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RESEARCH

Quantification of rearrangements and evolution of mitochondrial gene order of Acari (Chelicerata: Arachnida)

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Abstract

Invertebrate mitogenomes are generally fixed with formal 37 genes: 13 PCGs encoded subunits of OXPHOS, 2 ribosomal RNA (rRNA) functional in the translation of these PCGs and 22 transfer RNA (tRNA) genes. The order of these genes varies greatly among organisms and named rearrangement. Rearrangement patterns of mitochondrial genomes may shed light on mutation processes and evolutionary relationships of organisms. Mitochondrial gene organization is highly variable among Acari, so rearrangement is a very common mitogenomic pattern in this group. In this study, 258 unique Acari (Acariformes + Parasitiformes) mitogenomes were downloaded from NCBI and studied about rearrangement patterns. Sixty-seven mitotypes were determined among Acari and the most rearranged genes were trnL1 and *nad2*. Following that, trnI, trnS1, trnN, trnE, trnT, and trnP genes are remarkably mobile (RF > 95%). Conversely, *atp6*, *cox3*, trnG, and *cytb* genes also appears to be quite stable (RF < 20%). Within Acari, mean distance calculations are varied from 1.210 in *atp8* to 0.155 in rrnS. Contrary to expectations, among Acari mobile tRNA genes appear to be conserved in sequences, whereas PCGs have higher distance values and seem to be mutated. Consistently, tRNA genes seem saturated, but some PCGs (*atp6*, *cox* genes, *cytb*, *nad1*, *and nad6*) are not saturated. These values do not correlate with each other ($p > 0.005$). This discrepancy may indicate that the genes were rearranged after mutation load; consistent with this, DAMBE saturation values are also not correlated with RF values. Parasitiformes mitogenomes are more mobile than Acariformes mitogenomes and may be under the effect of selective sweeping.

Keywords Mitogenome · Rearrangement · Gene order · Mitotype · Acari

Abbreviations

DAMBE	Data Analysis in Molecular Biology and Evolution
IGS	Intergenic spacers
INSDC	International Nucleotide Sequence Database Collaboration (ENA/GenBank/DDBJ)
iTOL	Interactive Tree Of Life
M(x)	Mitotype (x), unique mitochondrial gene orders
ML	Maximum likelihood
MLGO	Maximum Likelihood for Gene Order Analysis
mtDNA	Mitochondrial genome
NCBI	National Center for Biotechnology Information
PCG	Protein coding genes
qMGR	Quantifying mitochondrial genome rearrangement
RF	Rearrangement frequency
rRNA	Ribosomal ribonucleic acid
RS	Rearrangement Score
TDRL	Tandem duplication random loss
tRNA	Transfer ribonucleic acid

Introduction

The mitochondrial genome (mtDNA) is a flexible genome which encodes 13 protein subunits which are essential for the formation of four of the five OXPHOS complexes, 2 rRNA subunits (*rrnS* and *rrnL*) joint in the mitoribosome structure and the 22 tRNAs (one for each tRNA except for

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trnS and *trnL*) in arthropods (Boore 1999; Cameron 2014). Mitogenome also has a variable non-coding regulator region: D-loop region and intergenic spacers (IGSs), which are containing regulatory elements of replication, transcription, and potentially translation (Roberti et al. 2003; Aydemir et al. 2023). The mitogenomic data potentially contain two different information: (i) the preferences of nucleotides of genes and whole genome and (ii) the structural features, such as gene content, gene order, motifs of replication, and transcription. The mitogenomic structural features generally reflect differences in functional and evolutionary limitations and are also evolved by various mechanisms and at different evolutionary rates (Castro et al. 2002; Gissi et al. 2008; Cameron 2014).

The mobility of mitochondrial genes among mitogenomes give important clues about mitogenome structure and mitogenome evolution and this mobility resulted to gene rearrangements in mitogenome (Gissi et al. 2008). Several types of rearrangement events have been proposed by comparing closely related species using different genes: inversions (Asakawa et al. 1995), transpositions (Macey et al. 1997), reverse transpositions (Boore et al. 1998), and tandem duplication following random loss of one of the duplicated genes (TDRL) (Boore 2000). Mitochondrial rearrangement processes mainly originated from TDRL mutations (Boore and Brown 1997; Macey et al. 1997; Lavrov et al. 2002). Mitochondrial gene boundaries that maintain accelerated mitochondrial gene rearrangements may set some selective boundaries of mitochondrial genome organizations (Dowton et al. 2009). mtDNA rearrangements not only change mtDNA gene sequences and gene order but also change the importance and orientation of regulatory elements located throughout the mitogenome, especially in non-coding regions, like D-loop and intergenic regions (Barshad et al. 2018). Paradoxically, it is also known that non-coding regions especially IGSs are evaluated as pseudogene residues of rearrangement processes (Serb 2003; Masta and Boore 2004; Mueller and Boore 2005; Akasaki et al. 2006). Even alternative initiation codons of mitochondrial PCGs were found to be related to mitochondrial rearrangement events in Echinoderms (Quek et al. 2021). It has been found that regions which potentially gain secondary structure may be particularly mediators for rearrangement mechanisms (Barshad et al. 2018). Particularly, tRNA clusters have been evaluated as rearrangement hotspots, and it has been suggested that processes such as replication slippage may trigger rearrangement. Accordingly, it is hypothesized that regulatory regions involved in transcription may also have such a function (Bernt et al. 2013). Therefore, it is not known whether mitogenome organization reflects transcription efficiency, selective forces, and mitochondrial phenotype.

Studies show that gene rearrangements are quite common in Arthropod mitogenomes (Shao et al. 2001, 2003; Masta and Boore 2004; Covacin et al. 2006). A positive and significant correlation has been determined between high rates of nucleotide substitution and gene rearrangements in hemipteroid insect mitochondrial genes differed by more than five breakpoints; in fact, it is suggested that nucleotide changes trigger gene order changes (Shao et al. 2003). In metazoan mitogenomes, the most varied genes, tRNAs, are generally evolutionary more mobile than protein-coding genes and accepted as a hotspots of rearrangement events (Dowton and Austin 1999; San Mauro et al. 2006; Gissi et al. 2008). In a recent and another study, it is hypothesized that mitochondrial genome mutations do not promote gene rearrangements, as previously proposed (Tyagi et al. 2020). It has not reached any consensus idea on the relationship of mitogenome organization and mitochondrial evolution. So, more studies with more components with different organismal orders are needed.

Within Acari, mitogenomes of Acariformes superorder show highly rearranged but not shared genome structure (Fahrein et al. 2007; Dermauw et al. 2009; Xue et al. 2016); for this reason, it has been suggested that mitochondrial gene order can be used as a phylogenetic marker (Basso et al. 2017; Wang et al. 2017). Nevertheless, in the results of the recent studies, this feature does not seem to be a powerful tool for superorders but can be used for families of Acari (Masta 2010; Yuan et al. 2010; Li et al. 2019; Li and Xue 2019). The tick-box, a region possibly functional as transcription signal that has been identified in Ixodida and has been demonstrated to be present in some other invertebrates, has also been proposed to mediate rearrangement processes. This region is a 17 bp DNA sequence that is located in the 3'-end of the polyadenylated *nad1* and rrnL genes and is similar to that found between trnQ and trnF (Montagna et al. 2012). In recent study, 37 different mitotypes were determined in Acari with the study include 204 specimens (Arribas et al. 2020). The ancestral gene order of Acari, named as mitotype 1 (M1) in this study, suggested in Arribas et al. 2020, was given in Fig. 1.

Acari includes 258 unique mitogenomes that is represented in the NCBI-GenBank database (released before May 2023). When the data are evaluated in terms of 2 traditional groups (Acariformes and Parasitiformes), only 22% of the sampling represent the more diverse Acariformes superorder (Pepato et al. 2010).

In this study, mitochondrial gene organizations of Acari were evaluated on larger sampling and comparatively discussed in the perspective of phylogeny, mutation load processes and mitotypes.

Materials and methods

Determination of unique gene orders and frequently rearranged genes

The mitogenome sequences of 258 Acari were downloaded from NCBI and used for comparative analyses of mitochondrial gene order (Table 1). Two hundred fifteen of the

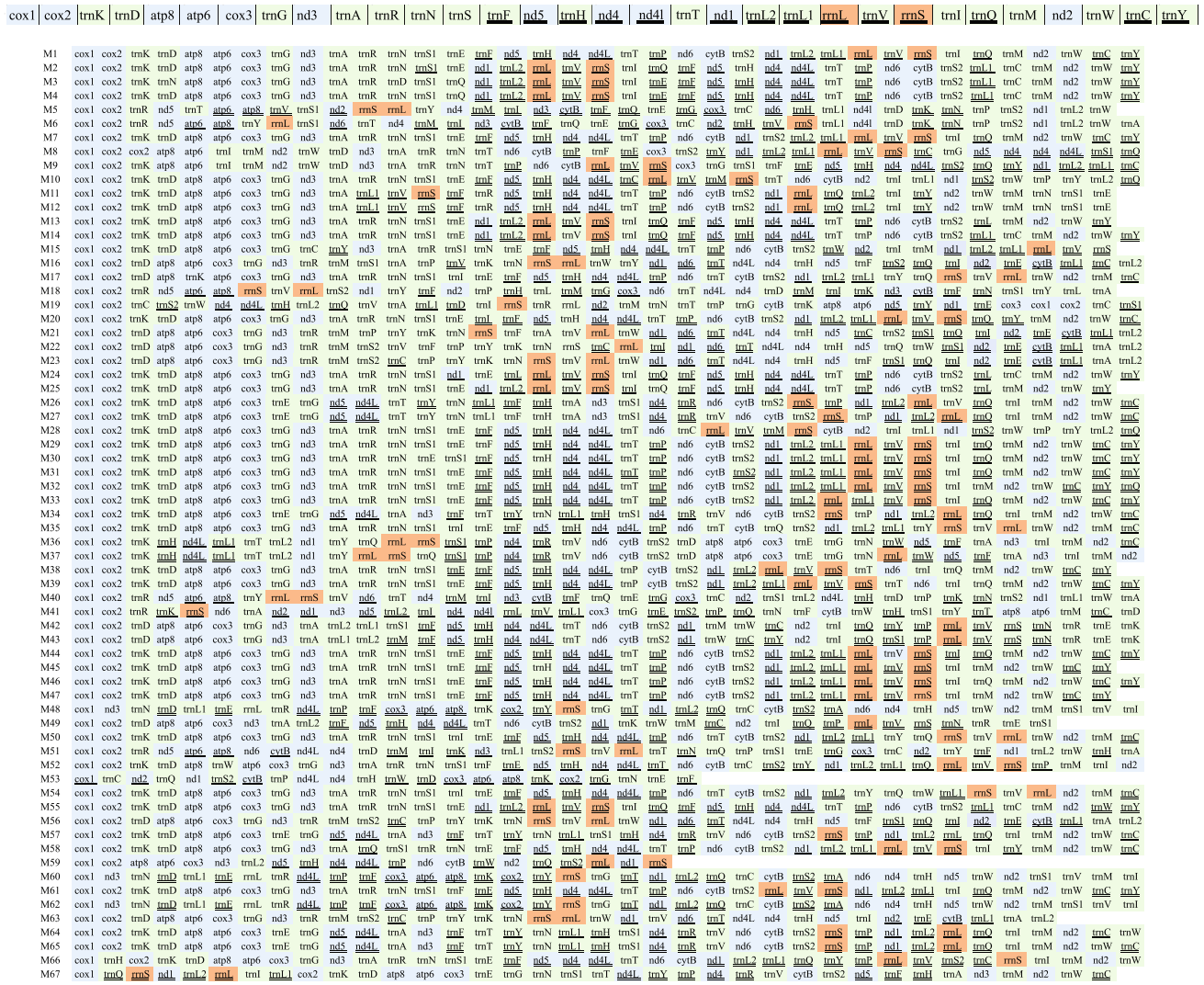

Fig. 1 Sixty-seven mitotypes, including generally accepted ancestral gene order (mitotype 1- M1), determined in Acari sampling include 257 unique mitogenomes

data are verified; RefSeq data and 43 INSDC (GenBank) data were selected and added to the dataset to represent the families without any RefSeq representatives. In the whole specimen, the superorder Acariformes represented with 55 and the superorder Parasitiformes represented with 203 species. In Acariformes, 23 species represent the order of Sarcoptiformes (19 Astigmata and four Oribatida), and 32 species represent the order of Trombidiformes (10 Anystina, 16 Eleutherengona, and six Eupodina). Within Parasitiformes, Mesostigmata has 24, Holothyrida has one, and Ixodida has 178 representative mitogenomes. The combined dataset comprises 26 superfamilies (Table 1).

Gene rearrangement events in Acari were mapped via CREx with a presumed ancestral gene order of Tardigrada, *Hypsibius dujardini* (NC_014848) (Bernt et al. 2007). CREx programme based on the common interval algorithm for pairwise comparison and determined the set of rearrangement events (transpositions, inversions, inverse transpositions, TDRL). With comparison of the "typical invertebrate arrangement," rearrangement frequency (RF) of each gene and rearrangement score (RS) of each species were calculated via qMGR (Quantifying Mitochondrial Genome Rearrangement, http://qmgr.hnnu.edu.cn/) (Zhang et al. 2020).

To determine the relationship between evolutionary forces and mitochondrial gene orders, rearrangement frequencies and mutational exposure of genes were compared. The overall mean distance values were calculated via MEGA v11. The saturation indexes for each gene were evaluated via DAMBE 7 (data analysis for molecular biology and evolution, http://dambe.bio.uottawa.ca/). DAMBE is a software package for phylogenetic analysis (alignment, substitution saturation

Table 1 The sampling of Acari includes 257 unique species downloaded from the NCBI database with the information of mitotypes

Organism	NCBI accesion	Length	%GC	Taxonomy
Scatoglyphus polytrematus	MT133686	13,966	29.8%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Acaridae incertae sedis; Scatoglyphus
Rhizoglyphus robini	NC_038058	14,244	32.2%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Rhizoglyphinae; Rhizoglyphus
Sancassania berlesei	NC_024637	14,273	32.6%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Rhizoglyphinae; Sancassania
Thyreophagus entomophagus	NC_066986	14,242	29.0%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Rhizoglyphinae; Thyreophagus
Aleuroglyphus ovatus	NC_023778	14,328	31.7%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Tyrophaginae; Aleuroglyphus
Tyrophagus putrescentiae	NC_026079	13,288	29.9%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Tyrophaginae; Tyrophagus
Tyrophagus longior	NC_028725	13,271	30.3%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Acaridae; Tyrophaginae; Tyrophagus
Lardoglyphus konoi	MW784238	14,269	30.0%	Acariformes; Sarcoptiformes; Astigmata; Acaroidea; Lardoglyphidae; Lardoglyphus
Chortoglyphus arcuatus	NC_067498	14,865	28.0%	Acariformes; Sarcoptiformes; Astigmata; Glycyphagoidea; Chortoglyphidae; Chortoglyphus
Blomia tropicalis	NC_062715	15,129	34.5%	Acariformes; Sarcoptiformes; Astigmata; Glycyphagoidea; Echimyopodidae; Blomia
Lepidoglyphus destructor	NC_062716	14,654	35.8%	Acariformes; Sarcoptiformes; Astigmata; Glycyphagoidea; Glycyphagidae; Lepidoglyphus
Carpoglyphus lactis	NC_048990	14,060	29.8%	Acariformes; Sarcoptiformes; Astigmata; Hemisarcoptoidea; Carpoglyphidae; Carpoglyphus
Histiostomatidae sp.	MH921997	14,711	29.8%	Acariformes; Sarcoptiformes; Astigmata; Histiostomatoidea; Histiostomatidae
Histiostoma blomquisti	NC_031377	15,892	29.8%	Acariformes; Sarcoptiformes; Astigmata; Histiostomatoidea; Histiostomatidae; Histiostoma
Histiostoma feroniarum	NC_038207	13,896	27.8%	Acariformes; Sarcoptiformes; Astigmata; Histiostomatoidea; Histiostomatidae; Histiostoma
Dermatophagoides pteronyssinus	NC_012218	14,203	27.4%	Acariformes; Sarcoptiformes; Astigmata; Psoroptidia; Analgoidea; Pyroglyphidae; Dermatophagoidinae; Dermatophagoides
Dermatophagoides farinae	NC_013184	14,266	28.6%	Acariformes; Sarcoptiformes; Astigmata; Psoroptidia; Analgoidea; Pyroglyphidae; Dermatophagoidinae; Dermatophagoides
Trouessartia rubecula	NC_041090	14,125	26.7%	Acariformes; Sarcoptiformes; Astigmata; Psoroptidia; Analgoidea; Trouessartiidae; Trouessartia
Psoroptes ovis	NC_024675	14,247	28.9%	Acariformes; Sarcoptiformes; Astigmata; Psoroptidia; Sarcoptoidea; Psoroptidae; Psoroptes
Oribatula sp.	MH921998	15,220	34.6%	Acariformes; Sarcoptiformes; Oribatida; Brachypylina; Oripodoidea; Oribatulidae; Oribatula
Oribatula sakamorii	MT232643	14,494	29.2%	Acariformes; Sarcoptiformes; Oribatida; Brachypylina; Oripodoidea; Oribatulidae; Oribatula
Paraleius leontonychus	LT984407	14,186	35.3%	Acariformes; Sarcoptiformes; Oribatida; Brachypylina; Oripodoidea; Scheloribatidae; Paraleius
Steganacarus magnus	NC_011574	13,818	25.4%	Acariformes; Sarcoptiformes; Oribatida; Mixonomata; Phthiracaroidea; Steganacaridae; Steganacarus
Hygrobates longiporus	NC_049059	13,721	27.6%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Hygrobatoidea; Hygrobatidae; Hygrobates
Hygrobates turcicus	NC_068260	15,006	28.8%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Hygrobatoidea; Hygrobatidae; Hygrobates
Unionicola foili	NC_011036	14,738	27.0%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Hygrobatoidea; Unionicolidae; Unionicolinae; Unionicola; Parasitatax

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Unionicola parkeri	NC_014683	14,734	27.2%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Hygrobatoidea; Unionicolidae; Unionicolinae; Unionicola; Unionicolides
Lebertia trifurcilla	NC_065315	14,347	25.5%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Lebertioidea; Lebertiidae; Lebertia
Sperchon plumifer	NC_039813	14,646	26.4%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Hydracarina; Sperchontoidea; Sperchontidae; Sperchon
Leptotrombidium pallidum	NC_007177	16,779	29.0%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Trombiculoidea; Trombiculidae; Leptotrombidium
Leptotrombidium deliense	NC_007600	13,731	30.0%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Trombiculoidea; Trombiculidae; Leptotrombidium
Leptotrombidium akamushi	NC_007601	13,698	32.5%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Trombiculoidea; Trombiculidae; Leptotrombidium
Walchia hayashii	NC_010595	14,857	27.0%	Acariformes; Trombidiformes; Prostigmata; Anystina; Parasitengona; Trombiculoidea; Trombiculidae; Walchia
Pyemotes zhonghuajia	NC_062623	10,555	21.4%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Heterostigmata; Pyemotoidea; Pyemotidae; Pyemotes
Demodex brevis	KM114225	14,211	31.0%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Cheyletoidea; Demodicidae; Demodex
Demodex folliculorum	NC_026102	14,150	29.9%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Cheyletoidea; Demodicidae; Demodex
Amphitetranychus viennensis	NC_032381	13,085	15.2%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Amphitetranychus
Panonychus ulmi	NC_012571	13,115	14.4%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Panonychus
Panonychus citri	NC_014347	13,075	14.5%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Panonychus
Stigmaeopsis miscanthi	MZ726369	15,171	19.6%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Stigmaeopsis
Tetranychus evansi	MN417333	13,064	15.5%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus urticae	NC_010526	13,103	15.7%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus cinnabarinus	NC_014399	13,092	15.6%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus kanzawai	NC_024676	13,091	15.5%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus ludeni	NC_024677	13,064	15.5%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus malaysiensis	NC_024678	13,049	16.6%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus phaselus	NC_024679	13,084	16.1%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus pueraricola	NC_024680	13,084	15.8%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Tetranychus truncatus	NC_024874	13,089	15.5%	Acariformes; Trombidiformes; Prostigmata; Eleutherengona; Raphignathae; Tetranychoidea; Tetranychidae; Tetranychus
Spinibdella lignicola	NC_067576	14,196	21.4%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Bdelloidea; Bdellidae; Spinibdella
Rhinotergum shaoguanense	NC_034150	13,646	27.0%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Eriophyoidea; Diptilomiopidae; Rhinotergum
Epitrimerus sabinae	NC_029208	13,531	33.7%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Eriophyoidea; Eriophyidae; Phyllocoptinae; Phyllocoptini; Epitrimerus
Leipothrix sp.	KX027362	14,216	32.9%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Eriophyoidea; Eriophyidae; Phyllocoptinae; Phyllocoptini; Leipothrix

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Phyllocoptes taishanensis	NC_029209	13,475	33.6%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Eriophyoidea; Eriophyidae; Phyllocoptinae; Phyllocoptini; Phyllocoptes
Halotydeus destructor	NC_063625	14,691	27.9%	Acariformes; Trombidiformes; Prostigmata; Eupodina; Eupodoidea; Penthaleidae; Halotydeus
Allothyrus sp.	KC769586	14,578	21.2%	Parasitiformes; Holothyrida; Holothyroidea; Allothyridae; Allothyrus
Argas sp.	KC769588	14,450	26.3%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas africolumbae	NC_019642	14,440	26.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas lagenoplastis	NC_023369	14,478	27.4%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas miniatus	NC_023371	14,416	25.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas walkerae	NC_037523	14,437	25.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas persicus	NC_053794	14,426	27.3%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas ricei	NC_067900	14,450	25.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Argas sp.	ON800829	14,454	25.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Argas
Navis striatus	NC_037522	14,487	23.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Navis
Ogadenus brumpti	NC_033855	14,516	30.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Ogadenus
Proknekalia peringueyi	KY457517	14,584	24.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Proknekalia
Secretargas transgariepinus	KY457523	14,534	28.5%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Argasinae; Secretargas
Alectorobius capensis	NC_005291	14,418	26.5%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius atacamensis	NC_067906	14,430	27.2%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius cerradoensis	NC_067907	14,415	28.5%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius fonsecai	NC_067910	14,404	25.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius guaporensis	NC_067912	14,416	26.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius microlophi	NC_067914	14,409	25.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius mimon	NC_067915	14,410	28.2%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius peropteryx	NC_067917	14,404	27.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius peruvianus	NC_067918	14,401	33.3%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius puertoricensis	NC_067919	14,424	25.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius rietcorreai	NC_067920	14,430	28.2%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius rioplatensis	NC_067921	14,451	27.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius rudis	NC_067922	14,395	27.0%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius amblus	ON756083	14,401	25.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Alectorobius spheniscus	ON756088	14,482	26.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Alectorobius
Antricola mexicanus	NC_023340	14,415	25.4%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Antricola
Carios vespertilionis	NC_060373	14,521	26.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Carios
Chiropterargas confusus	KY457514	14,287	25.4%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Chiropterargas
Chiropterargas boueti	NC_056777	14,307	23.4%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Chiropterargas

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Nothoaspis amazoniensis	NC_033900	14,416	27.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Nothoaspis
Ornithodoros costalis	KJ133591	14,442	27.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros kalahariensis	KJ133598	14,409	31.5%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros moubata	NC_004357	14,398	27.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros porcinus	NC_005820	14,378	29.0%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros rostratus	NC_023372	14,452	27.0%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros brasiliensis	NC_023373	14,489	26.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros zumpti	NC_033857	14,434	30.5%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros savignyi	NC_037525	14,401	34.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros sonrai	NC_039688	14,430	26.0%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros turicata	NC_039829	14,458	26.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros tholozani	NC_039830	14,407	30.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros parkeri	NC_039831	14,437	25.6%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros hermsi	NC_039832	14,430	28.0%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros coriaceus	NC_039857	14,423	30.3%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros compactus	NC_067908	14,400	27.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros erraticus	NC_067909	14,408	27.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros furcosus	NC_067911	14,436	27.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros noorsveldensis	NC_067916	14,420	30.2%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros tabajara	NC_067923	14,466	28.2%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros tartakovskyi	NC_067924	14,398	30.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros asperus	NC_067925	14,421	28.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros phacochoerus	NC_068139	14,554	28.8%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Ornithodoros waterbergensis	NC_068140	14,386	28.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Ornithodoros
Otobius megnini	NC_023370	14,430	25.1%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Otobius
Otobius lagophilus	NC_067913	14,535	29.7%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Otobius
Reticulinasus faini	NC_037524	14,433	23.3%	Parasitiformes; Ixodida; Ixodoidea; Argasidae; Ornithodorinae; Reticulinasus
Amblyomma marmoreum	KY457516	14,677	22.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma geoemydae	MK814531	14,780	22.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Amblyomma triguttatum	NC_005963	14,740	21.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma fimbriatum	NC_017759	14,705	22.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma cajennense	NC_020333	14,780	24.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma americanum	NC_027609	14,709	23.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma sculptum	NC_032369	14,780	23.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma javanense	NC_043872	14,780	20.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma ovale	NC_050255	14,760	23.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma testudinarium	NC_062071	14,976	19.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma gervaisi	NC_067858	14,709	20.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma latum	NC_067859	14,658	20.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma sparsum	NC_067860	14,681	20.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma hebraeum	NC_067897	14,655	22.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma maculatum	NC_067898	14,801	21.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma mixtum	NC_067899	14,821	23.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma tholloni	NC_067901	14,661	24.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma patinoi	NC_072689	14,779	23.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma tonelliae	NC_072690	14,731	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Amblyomma sp.	OM368313	14,760	21.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Amblyomminae; Amblyomma
Archaeocroton sphenodonti	NC_017745	14,772	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Archaeocroton
Bothriocroton concolor	NC_017756	14,809	24.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Bothriocrotoninae; Bothriocroton
Bothriocroton undatum	NC_017757	14,769	23.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Bothriocrotoninae; Bothriocroton
Haemaphysalis kolonini	MZ054209	14,948	21.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis flava	NC_005292	14,686	23.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis formosensis	NC_020334	14,676	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis inermis	NC_020335	14,846	21.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis concinna	NC_034785	14,675	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis japonica	NC_037246	14,685	22.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis longicornis	NC_037493	14,718	22.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Haemaphysalis hystricis	NC_039765	14,716	22.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis bancrofti	NC_041076	14,673	21.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis montgomeryi	NC_058312	14,681	21.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis sulcata	NC_062063	14,679	23.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis punctata	NC_062064	14,697	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis danieli	NC_062065	14,739	18.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis tibetensis	NC_062066	14,715	22.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis qinghaiensis	NC_062067	14,683	22.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis doenitzi	NC_062158	14,671	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis campanulata	NC_062159	14,691	21.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis yeni	NC_062160	14,690	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis kitaokai	NC_062161	14,936	22.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis cornigera	NC_062162	14,681	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis mageshimaensis	NC_062163	14,721	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis colasbelcouri	NC_062164	14,885	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis nepalensis	NC_064124	14,720	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Haemaphysalis bispinosa	NC_071765	14,732	21.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Haemaphysalinae; Haemaphysalis
Hyalomma truncatum	KY457529	14,731	22.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma aegyptium	MW546280	14,707	20.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma anatolicum	MW546283	14,731	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma excavatum	MW546284	14,733	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma rufipes	MW884229	14,761	20.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma asiaticum	NC_053941	14,723	21.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma marginatum	NC_056189	14,764	20.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Hyalomma scupense	NC_062166	14,721	20.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Hyalomminae; Hyalomma
Ixodes (Pholeoixodes) *sp.*	MW021452	14,543	27.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes hexagonus	NC_002010	14,539	27.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes persulcatus	NC_004370	14,539	22.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes holocyclus	NC_005293	15,007	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes uriae	NC_006078	15,053	25.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes ricinus	NC_018369	14,566	21.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes pavlovskyi	NC_023831	14,575	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes tasmani	NC_041086	15,227	22.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes nipponensis	NC_058242	14,505	22.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes vespertilionis	NC_058244	14,559	25.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes acutitarsus	NC_061225	14,475	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Ixodes granulatus	NC_061226	14,540	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes sinensis	NC_062059	14,534	22.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes simplex	NC_062060	14,556	24.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes ovatus	NC_062061	14,512	26.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes nuttallianus	NC_062062	14,604	25.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes kuntzi	NC_062157	14,524	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes australiensis	NC_062625	15,217	21.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes barkeri	NC_062626	15,259	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes woyliei	NC_062627	15,062	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes fecialis	NC_062628	15,256	22.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes confusus	NC_062629	14,939	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes cornuatus	NC_062630	14,985	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes hirsti	NC_062631	15,040	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes myrmecobii	NC_062632	14,995	21.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes trichosuri	NC_062633	15,001	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes columnae	NC_067861	14,524	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes pacificus	NC_067902	14,576	23.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes rubicundus	NC_067903	14,532	20.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes scapularis	NC_067904	14,543	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Ixodes angustus	NC_067905	14,529	25.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Ixodinae; Ixodes
Dermacentor rhinocerinus	KY457527	14,708	23.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor nitens	NC_023349	14,839	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor silvarum	NC_026552	14,945	21.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor nuttalli	NC_028528	15,086	21.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor everestianus	NC_042764	15,191	21.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor auratus	NC_059724	14,766	22.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor andersoni	NC_061057	14,806	20.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor variabilis	NC_061217	14,837	21.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor steini	NC_062068	14,773	23.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor marginatus	NC_062069	15,178	21.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor niveus	NC_062070	15,110	21.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor sinicus	NC_062165	14,996	21.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor albipictus	NC_067093	14,822	22.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor reticulatus	NC_068757	14,801	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Dermacentor sp.	OM368308	15,307	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Dermacentor
Rhipicentor nuttalli	NC_039828	14,779	21.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicentor
Rhipicephalus microplus	NC_023335	14,905	20.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Boophilus

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Rhipicephalus australis	NC_023348	14,891	20.1%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Boophilus
Rhipicephalus geigyi	NC_023350	14,948	19.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Boophilus
Rhipicephalus decoloratus	NC_052828	15,268	20.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Boophilus
Rhipicephalus annulatus	NC_067926	15,156	19.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Boophilus
Rhipicephalus sanguineus	NC_002074	14,710	22.0%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus turanicus	NC_035946	14,717	22.2%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus appendiculatus	NC_052829	15,001	22.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus linnaei	NC_060409	14,711	22.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus camicasi	NC_061616	14,725	22.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus haemaphysaloides	NC_062072	14,744	22.3%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus evertsi	NC_067927	14,743	23.6%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus maculatus	NC_067928	14,714	25.4%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus simus	NC_067929	14,721	23.8%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus zambeziensis	NC_067930	14,739	22.7%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Rhipicephalus rutilus	NC_072952	14,718	21.9%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Rhipicephalinae; Rhipicephalus; Rhipicephalus
Robertsicus elaphensis	NC_017758	14,627	19.5%	Parasitiformes; Ixodida; Ixodoidea; Ixodidae; Robertsicus
Nuttalliella namaqua	NC_019663	14,425	21.4%	Parasitiformes; Ixodida; Ixodoidea; Nuttalliellidae; Nuttalliella
Microdiplogynium sp.	MK270523	14,447	28.3%	Parasitiformes; Mesostigmata; Antennophorina; Celaenopsoidea; Diplogyniidae; Microdiplogynium
Quadristernoseta cf. intermedia	MK270521	14,423	27.8%	Parasitiformes; Mesostigmata; Antennophorina; Celaenopsoidea; Diplogyniidae; Quadristernoseta
Quadristernoseta cf. longigynium	MK270522	14,426	26.0%	Parasitiformes; Mesostigmata; Antennophorina; Celaenopsoidea; Diplogyniidae; Quadristernoseta
Stylochyrus rarior	NC_013474	14,900	27.3%	Parasitiformes; Mesostigmata; Gamasina; Ascoidea; Ologamasidae; Stylochyrus
Dermanyssus gallinae	NC_054303	16,184	19.3%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Dermanyssidae; Dermanyssus
Coleolaelaps cf. liui	MK270524	14,500	29.9%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Laelapidae; Coleolaelaps
Hypoaspis linteyini	NC_046028	14,529	23.1%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Laelapidae; Hypoaspis
Ptilonyssus chloris	NC_045208	14,433	16.2%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Rhinonyssidae; Ptilonyssus
Tinaminyssus melloi	NC_045209	14,759	27.7%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Rhinonyssidae; Tinaminyssus
Varroa destructor	NC_004454	16,476	20.0%	Parasitiformes; Mesostigmata; Gamasina; Dermanyssoidea; Varroidae; Varroa
Macrocheles glaber	NC_046025	14,753	25.0%	Parasitiformes; Mesostigmata; Gamasina; Eviphidoidea; Macrochelidae; Macrocheles

Table 1 (continued)

Organism	NCBI accesion	Length	%GC	Taxonomy
Macrocheles muscaedomesticae	NC_046026	14,526	24.7%	Parasitiformes; Mesostigmata; Gamasina; Eviphidoidea; Macrochelidae; Macrocheles
Cycetogamasus diviortus	NC_069643	14,450	29.3%	Parasitiformes; Mesostigmata; Gamasina; Parasitoidea; Parasitidae; Cycetogamasus
Parasitus wangdunqingi	MK270528	14,541	27.9%	Parasitiformes; Mesostigmata; Gamasina; Parasitoidea; Parasitidae; Parasitinae; Parasitus
Parasitus fimetorum	NC_061975	14,619	29.6%	Parasitiformes; Mesostigmata; Gamasina; Parasitoidea; Parasitidae; Parasitinae; Parasitus
Blattisocius keegani	MH120211	17,314	21.1%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Blattisociidae; Blattisocius
Blattisocius tarsalis	NC_046027	16,454	27.6%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Blattisociidae; Blattisocius
Amblyseius tsugawai	MW729376	15,853	23.0%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Amblyseius
Amblyseius swirskii	MW729377	16,903	20.9%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Amblyseius
Euseius nicholsi	KM999989	15,524	22.1%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Euseius
Neoseiulus womersleyi	MW762685	16,385	23.4%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Neoseiulus
Neoseiulus californicus	NC_069213	17,596	22.4%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Neoseiulus
Phytoseiulus persimilis	GQ222414	16,199	20.2%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Amblyseiinae; Phytoseiulus
Galendromus occidentalis	NC_009093	24,961	24.0%	Parasitiformes; Mesostigmata; Gamasina; Phytoseioidea; Phytoseiidae; Typhlodrominae; Galendromus

tests, distance-based analysis), data analysis (sequence retrieval, editing, manipulation, and conversion), molecular biology (codon adaptation index, effective number of codons, protein isoelectric point profiling), and evolution (maximum parsimony and maximum-likelihood methods for tree reconstructions, molecular clock hypothesis tests). Both distance and saturation values were comparatively evaluated with RF values (Xia 2018; Tamura et al. 2021). On the other hand, with the base of species level, overall between distances of each species of whole mitogenome sequences and CREx pairwise breakpoints were compared (Bernt et al. 2007).

Initiation codons of all PCGs were determined and statically tested to be linked to rearrangement or evolutionally events.

Construction of phylogenetic trees

Acari phylogeny of mitogenome was constructed using a dataset of three protein coding (*cox1*, *cytb*, and *nd6*) and rrnS genes of each species. *Drosophila melanogaster* (Arthropoda: Diptera, NC_024511) and *Apis mellifera* (Arthropoda: Hymenoptera, NC_024511) species were used as outgroups for phylogenetic analysis. Translation-aligned PCGs and MAFFT-aligned rrnS gene were merged using Sequence Matrix v.1.8 (Vaidya et al. 2011). The optimal nucleotide substitution model was estimated by PartitionFinder v1.1.1 under default options (Lanfear et al. 2012). The maximum likelihood (ML) approach was employed to infer phylogenetic trees using RaxML, applying the proposed GTR + G + I (GTR + Gamma model of rate heterogeneity + invariable sites) substitution model under 1000 bootstrap replicates (Huelsenbeck and Ronquist 2001; Stamatakis 2006; Ronquist et al. 2012). Visualization of the trees was performed using iTOL v 6.9.1 (İnteractive Tree of Life) (https://itol.embl.de/upload.cgi).

Reconstruction of ancestral genomic orders

ML tree was inferred through phylogeny reconstruction based on the gene adjacency option available on the MLGO (Maximum Likelihood for Gene Order Analysis) web server (Hu et al. 2014). The analysis utilized a gene order matrix that included all standard genes, encompassing all copies of duplicated genes while excluding non-coding regions from each mitogenome. The confidence levels of branch points within the tree were assessed using 1000 bootstrap replicates. This likelihood-based phylogenetic inference tool treats gene order data as binary characters, thereby providing bootstrap support for genomic changes and enhancing the robustness of the phylogenetic conclusions.

Results and discussion

Mitogenomes of Acari shows highly variable gene content between 21 (NC_011574: *Steganacarus magnus*) and 50 (NC_007601: *Leptotrombidium akamushi*) genes. In the mitogenome of *Steganacarus magnus* (Acariformes: Oribatida: Steganacaridae), 16 of 22 tRNA genes were absent; on the other hand, the mitogenome of *Leptotrombidium akamushi* (Acariformes: Prostigmata: Trombiculidae) has two copies of *cox3*, *cytb*, *atp8*, *atp6*, *nad1*, *nad6*, *nad4*, *nad4L*, trnH, trnK, trnE, trnY, and trnW genes (Fig. 1).

As a result of CREx analysis, 67 mitotypes were determined among Acari (Fig. 1). Fifty-six of these mitotypes were represented as unambiguous synapomorphies, and 11 different gene orders were shared, minimum two and maximum 85 species (Fig. 1, Table S1). Remarkably, mitotypes were determined for both individuals of the same genus in the sampling of Acari.

From Tardigrada reference to Acari, minimum 12 and maximum 32 rearrangement breakpoints were detected via CREx (Table S1). In the mitogenome of *Steganacarus magnus,* 12 rearrangement breakpoints were parsimoniously differentiated to reference mitogenome, with reversals of trnF and trnS2; and following reversals and TDRLs of trnL2 and trnW. The most divergent gene order was determined in *Amblyseius* species (Parasitiformes; Mesostigmata; Gamasina). From reference Tardigrada mitotype to *Amblyseius swirskii*, transpositions of *nad1*- trnL2 and trnK/trnD-trnN gene clusters and reversal of trnD gene; transpositions and following reversals of *atp8*/*atp6* and trnG/*cox3* genes were determined. Additionally, large TDRL patterns were determined within *nd* gene clusters.

As a result of qMGR, the most rearranged genes among Acari were trnL1 and *nad2* when compared to Tardigrada and the "typical invertebrate arrangement" reference. The high rearrangement frequency of the *nad2* gene, contrary to what is expected from tRNAs, is due to its completely differentiated arrangement relative to common invertebrate mitochondrial gene order (Aydemir and Korkmaz 2020). Following that, trnI, trnS1, trnN, trnE, trnT, and trnP genes are remarkably mobile (RF > 95%). Conversely, *atp6*, *cox3*, and trnG genes also appear to be quite stable (RF < 15%). *cytb* gene (RF = 18.72) was also found to be stable despite highly mobile neighboring tRNAs and *nad6* (RF = 57.33). The most conserved mitochondrial gene clusters cover *atp6*- *cox3*- trnG- *nad3*- trnA and *nad6*- trnH- *nad4* genes (Table S2).

The "overall mean distance" was calculated from the alignment files of each gene in Acari mitogenomes. The distance values were varied from 1.210 in *atp8* to 0.155 in rrnS (Table S3). According to distance results, it can be said that rRNA genes are highly conserved; contrary to the general pattern in invertebrate mitogenomes, protein-coding genes have proportionally higher distance values than tRNA genes (Table S3). As a result of DAMBE analyses, *atp6*, *cox1*, *cox2*, *cox3*, *cytb*, *nad1*, and *nad6* genes seemed non-saturated (Table S4). This indicates that these genes still suffer substitution, accumulate variations, and are not under the force of purifying selection. Therefore, in Acari mitogenomes, it is assumed that PCGs are thought to be subject to more mutations than tRNA genes.

Initiation codons or initiative amino acids are not statically co-affected or related with mitochondrial rearrangement patterns (Fig. S1).

The phylogenetic tree of Acari which shows mitotypes is given in Fig. 2.

Mitochondrial gene order of Parasitiformes

Among Parasitiformes (Holothyrida, Ixodida, and Mesostigmata), 37 mitotypes were determined. Seventeen mitotypes were determined in the Ixodida, which had the most representatives in Parasitiformes. Two dominant mitotypes were shared within the order Ixodida with few exceptions, mitotype 2 seems to derive from mitotype 1, which is shared with some Mesostigmata and a Holothyrida species and accepted as an ancestral gene order (Arribas et al. 2020) (Fig. 1). From mitotypes 1 to 2, transpositions of *nad1*-trnL2 and rrnL-trnV-rrnS-trnI-trnQ gene clusters were recommended as a potential scenario. This pattern consistent with the Parasitiformes is the evolutionally basal arachnids (Arribas et al. 2020). Phytoseiidae (Mesostigmata: Phytoseioidea) species have the highest breakpoint numbers within Parasitiformes (Table S1). Every Mesostigmata species show different mitotypes, except Antennophorina, Rhinonyssidae, and Parasitoidea species.

According to the qMGR results, the rearrangement frequencies are lower in Parasitiformes (mean RF = 43.93%) than in Acariformes (detailed below). trnL1, trnP, and *nad2* genes are remarkably mobile (100%). On the other hand, *atp6*-*cox3*-trnG-*nad3*-trnA and *nad6*-trnH-*nad4* gene clusters and *cytb* and trnV genes have the lowest rearrangement frequencies (RF < 8%).

Mitochondrial gene order of Acariformes

Among Acariformes (Trombidiformes + Sarcoptiformes), 30 mitotypes were determined via CREx; 20 and 10 of these were represented in Trombidiformes and Sarcoptiformes, respectively (Fig. 1). Species of the same genus contain differences in terms of gene order among Acariformes (e.g., *Unionicola, Leptotrombidium* for Trombidiformes and *Histiostoma*, *Dermatophagoides* for Sarcoptiformes species). Within Acariformes, minimum 2 and maximum 34

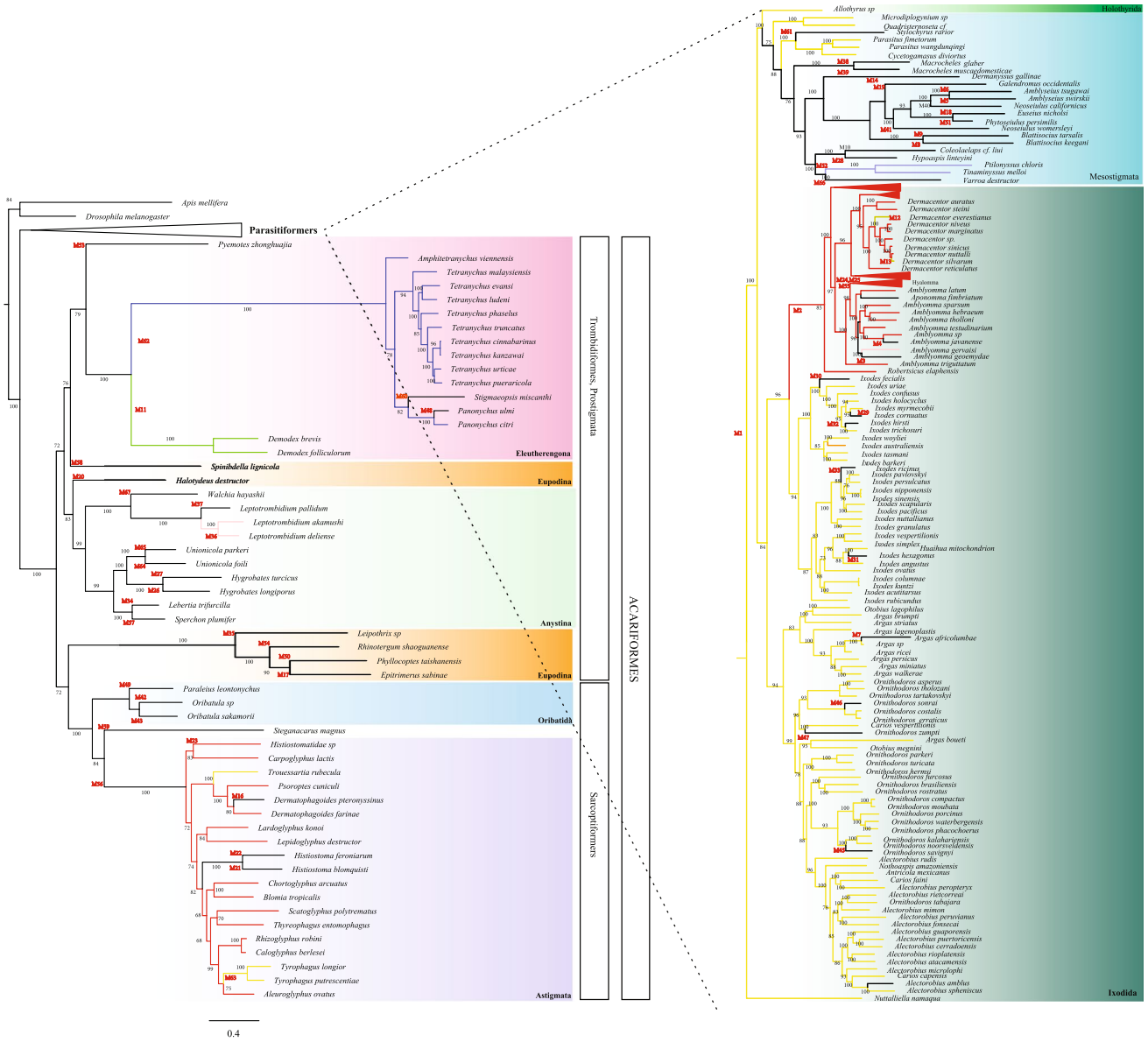

Fig. 2 ML-based phylogenetic tree of 257 unique representatives of each family of Acari based on concatenated sequences of *cox1*, *cytB*, *nad6*, and rrnL genes with insect outgroups (*Drosophila melanogaster* (Diptera) and *Apis mellifera* (Hymenoptera)). Numbers at nodes indicate bootstrap support values ≥ 90%. Branch colors represent mitotypes of Acari

rearrangement breakpoints were determined. The 2-valued rearrangement breakpoints display reversal and are retained between species *P. ulmi*- *P. citri* (reversal of trnK) and *L. trifurcilla*- *U. parkeri* (reversal of trnP). The 34-valued changes were determined between *P. ulmi* and some species and generally include 3 reversals and a reverse transposition event.

Consistent with the CREx results, the rearrangement frequencies are quite high in Acariformes according to the qMGR (mean RF = 69.80%). Thirteen genes seem to be remarkably mobile (> 95%) among Acariformes as a result of qMGR: trnI (100%), trnL1 (100%), *nad2* (100%), trnM (100%), trnS1 (99.07%), trnY (99.07%), trnQ (99.07%), trnN (98.14%), trnE (98.14%), trnT (97.22%), trnR (95.37%), and rrnL (95.37%) (Table S2). *atp6-cox3* gene clusters are relatively stable (RF < 50%) across Acariformes. This gene cluster, which includes additional trnG, *nad3*, and trnA genes in Parasitiformes, may be under the effect of selective sweeping (Stephan 2019). The force of positive selection of non-saturated *atp6- cox3* gene cluster may be inhibited to be mutated or accumulated the mutation around this region, which included relatively conserved/rearrangement stable and/or saturated genes, like trnG, *nad3*, and trnA.

Trombidiformes order seems to have the most diverged mitochondrial gene order within Acariformes. Shared gene

order at the level of subgroups or even at the family and genus are extremely rare (Fig. 1, Table S1).

Leptotrombidium species display different mitotypes (Fig. 1). *L. pallidum* has a transposition event compared to *L. deliense* and L. *akamushi*. *Unionicola* species differ in terms of the transposition of trnW- trnC genes. More dramatically, between *Hygrobates* species, the scenario of transposition of trnV and 5 reversals were determined. This pattern seems uncertain because it is too variable to be parsinomically appropriate; however, the fact that both sequences are verified RefSeq data increases reliability and indicates that the group is still ongoing non-saturated changes. Therefore, the Parasitengona group appears to have a highly variable gene order. Eleutherengona shows three highly variable gene order patterns: *Pyemotes zhonghuajia,* Cheyletoidea, and Tetranychoidea gene orders. Among Raphignathae (Cheyletoidea + Tetranychoidea), conserved mitochondrial gene order was detected, except for some minimal changes of pattern like reversals and/or transpositions. On the other hand, *Pyemotes zhonghuajia* seems to vary considerably, with two TDRL and four reversal events. Within Eupodina, all represent species have divergent mitochondrial gene orders (Fig. 1).

The order of Sarcoptiformes, especially the suborder Astigmata, displays conserved gene order patterns. Within Astigmata, two different gene order patterns are common, with a difference of 7-valued rearrangement breakpoints. Other rare patterns show 10- and 11-valued changes. Suborder Oribatida seems to vary more dramatically to Astigmata and exhibits differentiation with higher valued steps (Fig. 1).

Conclusion

The 257 species sampling to represent Acari mitogenomes shared 67 different mitotypes and 56 of these represented only one representative. In addition to the necessity to work with a larger number of sampling, it can be said that a large degree of rearrangement tendency was detected in Acari. As a consensus of results, rearrangemently passive genes seem to be not saturated and rearrangemently mobile genes, especially tRNA genes, seem to be conserved among Acari. Additionally, initiation codons of PCGs were not statistically related to mitochondrial gene order across Acari. Therefore, hypervariability of mitochondrial gene order seems to be linked to the taxonomy of species, hypothesizing that mitochondrial rearrangement events are multiparamater processes linked to evolution and genomics.

This finding confirms that genomic regions that probable RNA secondary structure mediate rearrangement patterns. However, some genomic regions that appear to be transcriptionally important, such as tick-boxes, need to be tested with more data to understand the relationship between transcription efficiency and rearrangement processes. On the other hand, it is assumed that non-coding D-loop and intergenic regions that can both form secondary structures and be evaluated as rearrangement residues may also be significant in rearrangement mechanisms. This is because 57 of the 67 gene sequences detected are specific. However, more representatives need to be studied.

On the other hand, because of extensive genome rearrangements, the control region has also become fragmented to 44–746 bp long and its location appears to vary greatly among species. However, it can be said that control regions are generally located nearly around rRNA genes (Jeyaprakash and Hoy 2007; Yang and Li 2016). Consistently, overall mean distances were the least valued in rRNA genes (Table S3). Accordingly, it can be said that neighboring rRNA genes are also protected by selective sweeping to protect the control region or vice versa. It is known that nucleotide substitution frequencies are related to gene rearrangement rates (Shao et al. 2003; Xu et al. 2006). It is not yet known which of these is the cause and which is the result.

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Author contribution HBA designed the study, conducted analysis, wrote the main manuscript text and prepared all figures.

Data availability No datasets were generated or analysed during the current study.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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