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# The mitochondrial genome of *Octostruma stenognatha* and its phylogenetic implications

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**Abstract** New sequencing technologies are providing a large-scale proliferation of sequence data, including complete mitochondrial genomes as a side effect of target capture methods. In this study, we use massively parallel sequencing to provide the nearly complete mitochondrial genome of the ant *Octostruma stenognatha*. The annotation of the genome revealed an interesting pattern that agrees with a recent deep reorganization in the systematics within the Formicidae family. This is the first mitogenome for the genus in a lineage, where the scarcity of mitochondrial information has restricted our understanding of its evolutionary history. This is a valuable example of the power and velocity with which products from new sequencing technologies can increase our capacity to understand evolutionary biology, especially in non-model species.

**Keywords** Mitogenome · Ultraconserved elements · Formicidae · Ants

## Introduction

The advent of massively parallel sequencing has provided unprecedented opportunities to investigate many aspects of the tree of life (Dunn et al. 2014). Interestingly, in addition

to the availability of information on nuclear genomes, the nature of many new sequencing methods has also improved our understanding of traditional sources of molecular information, such as mitogenomes (Tan et al. 2015). Mitogenomic sequences have been applied to infer relationships between organisms as soon they became most commonly available (e.g., Smith et al. 1993; Boore et al. 1998). The small size of the mitochondrial genome when compared with the nuclear allows studies involving phylogenetics, evolutionary biology, and phylogeography in a computationally feasible way (e.g., Perseke et al. 2013; Havird and Santos 2014; Shen et al. 2015). In general, modifications in mitochondrial gene order are uncommon (Boore 1999) and rarely display homoplasy (Le et al. 2000). These observations indicate the possibility of phylogenetic inferences based on gene order of the mitochondrial genome, which have been broadly applied in the field (e.g., Sankoff et al. 2000; Yuan et al. 2012; Liu et al. 2013). Mitochondrial genomes have also been shown as a powerful tool for the reconstruction of high-level phylogenetic relationship in Hymenoptera (Mao et al. 2015) and as well for basal inferences in the clade (Song et al. 2016).

The order Hymenoptera includes several clades with enormous evolutionary success, such as wasps, bees, and ants, with the latter being a dominant terrestrial taxon since Cretaceous (Dlussky et al. 2003). Despite their ecological importance (Hölldobler and Wilson 1990) and economic impacts (Way and Khoo 1992; Gutrich et al. 2007; Pérez et al. 2010), only few nuclear and mitochondrial genomes have been described for the family Formicidae to date (e.g., Gotzek et al. 2010; Hasegawa et al. 2011; de Melo Rodvalho et al. 2014; Duan et al. 2016; Liu et al. 2016). In this article, we take advantage of advances in massively parallel sequencing to provide the first mitogenome of the ant genus *Octostruma* using the strategy of assembling the genome

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from captured off-target data. This procedure is well known to provide accurate information widely in the field from humans (Picardi and Pesole 2012) to non-model amniotes (do Amaral et al. 2015). Finally, we interpret the obtained results in light of recent taxonomic changes in Myrmicinae.

## Materials and methods

Total DNA was extracted from a single specimen of *Octostruma stenognatha* from Horto Dois Irmãos, Recife, state of Pernambuco, Brazil (08°00'32"S, 34°56'40"W). Voucher specimens from the same nest series are deposited in the myrmecological collection of the Museu de Zoologia da Universidade de São Paulo, Brazil. DNA was extracted using the kit PureLink™ Genomic DNA (Invitrogen, USA), and double strand DNA concentration was measured on a Qubit 2.0 Fluorometer (Life Technologies, Inc.) using the dsDNA High-Sensitivity Assay Kit. The initial DNA concentration for this sample was 0.56 ng/μl. Because of this low concentration, instead of running a traditional electrophoresis gel, we checked DNA integrity using a Bioanalyzer (Agilent Technologies), which showed highly fragmented DNA (possibly because of the age, size, and preservation of the specimen, which was collected almost 15 years ago). Therefore, the sample was not sheared prior to library preparation for Illumina sequencing.

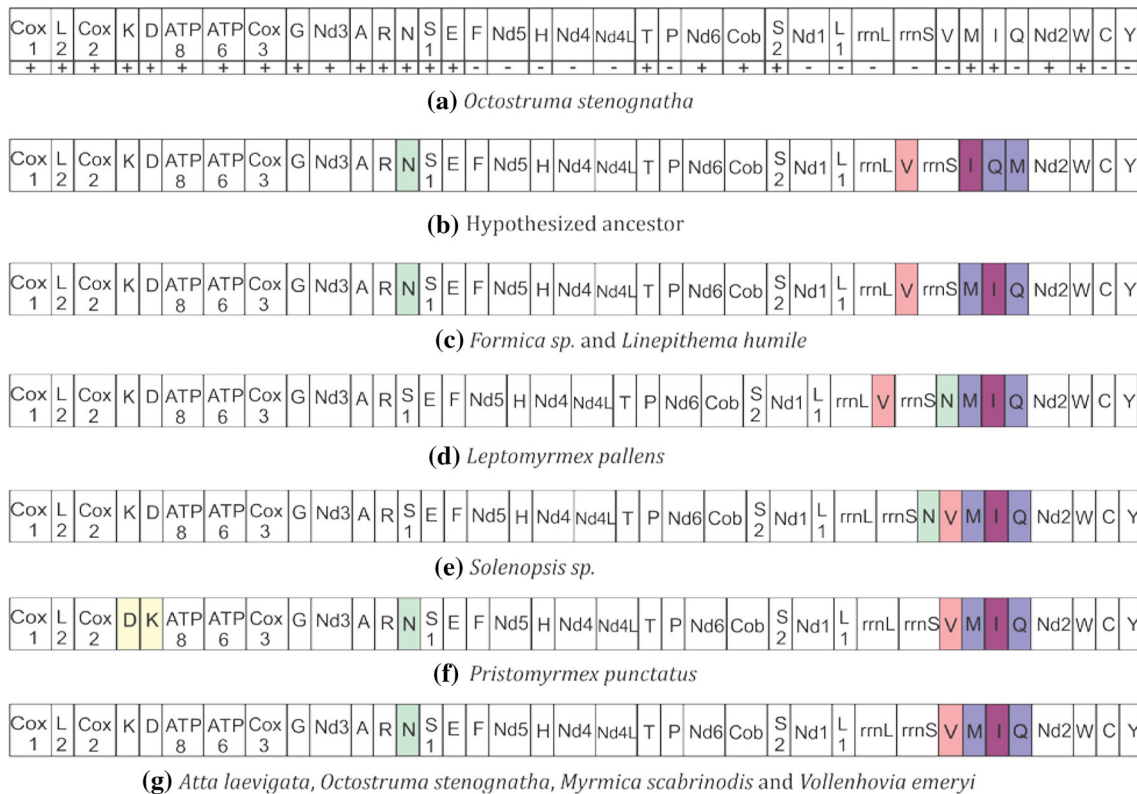
The KAPA Hyper prep kit (Kapa Biosystems) and protocol was chosen to process the Illumina libraries. A bead technique (Fisher et al. 2011) was used with an alternative for SPRI beads (Rohland and Reich 2012) in the library preparation. We used approximately 30 ng of total starting DNA and all reactions, except PCR, were carried out using ¼ of volume indicated by the manufacturer (M. Branstetter pers. com.). The sample was individually labeled using the iTru dual-indexing adapter system (B. Faircloth and T. Glenn, pers. com.), which are similar to the TruSeq layout barcodes (Faircloth and Glenn 2012), and we obtained 4.96 ng/μl of adapter ligated DNA from 16 PCR cycles. A target enrichment system (Gnirke et al. 2009) was performed to obtain ultraconserved elements (UCEs) specifically designed for Hymenoptera (Faircloth et al. 2014) using a modified protocol from Faircloth et al. (2012). We pooled our sample with seven other samples as part of another study for target enrichment (Ströher et al. unpublished results). The pool was concentrated to 147 ng/μl in a vacuum centrifuge and later enriched for 1510 UCEs using manufactured RNA capture probes (MyBaits, Mycarray, Inc.) and followed the manufacturer's indications except for the on-bead (biotinized) PCR. Two washes were performed to remove off-target sequences; however, this is not totally efficient, leaving copies of mitochondrial DNA in the library. Bioanalyzer (Agilent Technologies) was also used

to measure the size of the enriched material, followed by a real-time PCR to access the library concentration adopting the Kapa Library Quantification kit (Kapa Biosystems, Inc.). The pool was combined with five other pools at equimolar ratios and sequenced on Illumina HiSeq 2000 sequencer, using 100-bp paired-end reads at the University of California Santa Cruz, Genome Technology Center.

After sequencing, we used the Illumina bcl2fastq Conversion Software v1.8.4 to convert BCL files into FASTQ and to separate multiplexed samples. Sequence quality control was evaluated using FastQC 0.11.3 (Andrews 2010). This sample produced a total of 2,823,754 sequences. The Trimmomatic tool (Lohse et al. 2012), implemented through Illumiprocessor (Faircloth 2013), was used to remove low-quality regions, barcodes, and adapters. Phyluce (Faircloth 2016) was used to perform the assembly using the default Trinity tool (Grabherr et al. 2011) generating 25,820 contigs with mean length of 358 bp. The resulted contigs were processed with the phyluce workflow for UCEs analysis using a minimum of 80X coverage and 80% identity. A total of 651 unique UCEs were recovered for this sample. As predicted in this kind of large-scale sequencing (Hung et al. 2013), off-target regions are also captured and sequenced in a sufficient way to produce the mitochondrial genome in one contig, usually identified as the longest one. With this result, we performed the mtDNA genome annotation using MITOS (Bernt et al. 2013) with the Invertebrate genetic code, and the base composition was calculated using Geneious 8.1.5 (Kearse et al. 2012). The DNA sequence is available in GenBank with the accession number KX758608.

## Results and discussion

The mitogenome of *Octostruma stenognatha* presented here for the first time is composed of 37 genes (22 tRNAs, 2 rRNAs, and 13 protein-coding genes), for a total of 14,183 bp without the control region (Fig. 1a). As observed in other hymenopterans (Wei et al. 2010; Xiao et al. 2011), the base composition in the mtDNA genome of *O. stenognatha* is highly A + T-rich, with only 19.4% being G + C. This is very similar to the base pair composition found in another member of Attini tribe, *Atta laevigata*, where base composition is 80.8% A + T (de Melo Rodovalho et al. 2014). In *Octostruma stenognatha*, 14 genes are encoded by the minus strand and 23 by the plus strand. Regarding the absence of the control region, the challenges in sequencing and assembling this particular part of the mitogenome in insects are recognized for a long time and appear to be related with the high A + T composition allied with repeats sections (Saito et al. 2005; Cameron et al. 2008). Therefore, our result is not unpredicted, since other studies were



**Fig. 1** a Mitogenome gene order of *Octostruma stenognatha* and corresponding strand. **b** Hypothetical ancestor (Boore et al. 1998). **c–f** Colored boxes indicate differences in gene order in relation to the hypothetical ancestor in the indicated species. Single letters refer to tRNAs

specific designed for the sequencing of insects, and mitogenomes also had no success in recovering the control region (Mao et al. 2012; Ramakodi et al. 2015).

Although some mitochondrial gene order rearrangement, especially in tRNAs, can be observed in Hymenoptera (Dowton and Austin 1999), only a few changes could be observed in *Octostruma stenognatha* when compared with the hypothetical pancrustacean ancestral (Boore et al. 1998) (Fig. 1b). That is not true in other hymenopterans, such as wasps, in which the gene order rearrangement is widespread, not only for tRNAs, but also for protein-coding genes (Xiao et al. 2011). Several models have been suggested to explain how mitochondrial genes are rearranged, but this issue is still poorly understood (Cameron 2014). Therefore, when comparing the available ants mitogenomes with other hymenopterans, the gene arrangement is relatively stable (e.g., Gotzek et al. 2010; Hasegawa et al. 2011; Berman et al. 2014; de Melo Rodovalho et al. 2014; Yang et al. 2016) indicating that this can be a characteristic in the Formicidae family. The position of the trnV gene, after and not between the ribosomal genes, is unusual when compared with other ants (Berman et al. 2014; Yang et al. 2016) and the hypothetical ancestral gene order (Gotzek et al. 2010), although this feature can be found in some Myrmicine ants (e.g., Hasegawa et al. 2011; Babbucci et al. 2014) and is not

exclusive to Hymenoptera (Mao et al. 2015). The higher mobility of tRNAs in relation to other genes is expected, given that shifts in gene order are not equally frequent across mitogenomes (Moritz 1987). Although phylogenetic inference using gene order can be problematic when homoplasy can occur in the group, this feature can still be accounted for (Babbucci et al. 2014). An example in Hymenoptera is the paraphyly and basal position of Symphyta that was recently supported by the use of new mitochondrial genomes (Song et al. 2016).

A recently proposed new hypothesis for the phylogenetic relationships within the ant group Myrmicinae (Ward et al. 2014) has challenged some earlier ideas about the evolutionary relationships within the subfamily—the largest among ants. Based on 11 nuclear genes, Ward et al. (2014) reduced drastically the number of tribes from 25 to 6. In one of the most noteworthy changes, the tribe Attini is not restricted to fungus-growing species, but rather includes other genera, such as *Octostruma*. This genus has a long history of instability in its taxonomy, with its systematic position being first described as a subgenus of *Rhopalothrix* (Forel 1917). Only 30 years later, *Octostruma* was elevated to genus (Brown 1948), being subsequently allocated into the tribe Basicerotini (Brown 1949). The genus remained stable in that position for more than 50 years, until being

transferred to the tribe Dacetini (Baroni Urbani and De Andrade 1994). However, Bolton (1994) almost immediately restored the position of *Octostruma* within Basicerotini. In 2007, Baroni Urbani and De Andrade not only returned *Octostruma* to Dacetini, but also considered this genus a junior synonym of *Basiceros*. This classification was not adopted by most of the subsequent authors, so that *Octostruma* appears as a valid genus in the paper by Ward et al. (2014), as it was finally transferred to the tribe Attini. The fact that *Octostruma stenognatha* has an identical mitochondrial gene order as *Atta laevigata* (de Melo Rodovalho et al. 2014) corroborates the recent change of the genus inside the Attini tribe (Ward et al. 2014). In addition, as a final corroboration that the annotation of the mitogenome was correct, we recovered the place of the trnN gene as the same as the ancestral, position that is being claimed to be the “authentic” one for ants with mitogenomes already sequenced (Babuccci et al. 2014), as opposed to other findings (Gotzek et al. 2010; Berman et al. 2014). The *Octostruma* mitogenome has also high similarity with another member of the tribe Attini: *Wasmannia auropunctata* (Duan et al. 2016), the only possible divergence it is an inversion between the control region and the trnV gene that cannot be verified in this study.

## Conclusions

The recent technological advances are accelerating the number of mitogenomes available. Using massively parallel sequencing, we provide here the first mitochondrial genome for the *Octostruma* genus. The characteristics of this mitogenome are very similar to other hymenopterans and comparing this genome with those of other ants is consistent with recent taxonomic changes in the Myrmicinae clade. We expect that soon we will be able to compare genomes widely in Formicidae, making possible a better understanding of the evolutionary history in this family.

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