ228818, *T. solium*: NC004022, *T. pisiformis*: GU569096 and *T. hydatigena*: GQ228819. *T. serialis*: AM503319, *T. crassiceps*: NC002547, *T. solium*: NC004022, *T.asiatica*: NC004826, AB533175, AB608739, and *E. granulosus*: NC008075

Table 3 Pairwise comparison of nucleotide sequence differences (%) in 12S rRNA gene among *T. saginata* isolates and some other taeniids

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
1. *T. saginata*.N																													
2. IRTSSR1	0.005																												
3. IRTSSR2	0.007	0.002																											
4. IRTSSR3	0.005	0.005	0.007																										
5. IRTSSR4	0.014	0.014	0.016	0.014																									
6. IRTSSR5	0.007	0.002	0.005	0.007	0.012																								
7. IRTSSR6	0.007	0.007	0.009	0.007	0.016	0.009																							
8. IRTSSR7	0.012	0.012	0.014	0.004	0.004	0.014	0.014																						
9. IRTSSR8	0.005	0.005	0.007	0.005	0.014	0.007	0.007	0.012																					
10. IRTSSR9	0.005	0.005	0.007	0.000	0.014	0.007	0.007	0.007	0.005																				
11. IRTSSR10	0.009	0.009	0.012	0.009	0.009	0.007	0.012	0.016	0.009	0.009																			
12. IRTSSR11	0.006	0.005	0.007	0.005	0.019	0.007	0.012	0.012	0.009	0.005	0.014																		
13. IRTSSR12	0.009	0.005	0.007	0.009	0.014	0.002	0.012	0.016	0.009	0.009	0.009	0.005																	
14. IRTSSR13	0.012	0.012	0.014	0.012	0.012	0.009	0.014	0.019	0.012	0.012	0.007	0.016	0.012																
15. IRTSSR14	0.016	0.012	0.014	0.016	0.021	0.009	0.019	0.024	0.016	0.016	0.016	0.012	0.007	0.009															
16. IRTSSR15	0.016	0.012	0.014	0.012	0.026	0.014	0.009	0.019	0.016	0.012	0.021	0.007	0.012	0.019	0.014														
17. IRTSSR16	0.005	0.005	0.007	0.005	0.014	0.007	0.007	0.012	0.005	0.005	0.009	0.009	0.009	0.012	0.016	0.016													
18. IRTSSR17	0.009	0.009	0.007	0.009	0.019	0.012	0.012	0.016	0.009	0.009	0.014	0.014	0.014	0.016	0.021	0.021	0.005												
19. IRTSSR18	0.014	0.012	0.009	0.014	0.024	0.014	0.016	0.021	0.009	0.014	0.019	0.016	0.016	0.021	0.024	0.024	0.014	0.014											
20. IRTSSR19	0.012	0.007	0.009	0.007	0.021	0.009	0.014	0.014	0.012	0.007	0.016	0.007	0.012	0.014	0.014	0.014	0.012	0.016	0.019										
21. IRTSSR20	0.007	0.002	0.005	0.002	0.016	0.005	0.009	0.009	0.007	0.002	0.012	0.002	0.007	0.014	0.014	0.009	0.007	0.012	0.014	0.005									
22. IRTSSR21	0.007	0.002	0.005	0.007	0.016	0.005	0.009	0.014	0.007	0.007	0.012	0.007	0.007	0.014	0.014	0.014	0.007	0.007	0.014	0.009	0.005								
23. IRTSSR22	0.012	0.012	0.014	0.012	0.021	0.014	0.005	0.019	0.012	0.012	0.016	0.016	0.016	0.019	0.024	0.014	0.012	0.016	0.021	0.019	0.014	0.014							
24. IRTSSR23	0.009	0.009	0.012	0.009	0.019	0.012	0.002	0.016	0.009	0.009	0.014	0.014	0.014	0.016	0.021	0.012	0.009	0.014	0.019	0.016	0.021	0.012	0.002						
25. IRTSSR24	0.009	0.009	0.007	0.009	0.019	0.012	0.002	0.016	0.009	0.009	0.014	0.014	0.014	0.016	0.021	0.012	0.009	0.009	0.014	0.016	0.012	0.012	0.007	0.005					
26. IRTSSR25	0.012	0.007	0.009	0.012	0.021	0.009	0.005	0.019	0.012	0.012	0.016	0.012	0.012	0.019	0.019	0.009	0.012	0.016	0.019	0.014	0.009	0.009	0.009	0.007	0.007				
27. IRTSSR26	0.007	0.002	0.005	0.007	0.016	0.005	0.009	0.014	0.007	0.007	0.012	0.007	0.007	0.014	0.014	0.014	0.007	0.012	0.014	0.009	0.005	0.005	0.014	0.012	0.012	0.005			
28. IRTSSR27	0.007	0.007	0.009	0.007	0.016	0.009	0.005	0.014	0.007	0.007	0.012	0.012	0.012	0.014	0.019	0.014	0.007	0.012	0.016	0.014	0.009	0.009	0.009	0.007	0.007	0.009	0.009		
29. IRTSSR28	0.005	0.005	0.007	0.005	0.014	0.007	0.007	0.012	0.005	0.005	0.009	0.009	0.009	0.012	0.016	0.016	0.005	0.009	0.014	0.012	0.007	0.007	0.012	0.009	0.009	0.007	0.002	0.007	
30. IRTSSR29	0.002	0.002	0.005	0.002	0.012	0.005	0.005	0.009	0.002	0.002	0.007	0.007	0.007	0.009	0.014	0.014	0.002	0.007	0.012	0.009	0.005	0.005	0.009	0.007	0.007	0.009	0.005	0.005	0.002

T. multiceps: GQ228818, FJ744755; *T. saginata*: NC009938, *T. solium*: NC004022, *T. pisiformis*: GU569096; *T. hydatigena*: GQ228819; *T. crassiceps*: NC002547; *T. solium*: NC004022; *E. granulosus*: NC008075

Results

All 105 isolates were successfully amplified on both CO1 and 12S rRNA genes. Sequence analyses of CO1 and 12S rRNA genes showed 11 and 29 representative profiles respectively, designated as IRTSCO1 to IRTSCO11 for CO1 and IRTSSR1 to IRTSSR29 for 12S rRNA (Table 1). The level of pairwise nucleotide variation between individual haplotypes of CO1 gene were determined to be 0.3–2.4 % while the overall nucleotide variation among all 11 haplotypes was 4.6 % (Table 2). For 12S rRNA sequence data, the level of pairwise nucleotide variation was found 0.2–2.5 % and the overall nucleotide variation was determined as 5.8 % among 29 haplotypes (Table 3). Total mutations were 19 and 26 in CO1 and 12S rRNA that occurred in 18 and 25 segregation sites respectively. Figure 2 showed dendrograms based on COI and 12S rRNA gene sequences using the Bayesian inference method.

Discussion

Molecular characterization of parasites of medical and veterinary importance is a crucial factor in understanding epidemiology and control of parasitic infections. *T. saginata* is a zoonotic parasite of human and cattle with a worldwide distribution. It constitutes considerable medical and economical losses in endemic countries including Iran. Annual monetary burden of bovine cysticercosis in Iran was estimated at about US$ 410,000 (Jahed Khaniki et al. 2010).

Several genomic regions have been used for phylogenetic studies of different *Taenia* species including 18S and 28S ribosomal RNA as well as mitochondrial genes (Yan et al. 2013; Hoberg 2006). In the present study, we investigated the mitochondrial CO1 and 12S rRNA genes diversity of 105 cattle isolates of *T. saginata* from Iran. CO1 is a universally accepted marker for the study of genetic variation and evolutionary biology of helminth parasites (Le et al. 2000). Intraspecific variation in *T. saginata* has been investigated in several studies (Hailemariam et al. 2013; Okamoto et al. 2010), however, more studies using larger sample size are required to improve our understanding on the significance of genetic variation within this important taeniid species.

Level of nucleotide variation in CO1 and 12S rRNA between *T. saginata* isolates from the present study and six other *Taenia* species was found to be 2.6–14.1 % and 2.8–19.5 %, respectively. This is in agreement with the expected level of nucleotide variations in CO1 in the genus *Taenia* that has been estimated to be 2.5–15.8 % by McManus and Bowles (1994).

As shown in Table 2, the level of pairwise nucleotide difference among the isolates of the present study and other *T. saginata* isolates is 2.4 % whereas pairwise comparison of CO1 sequences between isolates of the present study and *T. asiatica* is 2.6 %. Much higher pairwise differences have been observed between *T. saginata* and other *Taenia* species other than *T. asiatica* (6.3–15.8 %). *Taenia asiatica* formerly known as Taiwan taenia or Asian taenia; had been recognized in southeast Asia in 1980s (Fan 1988). This tapeworm was classified as a subspecies of *T. saginata* namely, *T. saginata asiatica*. Eom and Rim (1993) described it as a new species; *Taenia asiatica*. However, recent findings indicate probable hybridization between *T. saginata* and *T. asiatica* (Okamoto et al. 2010; Yamane et al. 2012). Regarding Mayr's definition of species, a species is defined as a group of organisms that are capable of interbreeding (Mayr 1996). In light of the fact that the two *Taenia* species are not reproductively isolated and the relatively low level of nucleotide difference between the two species shown in this study, it may be speculated that *T. saginata* and *T. asiatica* are either very closely related species or basically they are two subspecies of a single species.

Further studies on the molecular characterization of the parasite are clearly required from other geographical localities in different parts of the world. The present study provided mitochondrial data on the cattle isolates of *T. saginata* in Iran. In-depth studies on nuclear genes are essential to provide a comprehensive picture on the extent and significance of genetic variation within different *T. saginata* populations.

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