The complete mitochondrial genome of *Dermacentor (Indocentor) auratus* (Acari, Ixodidae)

Jean-Marc Chavatte* and Sophie Octavia

National Public Health Laboratory, National Centre for Infectious Diseases, Block G, Level 13, 16 Jalan Tan Tock Seng, Singapore 308442, Singapore

Received 4 October 2020, Accepted 6 January 2021, Published online 19 January 2021

**Abstract** – *Dermacentor (Indocentor) auratus* Supino, 1897 is a prominent ixodid vector of numerous pathogens of public health and veterinary importance. Using long-range PCR of two overlapping regions sequenced on an Illumina MiSeq machine, the complete mitochondrial genome of *D. auratus* is reported here. The resulting contigs were able to be assembled into a complete and circularised genome which had the general organisation of the mitochondrial genomes of the Metastriaties. It had a total length of 14,766 bp and contained 37 genes, including 13 protein-coding genes, 22 transfer RNA genes, and 2 ribosomal RNA genes, as well as 2 non-coding control regions and 3 tick-boxes. The phylogenetic analysis on the whole mitogenome confirmed the position of *D. auratus* within the *Dermacentor* clade.

**Key words:** *Dermacentor (Indocentor) auratus*, Mitochondrial genome, Long-range PCR, Illumina sequencing.

**Résumé** – Le génome mitochondrial complet de *Dermacentor (Indocentor) auratus* (Acari, Ixodidae), *Dermacentor (Indocentor) auratus* Supino, 1897 est un ixode, vecteur notable de nombreux pathogènes importants en santé publique et en médecine vétérinaire. Utilisant la PCR en fragment long sur deux régions chevauchantes combinée au séquençage sur une plate-forme Illumina MiSeq, le génome mitochondrial complet de *D. auratus* est présenté ici. Les contigs obtenus ont été assemblés en un génome circulaire complet conforme à l’organisation générale des génomes mitochondrial des Métastriaties. D’une longueur totale de 14766 pb, il contient 37 gènes, incluant 13 gènes codants des protéines, 22 gènes d’ARN de transfert et 2 gènes d’ARN ribosomaux, ainsi que 2 régions contrôles non-codantes et 3 motifs « tick-box ». L’analyse phylogénétique sur le mitogénome complet confirme la position de *D. auratus* au sein du clade *Dermacentor*.

**Introduction**

Ticks are the second largest pathogen transmitters globally, after mosquitoes [7], and tick-borne diseases (TBDs) have a colossal impact on livestock industries worldwide, and also constitute an important public health threat for humans [20]. The recent increase in TBD infections in the United States and globally, added to the increase travel fluxes and mobility, accentuates the risk of import of TBDs into new areas, as recently highlighted with the first imported case of human babesiosis in Singapore [15]. Following import, the risk of introduction and establishment of a TBD locally depends on the vector competency of the local tick populations. It is therefore important to inventory the tick fauna, particularly in areas where this has been overlooked or neglected [13] to perform risk assessments. Renewed interest in this field has lead to interesting reports such as the recent discovery of *Dermacentor (Indocentor) auratus* Supino, 1897 [24] in Singapore, from multiple hosts, including humans [14]. *Dermacentor auratus* is a competent vector of the highly pathogenic zoonotic Kyasanur Forest disease (KFD) virus [21] and the murine Lanjan Virus [25]. Several other pathogens have also been isolated from *D. auratus* such as *Anaplasma* spp., *Rickettsia* spp., *Francisella* spp., *Borrelia* spp. and *Hepatozoon* spp. [22, 23, 27], highlighting the veterinary and public health risks related to this species [14, 22, 23, 27].

Along with the report of the discovery of *D. auratus* in Singapore, preliminary molecular data on its mitogenome were provided with sequences of the cytochrome c oxidase I (*cox1*) and the large subunit ribosomal RNA (*lsu rRNA*) genes [14]. The sequences were deposited in GenBank under accession numbers MT371767 and MT371686 (*cox1*) and MT371591 and MT371592 (*lsu rRNA*), respectively [14] and were used as the starting point for the present work that reports the entire mitochondrial genome of *D. auratus*.

**Materials and methods**

DNA material from a *D. auratus* TKL1 isolate obtained in [14] was used. Assuming that the mitogenome of *D. auratus* is circular, similar to other Metastriate ticks, its amplification was...
attempted using two long-range PCRs targeting fragments of ≈9700 bp and ≈6200 bp spanning the whole, and overlapping at their extremities by 457 bp and 709 bp. The primers proposed by [4] and [9] and successfully used in [14] were cross-paired. The PCRs were run in a total volume of 30 μL containing 1X High Fidelity PCR Buffer, 2 mM of MgSO$_4$, 250 μM of each dNTP, 250 nM of each oligonucleotide primer, 0.06 U/μL of Platinum® Taq High Fidelity DNA Polymerase (Invitrogen™) and 3 μL of DNA template. The PCR assays were performed on a Veriti thermal cycler (Applied Biosystems), with the following conditions: initial denaturation at 95 °C for 2 min, followed by 35 cycles of annealing at 55 °C for 1 min, extension at 68 °C for 6 or 10 min depending on the fragment size (increased by 20 s at each cycle from the 11th cycle), and denaturation at 94 °C for 30 s, then terminated with a final cycle of annealing at 55 °C for 2 min and extension at 72 °C for 15 min.

PCR products were visualised by capillary electrophoresis on a QIAxcel® Advanced System (QIAGen™) equipped with a QIAxcel® DNA High Resolution Kit (QIAGen™), then purified using a QIAquick® PCR Purification Kit (QIAGen™), eluted in EB and stored at −30 °C until sequencing. Both fragments were prepared for next-generation sequencing (NGS) by a Nextera XT DNA Library Preparation Kit (Illumina™) and sequenced on a MiSeq System (Illumina™) to generate 300 bp paired-end reads. Fastq raw reads were trimmed using Trimmomatic v.0.36 [5] to remove low-quality bases and assembled with Shovill v.1.0.4 with SPAdes as the

| Table 1. Mitochondrial genome organisation of Dermacentor auratus with gene order, positions, lengths, nucleic acid composition, coding strand, and start and stop codons. |
|-----------------|-----------------|-----------------|-----------------|-----------------|
| Gene            | Position        | Length (bp)     | Nucleic acid    | Coding strand   | Codon           | Amino acid size |
|                 | Start | End  | AT (%) | GC (%) |                  | Start | Stop |
| tRNA-M          | 1     | 68   | 68     | 75     | 25   | +      | ATT  | TAA  | 319  |
| nad2            | 69    | 1028 | 960    | 83.7   | 16.3 | +      | ATT  | TAA  | 512  |
| trNA-W          | 1027  | 1088 | 62     | 82.3   | 17.7 | +      | ATT  | TAA  | 224  |
| trNA-Y          | 1094  | 1157 | 64     | 73.4   | 26.6 | −      | ATG  | T−   | 224  |
| cox1            | 1150  | 2688 | 1539   | 69.7   | 30.3 | +      | ATT  | TAA  | 512  |
| cox2            | 2693  | 3365 | 673    | 71     | 29   | +      | ATG  | T−   | 224  |
| trNA-K          | 3366  | 3432 | 67     | 70.1   | 29.9 | +      | ATG  | T−   | 224  |
| trNA-D          | 3433  | 3492 | 60     | 78.3   | 21.7 | +      | ATG  | T−   | 224  |
| atp8            | 3493  | 3654 | 162    | 84.6   | 15.4 | +      | ATG  | T−   | 53   |
| atp6            | 3648  | 4313 | 666    | 79     | 21   | +      | ATG  | T−   | 221  |
| cox3            | 4324  | 5101 | 778    | 73.8   | 26.2 | +      | ATG  | T−   | 221  |
|                 |         |       |        |        |      |        |      |      | 259  |
|                 |         |       |        |        |      |        |      |      | 114  |
| trNA-G          | 5102  | 5162 | 61     | 90.2   | 9.8  | +      | ATT  | TAA  | 512  |
| nad3            | 5163  | 5507 | 345    | 80.9   | 19.1 | +      | ATT  | TAA  | 224  |
| trNA-A          | 5507  | 5570 | 64     | 79.7   | 20.3 | +      | ATT  | TAA  | 224  |
| trNA-R          | 5575  | 5634 | 60     | 73.3   | 26.7 | +      | ATT  | TAA  | 224  |
| trNA-N          | 5635  | 5697 | 63     | 76.2   | 23.8 | +      | ATT  | TAA  | 224  |
| trNA-S1         | 5710  | 5765 | 56     | 82.1   | 17.9 | +      | ATT  | TAA  | 224  |
| trNA-E          | 5766  | 5825 | 60     | 78.3   | 21.7 | +      | ATG  | T−   | 224  |
| Tick Box 1      | 5826  | 5843 | 18     | −      |      | −      |      |      | 259  |
| tick1           | 5844  | 6762 | 919    | 76.9   | 23.1 | −      | ATT  | T−   | 306  |
| trNA-L2         | 6763  | 6828 | 66     | 72.7   | 27.3 | −      | ATG  | T−   | 306  |
| Tick Box 2      | 6829  | 6846 | 18     | −      |      | −      |      |      | 259  |
| trNA-V          | 6852  | 8017 | 1166   | 81.6   | 18.4 | +      | ATT  | T−   | 306  |
| ssu rRNA        | 8018  | 8078 | 61     | 77     | 23   | −      | ATG  | T−   | 306  |
| trNA-W          | 8079  | 8778 | 700    | 78.7   | 21.3 | −      | ATG  | T−   | 306  |
| CR1             | 8779  | 9089 | 311    | 65.9   | 34.1 | −      | ATG  | T−   | 306  |
| trNA-I          | 9090  | 9152 | 63     | 73     | 27   | −      | ATG  | T−   | 306  |
| trNA-Q          | 9160  | 9225 | 66     | 84.8   | 15.2 | −      | ATG  | T−   | 306  |
| Tick Box 3      | 9229  | 9246 | 18     | −      |      | −      |      |      | 259  |
| trNA-F          | 9257  | 9315 | 59     | 86.4   | 13.6 | −      | ATT  | T−   | 306  |
| nad5            | 9315  | 10,973 | 1659 | 79.4   | 20.6 | −      | ATT  | T−   | 306  |
| trNA-H          | 10,974 | 11,035 | 62   | 83.9   | 16.1 | −      | ATT  | T−   | 306  |
| nad4            | 11,036 | 12,350 | 1315 | 78.7   | 21.3 | −      | ATT  | T−   | 306  |
| nad4L           | 12,344 | 12,619 | 276  | 81.5   | 18.5 | −      | ATT  | T−   | 306  |
| trNA-T          | 12,622 | 12,682 | 61   | 85.2   | 14.8 | +      | ATT  | T−   | 306  |
| trNA-P          | 12,683 | 12,743 | 61   | 80.3   | 19.7 | −      | ATT  | T−   | 306  |
| nad6            | 12,746 | 13,180 | 435  | 83.2   | 16.8 | +      | ATT  | T−   | 306  |
| cycb            | 13,192 | 14,273 | 1082 | 73.9   | 26.1 | +      | ATT  | T−   | 306  |
| trNA-S2         | 14,274 | 14,338 | 65   | 81.5   | 18.5 | +      | ATT  | T−   | 306  |
| trNA-L1         | 14,340 | 14,400 | 61   | 72.1   | 27.9 | −      | ATT  | T−   | 306  |
| CR2             | 14,401 | 14,704 | 304  | 66.8   | 33.2 | −      | ATT  | T−   | 306  |
| trNA-C          | 14,705 | 14,761 | 57   | 78.9   | 21.1 | +      | ATT  | T−   | 306  |
assembler [1]. Contigs were aligned and scaffolded using the overlapping fragments to reconstruct the full mitogenome of *D. auratus* using CLC Main Workbench v8.0.1 (QIAGen®). Annotation was performed using MITOS [3] and manual search of homology and comparison. Transfer RNA secondary structure prediction was obtained using the Vienna RNA Websuite [10]. Multiple alignments of the *D. auratus* mitochondrial genomes obtained in this study with several mitogenomes (39 Ixodidae, 1 Argasidae and 1 Nuttalliellidae) retrieved from GenBank were performed with MUSCLE [8]. Phylogenetic analysis, performed with MEGAX [12], was inferred by the maximum likelihood (ML) method based on the GTR + Γ + I model of evolution [26]. The most appropriate model of nucleotide substitution was selected based on BIC score [19]. Reliability of tree topology, branch support and nodal robustness were assessed by non-parametric bootstrap using 1000 replicates.

The mitochondrial genome sequence obtained in this study was deposited in GenBank under accession number MW034677.

Results and discussion

Long-range PCRs, sequencing, and *de novo* assemblies generated 2 contigs of 9700 bp and 6194 bp, respectively with an average sequencing depth of 25- and 44-fold coverage, respectively. After reconstruction, the complete mitogenome of *D. auratus* was confirmed to be circular and showed a total length of 14,766 bp, with AT/GC contents of 77.2% and 22.8%, respectively. Genome annotation revealed homology to the other hard-tick mitochondrial genomes, where it contained 37 genes, including 13 protein-coding genes (*cox1* to *cox3*, *nad1* to *nad6*, *nad4L*, *atp6*, *atp8* and *cytb*), 22 transfer RNA genes (tRNAs), 2 ribosomal RNA genes (rRNAs), as well as 2 non-coding control regions (CR) and 3 tick-boxes. Details about the organisation, orientation and size of the genes and non-coding elements are listed in Table 1 and mapped in Figure 1.

The complete and annotated mitochondrial genome of *D. auratus* has been deposited in GenBank under the accession number MW034677.

Protein coding genes

Six of the protein-coding genes were initiated with an ATG codon (*cox2*, *atp6*, *cox3*, *nad4*, *nad4L* and *cytb*), six with an ATT codon (*nad1*, *nad2*, *cox1*, *atp8*, *nad3* and *nad5*), and one with an ATA codon (*nad6*). Eight of the protein-coding genes were terminated with the standard TAA codon (*nad2*, *cox1*, *atp8*, *atp6*, *nad3*, *nad5*, *nad4L* and *nad6*), and five with
the truncated termination codons TA (cytb) and T– (cox2, cox3, nad1 and nad4). Alternative start codons and truncated stop codons T– or TA– have been found in the mitogenomes of other Dermacentor species [11], other ticks [6, 16, 18, 28], and spiders [17]. The truncated stop codons are completed by polyadenylation of the mature transcript [18]. The length of the protein-coding genes ranged from 162 bp (atp8) to 1659 bp (nad5), and their AT/GC contents range from 69.7%/30.3% (cox1) to 84.6%/15.4% (atp8). Nine of the protein-coding genes (nad2, cox1, cox2, atp8, atp6, cox3, nad3, nad6 and cytb) were encoded on the positive strand, while the remaining four (nad1, nad4, nad4L and nad5) were encoded on the negative strand.

Ribosomal RNA genes

Both ssu rRNA and lsu rRNA genes were found with a length of 700 bp and 1166 bp, respectively similar to other ticks [6, 11, 16, 18, 28]. Their AT/GC compositions were 78.7%/21.3% and 81.6%/18.4% for ssu rRNA and lsu rRNA, respectively. They were both located on the negative strand between the trNA-L2 gene and the CR1 with the trNA-Y gene intercalated in between, this organisation follows the other Metastriates [18] (Fig. 1).

Transfer RNA genes

Twenty two tRNA genes were identified including 2 tRNA-L and 2 tRNA-S (Figs. 1, 2). Their size ranged from 56 bp (tRNA-S1) to 68 bp (tRNA-M) (Table 1). The majority of the tRNA genes (trNA-M, trNA-W, trNA-K, trNA-D, trNA-G, trNA-A, trNA-R, trNA-N, trNA-S1, trNA-E, trNA-I, trNA-T, trNA-S2 and trNA-C) were encoded on the positive strand, while the remaining eight were encoded on the negative strand (Fig. 1). The AT/GC content of the tRNAs ranged from 70.1%/29.9% (trNA-K) to 90.2%/9.8% (trNA-G). Prediction of the tRNA secondary structure showed that 20 of the tRNAs have the standard cloverleaf structure, while tRNA-S1 (anticodon TCT) and tRNA-C were missing the D-arm (Fig. 2). Mitochondrial tRNA-S secondary structure lacking the D-arms is a common feature in most animal species, including ticks [28]. Mitochondrial tRNA-C secondary structures are variable among tick species with some missing D-arm and/or T-arm and some having standard cloverleaf

Figure 2. Predicted secondary structure of the mitochondrial tRNA genes of Dermacentor (Indocentor) auratus obtained using the Vienna RNA Websuite [10].
structure; *D. auratus* was only lacking the D-arm, a feature previously observed in other tick species [27, 28] (Fig. 2). The sizes, coding strand and arrangement of the tRNA genes were similar to what is observed in the mitogenome of other *Dermacentor* species [11] and other ticks [6, 16, 18, 28].

**Non-coding sequences**

Duplicate CRs were found; they contained the regulatory elements of mitochondrion transcription and replication. CR1 and CR2 spanned 311 bp and 304 bp in length, respectively and shared a common identical core sequence of 249 bp (position 9080-8832 for CR1 and 14692-14444 for CR2). Their AT/GC content was 65.9%/34.1% and 66.8%/33.2%, respectively on their full length and 64.3%/35.7% for the core sequence. CR1 was located between *ssu rRNA* and *tRNA-I* and CR2 between *tRNA-L1* and *tRNA-C*, both on the negative strand. These locations have been observed in many other *Metastriates* [6,16,18,28]. Three non-coding motifs called “tick-boxes” were identified, a number identical to what was reported in *Metastriates* [18]. They are short post-transcriptional regulatory elements of 18 bp [18]. Tick-Boxes 1 and 2 shared an identical sequence, while Tick-Box 3 showed only 1 nucleotide difference. Tick-Box 1 was located on the negative strand at the

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**Figure 3.** Maximum likelihood phylogeny inferred on the mitochondrial genomes of *Dermacentor (Indocentor) auratus* obtained in this study (MW034677) (highlighted) and 41 other tick mitochondrial genomes retrieved from GenBank. Accession numbers of the sequences are provided between vertical bars. The mitogenomes of the Argasidae and Nuttalliellidae were used as outgroups to root the tree. The ML analysis used the GTR + Γ + I model of evolution [26]. Reliability of tree topology, branch support and nodal robustness were assessed by non-parametric bootstrap using 1000 replicates (only >70% shown). Analysis performed with MEGA X [12].
3' end of the nad1 gene, a position widely overlooked in many published tick mitochondrial genomes where the termination of the nad1 gene is extended to a full TAA stop codon and abuts or overlaps with the tRNA-E gene incorporating Tick-Box 1, as pointed out by [18]. Tick-Box 2 was located between the Isu RNA and the tRNA-L2 genes on the negative strand, while Tick-Box 3 was located between tRNA-Q and tRNA-F on the positive strand, following the general organisation of the other Metastriates [18].

**Phylogenetic analysis**

The ML analysis was performed on the mitochondrial genomes of *D. auratus* obtained in this study (MW034677) and 39 other Ixodidae, as well as 1 Argasidae and 1 Nuttalliellidae used as outgroups to root the tree (Fig. 3). The phylogenetic tree of the Ixodidae was strongly supported with the major genera clearly separated (bootstrap values 100%) (Fig. 3) and was monophyletic, following the recent establishment of the genera *Roberstitus* and *Archaeocroton* to accommodate *Amblyomma elaphense* and *Amblyomma sphenodonti* [2], which previously had controversial phylogenetic positions (Fig. 3) [2, 6, 16, 28]. Expectedly, *D. auratus* is clustered among the other *Dermacentor* species (Fig. 3).

**Dermacentor subgenera**

Up to seven subgenera were recognised within the genus *Dermacentor: Dermacentor, Indocentor, Asiacentor, Americentor, Serdjukovia, Kohlsiella* and *Olenvenia*, with the validity of the last three remaining controversial [29]. The type species of the subgenus *Indocentor* is *D. auratus*. The mitochondrial genome of *D. auratus* obtained here constitutes a useful reference for future studies on *Dermacentor* subgeneric classification. This will become particularly true when more sequences from different species become available, and reaching this point could be accelerated with the use of the simple protocol adopted here.

**Conclusion**

This study reports the complete mitochondrial genome of *D. (Indocentor) auratus* obtained using a simple method of amplification and sequencing based on two long-range PCRs and next generation sequencing. The mitogenome of *D. auratus* is circular and has the typical Metastriates tick mitochondrial genome organisation. All the genes were annotated and the secondary structure of the tRNAs was determined. Phylogenetic analyses indicated that *D. auratus* clustered with other *Dermacentor* species. The availability of the complete mitochondrial genome sequence of *D. auratus* will provide a useful reference to help in the rapid and accurate identification of this important vector of TBDs, as well as for further studies on the phylogeny and evolution history of hard ticks.

**Acknowledgements.** The authors are grateful to Dr Chew Ka Lip who collected the specimen and Dr Kwak Mackenzie who contributed to its identification. The authors declare that they have no conflict of interest.

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Cite this article as: Chavatte J-M, & Octavia S. 2021. The complete mitochondrial genome of Dermacentor (Indocentor) auratus (Acari, Ixodidae). Parasite 28, 6.