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GENETICS, EVOLUTION, AND PHYLOGENY - SHORT COMMUNICATION

The complete mitochondrial genome of *Eimeria anseris* from the wintering greater white-fronted goose in Shengjin Lake, China, and phylogenetic relationships among *Eimeria* species

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Abstract
Coccidiosis is recognized as one of the most widespread and pathogenic parasitic infections in migratory waterfowl throughout the world. It can be caused by several species of *Eimeria*. We sequenced the complete mitochondrial genome (mtDNA) of *Eimeria anseris* from wintering greater white-fronted geese (*Anser albifrons*) in China. The complete *E. anseris* mtDNA is 6179 bp in size and contains three protein-coding genes (CYT B, COI, and COIII), 12 gene fragments for large subunit ribosomal RNA (rRNA), and seven gene fragments for small subunit rRNA, but no transfer RNA genes. Available complete *Eimeria* mtDNA sequences are highly conserved in sequence: the sequences are all similar in length; with the same three protein-coding genes and fragmented rRNA genes; ATG is generally the start codon, and TAA and TAG are the most frequently used stop codons. Our molecular phylogenetic analyses show some species clustering into host-specific clades, but many species do not follow clear coevolutionary host segregating patterns. The results suggest that *Eimeria* spp. from turkeys and chickens are paraphyletic groups, while *Eimeria* species isolated from rabbits are a monophyletic group. *E. anseris*, which infects *A. albifrons*, and another group of *Eimeria* isolated from chickens form a closely related monophyletic clade.

Keywords Mitochondrial DNA · Coccidiosis · Phylogenetic relationship · *Eimeria anseris* · *Anser albifrons*

Introduction

Coccidiosis is recognized as one of the most widespread and pathogenic parasitic infections in migratory waterfowl throughout the world. It can be caused by several species of *Eimeria*, as well as other coccidian Apicomplexa (Traill et al. 2009; Hervías et al. 2013; Huang et al. 2014; Hafeez et al. 2015). *Eimeria* is an obligate intracellular protist parasite that has a complex life cycle in the intestinal mucosa of the host and is directly transmitted from one animal to another by contact with infected feces (Lin et al. 2011; Honma et al. 2011; Huang et al. 2014). *Eimeria anseris* is an important agent of coccidiosis that is distributed worldwide in domestic poultry, particularly ducks, geese, and swans in the family Anatidae. *E. anseris* can cause serious damage to the digestive tract of the host, resulting in malabsorption of nutrients and diarrhea, which often causes weight loss and can lead to death (Abbas et al. 2008; Ding et al. 2008).

Mitochondrial DNA (mtDNA) is short in length, without introns, and has short intergenic regions. It has been extensively used as a genetic marker, not only for phylogenetic analyses at many different taxonomic levels but also serving as an ideal model for studying gene rearrangement and genome evolution (Liu et al. 2013, 2014). Several complete mitochondrial DNA sequences have been published for *Eimeria* (Lin et al. 2011). Mitochondrial genome organization in *Eimeria* is quite different from that of most eukaryotes (Feagin et al. 2012; Ogedengbe et al. 2014; He et al. 2014). Complete *Eimeria* mtDNA is typically a little longer than 6 kb and contains three protein-coding genes (Cyt b, COI, and COIII), 12–19 gene fragments for large subunit (LSU) ribosomal RNA (rRNA), and 7–14 gene fragments for small subunit (SSU) rRNA (Lin et al. 2011; Ogedengbe et al.

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Table 1 GenBank accession numbers for the 20 complete mtDNA of *Eimeria* species in this study

Species	Accession number	Species	Accession number
Eimeria intestinalis	KP009592	*Eimeria tenella*	AB564272
Eimeria irresidua	KP025690	*Eimeria gallopavonis*	KJ608413
Eimeria magna	KF419217	*Eimeria acervulina*	KX094948
Eimeria vejdovskyi	KP025692	*Eimeria anseris*	This study
Eimeria media	KP025691	*Eimeria praecox*	KX094945
Eimeria mephitidis	KT203398	*Eimeria meleagrimitis*	KJ608414
Eimeria innocua	KR108296	*Eimeria meleagridis*	KJ608418
Eimeria dispersa	KJ608416	*Eimeria adenoeides*	KJ608415
Eimeria necatrix	KX094954	*Eimeria maxima*	KX094966
Eimeria mitis	KF501573	*Eimeria brunetti*	KX094959
Isospora sp.	KP658103		

2014; Tian et al. 2015; Hafeez et al. 2016). It is highly conserved, short in length, has no introns, and contains short intergenic spacer regions (Feagin et al. 2012; Ogedengbe et al. 2014; He et al. 2014). Unlike most eukaryotes, the mitochondrial genomes of *Eimeria* species do not possess 5S rRNA or transfer RNA genes (Ogedengbe et al. 2014). In spite of these conserved features, *Eimeria* mtDNA genome structures vary widely, reportedly including linear concatemers, linear genomes with terminal inverted telomeric repeats, and circular genomes (Ogedengbe et al. 2014).

The greater white-fronted goose (*Anser albifrons*) is a long-distance migratory waterfowl, and an important wetland indicator species within the family Anatidae, in the order Anseriformes (IUCN 2018). We previously found greater white-fronted geese to be infected with many parasites, including *E. anseris* (unpublished). *E. anseris* can cause serious coccidiosis disease, resulting in malabsorption of nutrients and diarrhea, which affects the life and survival of migratory waterfowl. *Anser albifrons* is large migratory colonial water bird that winters in wetlands and is prone to parasite infection. Attempts have been made to molecularly characterize geese parasites using various nuclear loci; however, the maternally derived and mitotically replicating mitochondrial genome may be more appropriate for molecular epidemiology.

Here, we report the characterization and organization of the complete *E. anseris* mitochondrial genome isolated from wintering greater white-fronted goose feces at Shengjin Lake, China. The purpose of the present study is not only to determine the genomic organization and structure of the mitochondrial genome of *E. anseris* but also to increase attention by public health and ornithological researchers to coccidiosis in waterfowl. Furthermore, our phylogenomic analysis will shed increased light on the coevolutionary relationship between *Eimeria* species and hosts.

Materials and methods

Sample collection, source, and identification of *E. anseris*

E. anseris oocysts were isolated from wintering greater white-fronted goose feces. A noninvasive sampling technique was used to collect fecal samples from wintering greater white-fronted geese from Wangba Village (30° 16′ 58.89″ N, 117° 0′ 14.64″ E) at Shengjin Lake, Anhui Province, China, from November 2017 through April 2018. *E. anseris* oocysts were washed in physiological saline (0.9% sodium chloride) and identified based on morphological characters. Isolation and pretreatment of oocysts followed the method of Yan et al. (2012). Total DNA was extracted from fecal samples using the TIANamp Stool DNA Kit from Tiangen Biotech CO., LTD (Beijing, China). The mtDNA was sequenced by GeneSky Biotech Co., Ltd. (Shanghai, China) using next-generation sequencing (NGS) technology.

Genome annotation and sequence analysis

DNA sequences were analyzed using the programs Seqman (DNASTAR 2001), BioEdit, and Chromas v. 2.22. The protein-coding and rRNA gene boundaries were identified by alignment with the mitochondrial genomes of other *Eimeria* species. The complete *E. anseris* mitochondrial genome sequence has been deposited in GenBank under accession number MH758793.

Phylogenetic analyses

To explore phylogenetic relationships among *Eimeria*, we collected all available complete *Eimeria* mtDNA sequences in GenBank, plus our sequence, and *Isospora* sp. mtDNA (KP658103) as an outgroup (Table 1). We aligned the 21-member coccidian data set, using ClustalX v. 2.1

(Thompson et al. 1997), as implemented in Mega 4.0 (Tamura et al. 2007), followed by manual adjustment.

Phylogenetic trees were then estimated using the maximum likelihood (ML) and Bayesian inference (BI) methods. ML and BI phylogenetic trees were reconstructed using PAUP* v. 4.0b8 (Strimmer and Haeseler 1996) and MrBayes. v. 3.1.2 (Strimmer and Haeseler 1996), respectively, specifying separate partitions for each gene within the Nexus format file (Strimmer and Haeseler 1996). ML analyses were performed in PAUP using tree bisection and reconnection (TBR) branch swapping (10 random addition sequences) and a general time-reversible model with invariant sites and among-site variation (GTR+I+Γ). This model was selected as the best-fit model of evolution using Modeltest v. 3.06 based on the Akaike information criterion (AIC). The support for internal branches in the ML tree was evaluated via the bootstrap test with 100 iterations.

Bayesian inference of phylogeny was performed using MrBayes (Ronquist and Huelsenbeck 2003) with the same best-fit substitution model as with the ML analysis. MrBayes simultaneously initiates two Markov chain Monte Carlo (MCMC) runs to provide a better estimated confirmation of convergence of posterior probability distributions. Analyses were run for one million generations until the average standard deviation of split frequencies was less than 0.01, which indicates that the convergence had most likely been reached. Chains were sampled every 1000 generations.

Results

Genome organization and arrangement

The complete *E. anseris* mtDNA is 6179 bp in size and contains three protein-coding genes (CYT B, COI, and COIII), 12 gene fragments for LSU rRNA, and seven gene fragments for SSU rRNA, but no transfer RNA genes (Fig. 1, Table 2). The longest gene is COI at 1476 bp in size, located between CYT B and LSUF. The shortest gene fragment is LUSC (16 bp), located between LSUG and SSUF. Overall base composition was as follows: A, 29.8%; C, 17.2%; G, 17.7%; and T, 35.3%. Overall A+T content is 65.1%, and the C+G content is 34.9%, with guanine being the rarest nucleotide, as in most all *Eimeria* mtDNAs (Fig. 2).

Table 2 Organization of complete *Eimeria anseris* mtDNA

Genes	Nucleotide no.	Size	Start codon	Stop codon
SSUA (SA)	1–82	82		
CYT B	128–1207	1080	ATG	TAA
COI	1211–2686	1476	ATT	TAA
LSUF	2727–2854	128		
LUSG	2848–2954	107		
LUSC	3073–3088	16		
SSUF	3227–3287	61		
LSU10	3288–3371	84		
SSUD (SD)	3442–3506	65		
SSU9	3516–3578	63		
LSU13	3617–3649	33		
LSUD	3729–3815	87		
SSU8	3852–3943	92		
LSU2	3960–4026	67		
LSUA	4047–4224	178		
COIII	4217–4996	780	ATT	TAG
LSU1	5035–5145	111		
LUSB	5221–5244	24		
LSU3	5278–5350	73		
SSUB	5397–5512	116		
LSUE	5613–5800	188		
SSUE	5900–5936	37		

Protein-coding genes and ribosomal RNA genes

The total, combined length of the three protein-coding sequence (CDS) regions is 3336 bp, which represents 53.60% of the entire mitochondrial genome. The longest CDS is COI (1746 bp), located between CYT B and LSUF. The shortest is

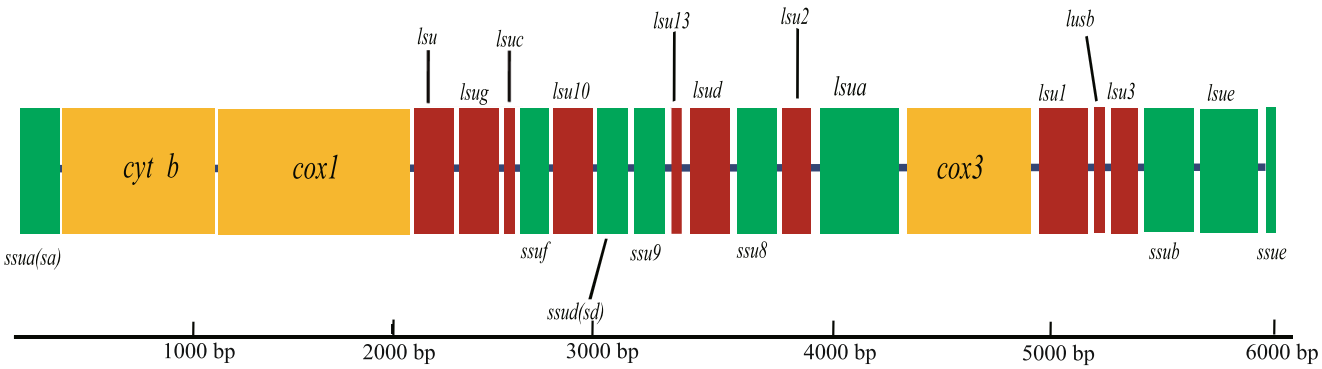

Fig. 1 Arrangement of *Eimeria anseris* mitochondrial genome. SSU rRNAs are colored green, protein-coding genes are colored orange, and LSU rRNAs are colored red

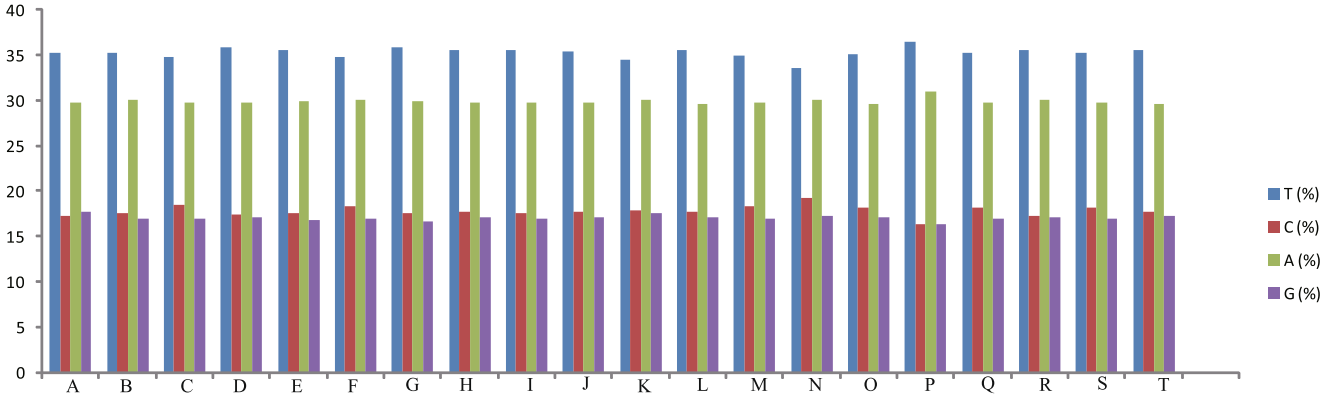

Fig. 2 Nucleotide composition (%) of *Eimeria* mitochondrial genomes used in the study. Notes: A, *E. anseri*; B, *E. acervulina*; C, *E. adenoeides*; D, *E. brunette*; E, *E. dispersa*; F, *E. gallopavonis*; G, *E. innocua*; H, *E. intestinalis*; I, *E. irresidua*; J, *E. magna*; K, *E. maxima*; L, *E. media*; M, *E. meleagridis*; N, *E. meleagrimitis*; O, *E. mephitidis*; P, *E. mitis*; Q, *E. necatrix*; R, *E. praecox*; S, *E. tenella*, T, *E. vejdovskyi*

COIII, which is between LSUA and LSU1, and is 780 bp in length. CYT B begins with an ATG start codon; COI and COIII begin with ATT. The standard stop termination codon TAA occurs in CYT B and COI, and COIII stops with TAG (Fig. 3, Table 2).

The *E. anseris* mtDNA contains 12 gene fragments for LSU rRNA (LSUF, LUSG, LUSC, LSU10, LSU13, LSUD, LSU2, LSUA, LSU1, LUSB, LSU3, and LSUE) and seven gene fragments for SSU rRNA (SSUA (SA), SSUF, SSUD (SD), SSU9, SSU8, SSUB, and SSUE), but no transfer RNA genes. The LSU rRNA gene fragments range in length from 16 to 188 bp; the longest is LSUE, and the shortest is LUSC. The longest SSU rRNA is SSUB, which has a length of 116 bp; the shortest is SSUF, which is 61 bp long.

Phylogenetic reconstructions

The complete mtDNA sequence ML and BI phylogenetic trees of the 20 *Eimeria* species share identical topologies and high-node support values (Fig. 4). The trees divide the sequences into two primary clusters. Some species cluster into clades associated with the parasites' hosts (e.g., species isolated from rabbits), but many species do not follow clear coevolutionary host segregating patterns (e.g., species isolated from both chickens and turkeys).

One primary cluster contains a very well-defined, monophyletic clade of *Eimeria* species, *E. praecox*, from chicken, sister to both *E. anseris*, which infects *A. albifrons*, and *E. acervulina*, also from chicken. This clade is sister to three other chicken-infecting species, *E. brunetti*, *E. mitis*, and *E. maxima*. The other major clade in this primary cluster contains *E. gallopavonis*, *E. adenoeides*, and *E. meleagridis*, found in turkey, sister to *E. tenella*, and *E. necatrix*, from chicken, all sister to *E. meleagrimitis*, from turkey.

The other primary cluster assorts *E. dispersa* and *E. innocua*, from turkey, sister to *E. mephitidis*, from striped skunk. *E. irresidua*, *E. intestinalis*, *E. magna*, *E. media*, and *E. vejdovskyi*, all from rabbit, form a well-supported clade.

In summary, *Eimeria* species that infect chickens and turkeys do not all assort to host-specific clades. Furthermore, *E. anseris*, which infects *A. albifrons*, belongs to a monophyletic clade with species that infect chicken.

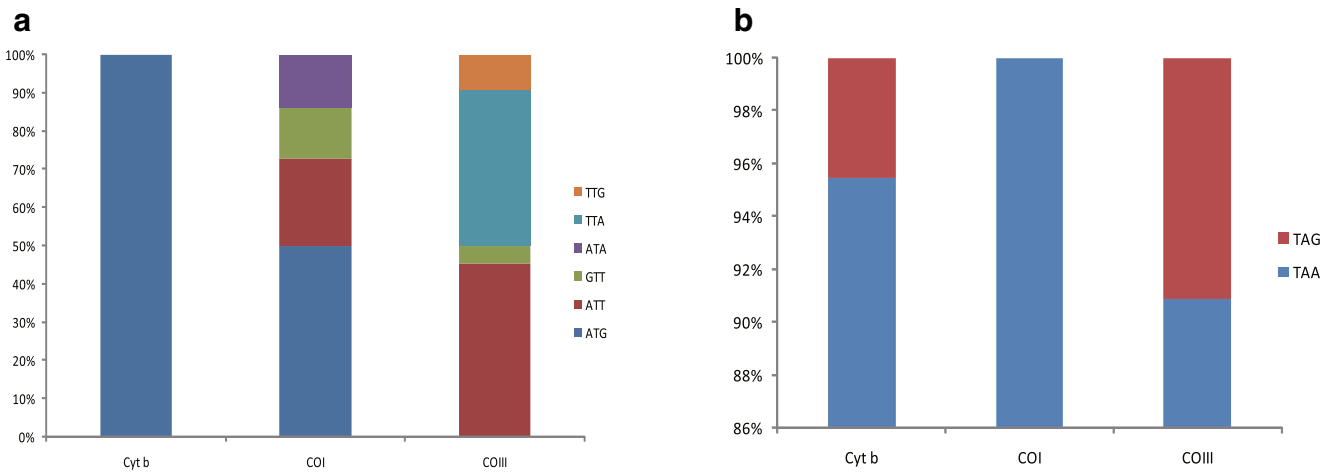

Fig. 3 Start codon use (**a**) and stop codon use (**b**) of three mitochondrial protein-coding genes, Cyt b, COI, and COIII, in 20 *Eimeria* species

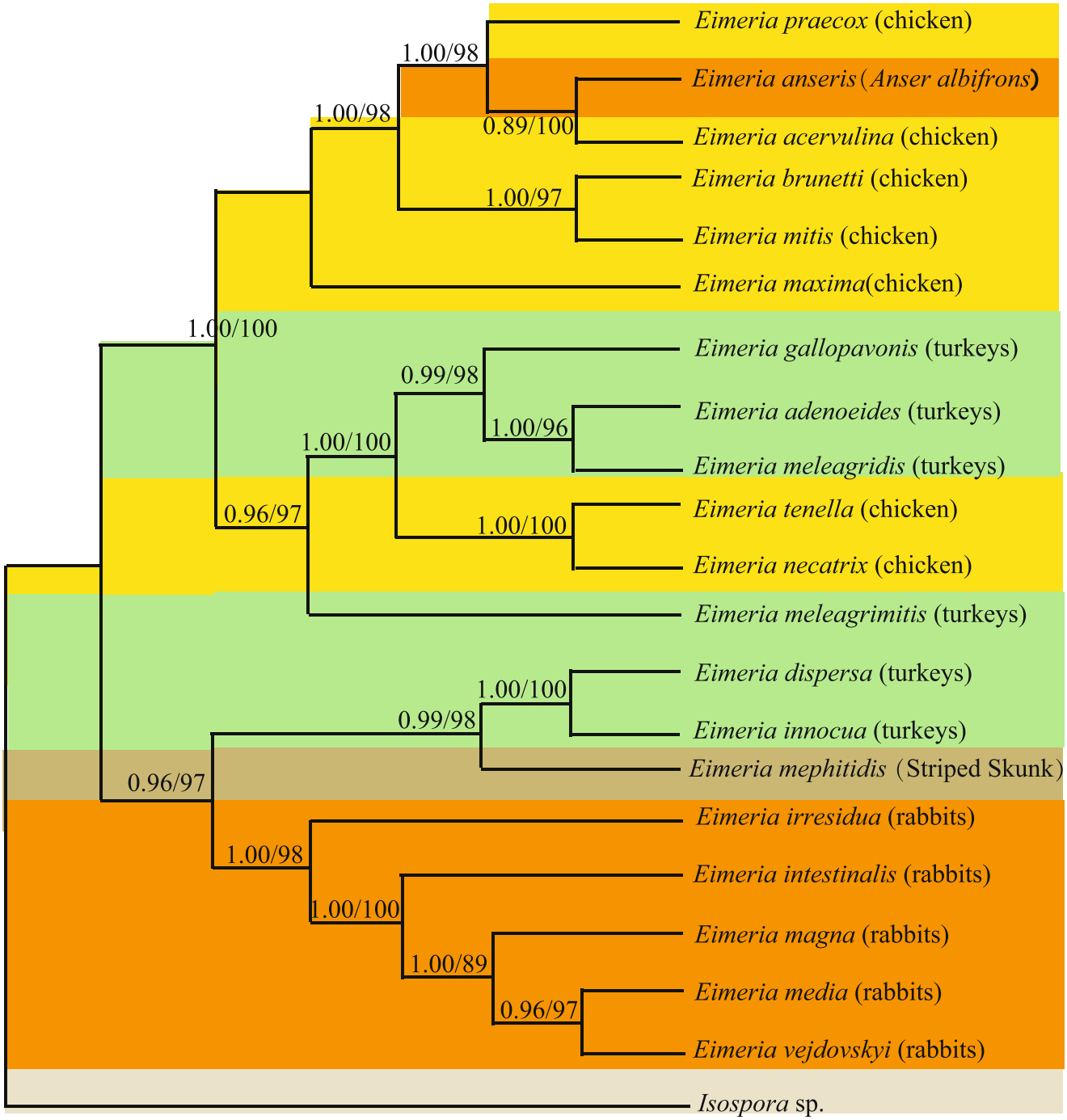

Fig. 4 Phylogenetic relationships of 20 *Eimeria* species based on complete mitochondrial DNA. Numbers at each node indicate Bayesian posterior probabilities (left) and maximum likelihood bootstrap proportions (right). *Isospora* is the outgroup

Discussion

Mitochondrial genome feature annotation

All sequenced *Eimeria* mitochondrial genomes are compact, with short intergenic spacer regions, and all are quite similar in length (Lin et al. 2011; Tian et al. 2015; Ogedengbe et al. 2014; Hafeez et al. 2015, 2016). The longest, *E. mitis*, is 6408 bp in length, and the shortest, *E. maxima*, is 6167 bp long (Table 3). Compared with 19 previously sequenced *Eimeria* mitochondrial genomes, *E. anseris* contains 4536 bp absolutely conserved sites, which represents 73.16% of the genome.

E. anseris mtDNA nucleotide composition is biased toward A and T, with T (35.3%) being the most common nucleotide and C (17.2%), the least common. This is different from

Table 3 Nucleotide composition (%) of study *Eimeria* mitochondrial genomes

Species	T (%)	C (%)	A (%)	G (%)	Total
Eimeria anseris	35.3	17.2	29.8	17.7	6179
Eimeria acervulina	35.3	17.6	30.1	17.0	6179
Eimeria adenoeides	34.8	18.4	29.8	17.0	6211
Eimeria brunetti	35.8	17.4	29.8	17.1	6156
Eimeria dispersa	35.6	17.6	29.9	16.8	6238
Eimeria gallopavonis	34.8	18.3	30.1	16.9	6215
Eimeria innocua	35.8	17.5	29.9	16.7	6247
Eimeria intestinalis	35.5	17.7	29.7	17.1	6247
Eimeria irresidua	35.6	17.6	29.8	17.0	6259
Eimeria magna	35.4	17.7	29.7	17.1	6249
Eimeria maxima	34.5	17.9	30.0	17.5	6167
Eimeria media	35.5	17.7	29.6	17.1	6245
Eimeria meleagridis	34.9	18.3	29.8	17.0	6212
Eimeria meleagrimitis	33.5	19.2	30.0	17.3	6165
Eimeria mephitidis	35.1	18.2	29.6	17.1	6175
Eimeria mitis	36.5	16.3	30.9	16.3	6408
Eimeria necatrix	35.2	18.2	29.8	16.9	6212
Eimeria praecox	35.5	17.3	30.1	17.1	6172
Eimeria tenella	35.2	18.1	29.8	16.9	6213
Eimeria vejdovskyi	35.5	17.7	29.6	17.2	6240

most *Eimeria* mtDNA, in which the rarest nucleotide is G (Fig. 2, Table 3) (Lin et al. 2011; Ogedengbe et al. 2014). Overall, *E. anseris* mtDNA A+T content is 65.1%, and C+G content is 34.9%, similar to other *Eimeria*, all with higher A+T content than C+G (Table 3) (Lin et al. 2011; Tian et al. 2015; Ogedengbe et al. 2014; Hafeez et al. 2015).

Protein-coding gene variation

E. anseris mtDNA initiation and termination codons follow the same pattern as other members of *Eimeria*. Most CDS regions in *E. anseris* use ATG as a start codon (Table 4). A few exceptions in our and in previous studies show *Eimeria* employing ATT, GTT, ATA, TTA, or TTG (Lin et al. 2011; Tian et al. 2015; Ogedengbe et al. 2014; Hafeez et al. 2015, 2016). Stop codons are also similar across species, with TAA and TAG occurring most frequently across all 20 *Eimeria* species (Lin et al. 2011; Tian et al. 2015; Ogedengbe et al. 2014; Hafeez et al. 2015, 2016). Specific examples from the three CDS regions of all 20 *Eimeria* species include the following: the CYT B initiation codon is ATG, and the termination codon is TAA in all, except in *E. falciformis*, which stops with TAG. COI starts with ATG, ATT, GTT, or ATA and ends with TAA in all 20 *Eimeria* species. And all COIII CDS regions end with TAA, but *E. anseris* and *E. acervulina* end with TAA.

Table 4 Predicted initiation and termination codons for three mitochondrial protein-coding genes in study *Eimeria* mitochondrial genomes

Species	Cyt b Initiation/termination codon	COI Initiation/termination codon	COIII Initiation/termination codon
Eimeria anseris	ATG/TAA	ATT/TAA	ATT/TAG
Eimeria acervulina	ATG/TAA	GTT/TAA	ATT/TAG
Eimeria adenoeides	ATG/TAA	ATG/TAA	ATT/TAA
Eimeria brunetti	ATG/TAA	GTT/TAA	ATT/TAA
Eimeria dispersa	ATG/TAA	ATG/TAA	TTG/TAA
Eimeria gallopavonis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria innocua	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria intestinalis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria irresidua	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria magna	ATG/TAA	ATT/TAA	ATT/TAA
Eimeria maxima	ATG/TAA	ATT/TAA	ATT/TAA
Eimeria media	ATG/TAA	ATA/TAA	ATT/TAA
Eimeria meleagridis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria meleagrimitis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria mephitidis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria mitis	ATG/TAA	ATG/TAA	TTA/TAA
Eimeria necatrix	ATG/TAA	ATT/TAA	ATT/TAA
Eimeria praecox	ATG/TAA	GTT/TAA	ATT/TAA
Eimeria tenella	ATG/TAA	ATT/TAA	ATT/TAA
Eimeria vejdovskyi	ATG/TAA	ATG/TAA	TTA/TAA

Phylogenetic relationships

Coevolution between *Eimeria* species and hosts has contributed to phylogenetic relationships within the genus, and the present study partially corroborates this assertion (Miska et al. 2010). This is seen in our research in that all *Eimeria* species isolated from rabbit, *E. irresidua*, *E. intestinalis*, *E. magna*, *E. media*, and *E. vejdovskyi*, are a monophyletic group (Vrba and Pakandl 2014; Liu et al. 2015; Hafeez et al. 2015, 2016). However, our phylogenetic analyses show that host swapping with subsequent divergence has also occurred in many species. Thus, some species from turkeys, *E. gallopavonis*, *E. adenoeides*, and *E. meleagridis*, in one highly supported, unique clade, do not group with the other turkey eimerians, *E. meleagrimitis*, *E. dispersa*, and *E. innocua*. Hence, *Eimeria* infecting turkeys are a paraphyletic group, which is a view different from previous research (Barta et al. 1997; Lew et al. 2003; Yabsley 2009; Miska et al. 2010; Ogedengbe et al. 2014). The results also show that some of the *Eimeria* species that infect chicken, *E. tenella* and *E. necatrix*, are more closely related to species that infect turkey. Thus, chicken-infecting *Eimeria* is also a paraphyletic group. Furthermore, *E. anseris*, which infects *A. albifrons*, and *E. praecox*, *E. acervulina*, *E. brunetti*, and *E. mitis*, all isolated from chicken, form one highly supported clade, sister to, though not as highly supported, *E. maxima*, also from chicken. This supports the view held by other researchers of a close phylogenetic relationship within these species (Poplstein and Vrba 2011; Ogedengbe et al. 2014).

The present study sequenced, annotated gene and genome organization, and reported for the first time the complete mtDNA sequence of *E. anseris*. The mt genome of *E. anseris* infecting *A. albifrons* is similar with respect to genome size, organization, start codon positions, and overall base composition as all other *Eimeria*. Coevolution between *Eimeria* species and hosts has contributed to phylogenetic relationships within the genus, and the present study partially corroborates this assertion using complete mtDNA. Our molecular phylogenetic analyses show some species clustering into clades associated with the parasites' hosts, but many species do not follow clear coevolutionary host segregating patterns. The mtDNA sequence provides useful genetic data for addressing further questions in the systematics and population genetics of these and related *Eimeria* of relevance to waterfowl. The nature of the *E. anseris* mt genome makes the sequence highly suited for the development of diagnostic assays as well, potentially providing genetic markers for molecular epidemiology and the study of coccidia phylogenetics.

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Compliance with ethical standards

No animal was harmed during the course of this research. All experimental procedures complied with current laws regarding animal welfare and research in China and were specifically approved by the Animal Research Ethics Committee of Anhui Medical University.

Competing interests The authors declare that they have no competing interests.

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