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Molecular characterization of a *mariner*-like element in the *Atta sexdens rubropilosa* genome

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ABSTRACT. Mobile elements are widely present in eukaryotic genomes. They are repeated DNA segments that are able to move from one locus to another within the genome. They are divided into two main categories, depending on their mechanism of transposition, involving RNA (class I) or DNA (class II) molecules. The *mariner*-like elements are class II transposons. They encode their own transposase, which is necessary and sufficient for transposition in the absence of host factors. They are flanked by a short inverted terminal repeat and a TA dinucleotide target site, which is duplicated upon insertion. The transposase consists of two domains, an N-terminal inverted terminal repeat binding domain and a C-terminal catalytic domain. We identified a transposable element with molecular characteristics of a *mariner*-like element in *Atta sexdens rubropilosa* genome. Identification started from a PCR with degenerate primers and queen genomic DNA templates, with which it was possible to amplify a fragment with *mariner* transposable-element homology. Phylogenetic analysis demonstrated that this element belongs to the *mauritiana* subfamily of *mariner*-like elements and it was named *Asmar1*. We found that *Asmar1* is homologous to a transposon described from another ant, *Messor bouvieri*. The predicted transposase sequence demonstrated that *Asmar1* has a truncated transposase ORF. This study is part of a molecular characterization of mobile elements in the *Atta* spp genome. Our finding of *mariner*-like elements in all castes of this ant could be useful to help understand the dynamics of *mariner*-like element distribution in the Hymenoptera.

Key words: Transposable element; *Mariner*-like element;
Leaf-cutter ant; *Atta sexdens rubropilosa*

INTRODUCTION

Mobile elements are present in all organisms in multiple copies; they have occupied different genomes for millions of years. There is an important division of classes involving these elements, which consider mainly the transposition mechanism. Class I elements transpose via an RNA intermediate, while Class II elements transpose via a cut and paste mechanism.

Class II elements are important tool for genetic transformation in many different organisms. A special transposable element widely used for transformation is the *mariner* element (Jacobson et al., 1986; Berghammer et al., 1999; Coates et al., 2000; Moreira et al., 2000). This element possesses common characteristics, such as: inverted terminal repeat (ITR) sequence at the extremities; ITR sites flanked by TA nucleotides, duplication of two base pairs in the insertion site (direct repeats); catalytic domain, which contains the D,D(34)D catalytic triad and the transposase domain; DNA-binding domain, which contains the nuclear localization signal and the helix-turn-helix motif, and finally a short size of about 1300 bp.

The *mariner* elements were first identified in *Drosophila melanogaster*, but are extensively distributed in nature, and can be found in a wide variety of insects and other arthropods. *Mariner* family members have also been identified in several organisms such as nematodes, marine species, fungi, plants, and mammals, including humans (Robertson, 1993; Capy et al., 1996; Jarvik and Lark, 1998; Leroy et al., 2003; Mandrioli, 2003; Halaimia-Toumi, et al., 2004).

Currently, these elements are members of a large transposon family, known as *mariner* and *mariner*-like elements (MLEs) (Lampe et al., 1996). There are over 13 subfamilies known of *mariner* elements, which typically contain approximately 40-56% identity in nucleotide and 23-45% identity in amino acids between the subfamilies and 25-100% identity in amino acids with a particular subfamily. The phylogenetic history of the *mariner* element family is known for extensive horizontal transfer between species, some separated by great phylogenetic distances (Robertson and Zumpano, 1997; Robertson and Martos, 1997; Lampe et al., 2003).

Many of these transposable elements belonging to the *mariner* family are non-functional; they accumulated some kind of mutations during evolution and thus transcribe inactive proteins. The number of MLEs per genome can vary tremendously from species to species (Hartl et al., 1997). Several species that had characterized parcial or full-length elements showed inactive MLEs, with multiple stop codons, deletions or frameshifts. They were observed in the genomes of insects: *Rhynchosciara americana* (Rezende-Teixeira et al., 2008, 2010), *Messor bouvieri* (Palomeque et al., 2006), *Musca domestica* (Yoshiyama et al., 2000), *Hessian* fly (Russell and Shukle, 1997), *Bombyx mori* (Robertson and Asplund, 1996; Robertson and Walden, 2003; Kumaresan and Mathavan, 2004), *Bactrocera tryoni* (Green and Frommer, 2001), *Ochlerotatus atropalpus* (Zakharkin et al., 2004), in Lepidoptera: *Antheraea mylitta* (Prasad and Nagaraju, 2003), *Mamestra brassicae* (Mandrioli, 2003), in nematode:

Meloidogyne chitwoodi (Leroy et al., 2003), and several other species. The prevalence of inactive copies of *mariner* elements in many genomes suggests that the vertical inactivation by mutation had an important, probably dominant, role in the evolution dynamic of *mariner* elements (Lohe et al., 1995).

The present study characterized a transposable element of *mariner* element family in the leaf-cutter ant genome, *Atta sexdens rubropilosa*. This insect social behavior and responses to pesticides have been well studied, but there is little data on other aspects of its biology. Recent data comparing the morphology and cytoskeleton organization of the salivary glands (the post-pharyngeal, hypopharyngeal, mandibular, and thoracic salivary gland) of different castes show a lack of molecular markers in this system (do Amaral and Machado-Santelli, 2008). It was the starting point for molecular characterization of mobile elements, which nowadays are considered important molecular markers. As observed in many invertebrates the element identified presented defective open reading frame (ORF), stop codons within the ORF and imperfect ITR sequences. However, the study of this element in this system can provide important information on the evolution and function of mobile elements, which always appear to collaborate with a variety of biological functions (revised by Khurana and Theurkaf, 2010; George et al., 2010).

MATERIAL AND METHODS

Animals

Ants of *A. s. rubropilosa* were collected at the Universidade de São Paulo campus, in the Brazilian State of São Paulo, and the wild ants bred in the laboratory.

Nucleic acid

Genomic DNA was extracted from an *A. s. rubropilosa* queen ant, added to 300 µL TMD (10 mM Tris-Cl, pH 8, 5 mM EDTA, and 0.3 M NaCl), and homogenized. This was then mixed with 12 µL 20% SDS and incubated at 65°C for 1 h in the presence of proteinase K (100 µg/mL), followed by one extraction with phenol:chloroform. DNA was precipitated in ethanol, washed with 70% ethanol, dried and dissolved in TE buffer (10 mM Tris-HCl, pH 8, and 1 mM EDTA). DNA was quantified in a NanoDrop ND1000 Spectrophotometer.

PCR, inverse PCR and DNA sequencing

PCR amplifications were made with degenerated primer to amplify the *Asmar1* element internal regions (pmar1R: 5'-TTTGCACAACAAGTTCAATTT-3' and pmar1F: 5'-TTTCTGGCAATTTACGGAT-3'). Primers were designed for inverse PCR (iAsmar1R: 5'-TCCAATTAAAGCAGAAAATCAA-3', iAsmar1F: 5'-TGGTGGGACTAAAAGGATCT-3') based on the internal sequences of *Asmar1*. The protocol of DNA circularization was described in Rezende-Teixeira et al. (2010). The PCR amplifications were performed using Platinum Taq DNA polymerase (Invitrogen Life Technologies) according to manufacturer instructions. Cycle conditions were 94°C for 2 min, 35 cycles of 94°C for 30 s; 55°C for 30 s; 72°C for 2 min and a final extension at 72°C for 7 min. The PCR products were cloned in pGemT-easy vector (Promega). Clones were sequenced using the BigDye terminator (PerkinElmer) and run on an ABI-3100 sequencer (PerkinElmer), using T7 and SP6 primers. The nucleotide sequences were analyzed in a Linux workstation with Phred, Phrap Crosmatch and Consed 17 programs (Ewing and Green, 1998; Ewing et al., 1998; Gordon et al., 1998). The BLAST analyses were done in the non-redundant GenBank database (Wheeler et al., 2000). The MLE sequences of *A. s. rubropilosa* were deposited in the GenBank database and have the following accession No.: *A. s. rubropilosa Asmar1* (JF717775).

RESULTS AND DISCUSSION

To amplify *mariner*-like transposable elements in the *A. s. rubropilosa* genome the primers initially used were designed to amplify *mariner* elements of *Rhynchosciara* diptera (Rezende-Teixeira et al., 2010). Given the high identity observed between these elements, the primers functioned perfectly, and the ORF internal region of a *mariner*-like family element was amplified, as expected (pmar1R: 5'-TTTGCACAACAAGTTCAATTT-3' and pmar1F: 5'-TTTCTGGCAATTTACGGAT-3'). To perform all PCRs queen ant DNA of *A. s. rubropilosa* was used.

Since the ORF internal region was known, a new primer pair was drawn from the amplified sequence of *A. s. rubropilosa*. These primers point to the ends of the transposon to carry out an inverse PCR to provide data of the complete sequence, flanking regions and target site.

The amplified sequence of element in *A. s. rubropilosa* was named *Asmar1*, and the consensus element is 1267 nucleotides in length and has the typical structure of an MLE; however, the ITRs are imperfect (Figure 1). An ATG starts at nucleotide 162, one defective ORF of 1035 bp encoding a putative transposase with 345 amino acid protein and 5 internal stop codons. The translation start site, which has been described in some full-length *mariner* elements, is located in a non-canonical Kozak's box (PuXXATGPu), which was also observed in the element *Asmar1* of *A. s. rubropilosa*. The last position of the subject contains a pyrimidine nucleotide (thymidine) in the place of one purine.

The D,D(34)D signature-sequence, which is also a characteristic of *mariner* elements, defines the second functional domain of the transposase, which is the catalytic domain (129 amino acids in *A. s. rubropilosa*). This domain is responsible for site-specific cleavage and junction in the transposition process (van Luenen et al., 1994; Craig, 1995). The active site of this domain is defined by three amino acid motifs, consisting of two aspartic acid (D) residues separated by 94 amino acids, followed by another aspartic acid residue separated by 34 amino acids (Robertson, 1993; Doak et al., 1994). The D,D(34)D catalytic triad that makes up the active site serves as a binding domain for the divalent cation (Mg^{2+}) required for catalysis (Prasad et al., 2003). The motif D,D(34)D was identified in the *Asmar1* transposase of *A. s. rubropilosa* with 81 residues, which were 100% aligned.

It was noted that some sequences (WVPHEL, DEKW, H/QDNAP, HPPYSPDLAPSD), highly conserved in the MLE family (Robertson, 1993; Prasad and Nagaraju, 2003), are also present in the *Asmar1* element, but some amino acids appear altered. The sequences found in *A. s. rubropilosa* are: WVP$\underline{\text{MN}}$L, DE$\underline{\text{MW}}$, HDNA$\underline{\text{R}}$, and HPPYSPD$\underline{\text{V}}$APSD. The underlined amino acids are shifts found in *Asmar1*. These sequences correspond to regions of aspartic acid residues that comprise the D,D(34)D catalytic triad and two motifs (WVPHEL and YSPDLAP), typical of *mariner* transposases described by Robertson (1993).

The ITRs are short sequences of about 28 bp flanking the mobile element, responsible

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TATTGTGAGTACAAATTAATTCGGTCCGTTTCTAACTGTTGTGAATGGTT
CATAGTGACAGCTGATTTTGGCGATTTCAGAAAGGTTAAACATCTACTAA
TAATATTCAGTTTATATCACTTTGAGTTTCATACAAAAACCTTGATTTTT
ACTGTGTTTGAAATGTCGAATTTTGTGTTAACTTAGCAGCATTTGAGAGA
               M  S  N  F  V  L  T  *  q  H  L  R  D
TTTTGATTTTCTGCTTTAATTGGAAGAAAAGTGCGGCTGAAGCCCATCGA
 F  D  F  L  L  *  L  k  k  S  A  A  E  A  H  R
ATGCTTGTCGAAGTTTATGGTAACACTGCTCCAACTGGTAAATCATGTAG
M  L  V  E  V  Y  G  N  T  A  P  T  G  K  S  C  R
GGAATGGTTTCGACGTTTCAAGGATGAGATTTCAGCGTTGAAGACAAGCC
 E  W  F  R  R  F  K  D  E  I  S  A  L  K  T  S  L
TCGCTCTGGACAGCCAAAAAATTCCGAAGACAAAGAATTGAGACATTACT
  A  L  D  S  Q  K  I  P  K  T  K  N  *  D  I  T
CGAAGAAGATCAGAGTCAAACGCAAGAGGAGCTTGCAGAATCATTGGGGA
R  R  R  S  E  S  N  A  R  G  A  C  R  I  I  G  D
TAACTCAAGCCGTATCTGTACGATTGAGAGCCATGAAGTCATGGGAATGA
 N  S  S  R  I  C  T  I  E  S  H  E  V  M  G  M  I
TTGAGAAACAAGGAAATTGGGTGCCTATGAACTTAAACCGAGAGACTTTG
  E  K  Q  G  N  W  V  P  M  N  L  N  R  E  T  L
AAAGGCGATTTTTCACTTGCGAACAGTTGATTCAAAGATAACAGAGAAAA
K  G  D  F  S  L  A  N  S  *  F  K  D  N  R  E  K
GGTTTTTTGCATCGGATTGTGAGACGAGATGTGGATATTCTACGACAATC
 V  F  C  I  G  L  *  D  E  M  W  I  F  Y  D  N  P
CCAAGAAGAAAAAATACTACGCTAAGCCTGATCAATCGTTGCCATCGATC
  K  K  K  K  Y  Y  A  K  P  D  Q  S  L  P  S  I
TCAACATCAACACCGAACATTCATGATTCAAAGATCATGCTTTGTATCTG
S  T  S  T  P  N  I  H  D  S  K  I  M  L  C  I  W
GTGGGACTAAAAGGATCTTGTTTACTATGAGCTGCTGAAACCTGGCGATT
 W  D  *  K  D  L  V  Y  Y  E  L  L  K  P  G  D  S
CCATTACGGGCGATCGGTATCGGCTACAATTGATTCGTTTGAGTCGTGTA
  I  T  G  D  R  Y  R  L  Q  L  I  R  L  S  R  V
TTGCAAGAAAAATGGCCGGAATACGAGCAAAGACATGTGATTTTGCAGCA
L  Q  E  K  W  P  E  Y  E  Q  R  H  V  I  L  Q  H
TGACAATGCTCGACCCCATGTTGCGAAAGTGGTCAAGACATACTTGGAAA
 D  N  A  R  P  H  V  A  K  V  V  K  T  Y  L  E  T
CGTTGAAATGGGAAGTCCTACCCCATCCGCCGTATTCTCCAGACGTTGCT
  L  K  W  E  V  L  P  H  P  P  Y  S  P  D  V  A
CCCTCTGACTATCACTTGTTTCGATCAATGGCACACGGTCTGGCTGACCA
P  S  D  Y  H  L  F  R  S  M  A  H  G  L  A  D  Q
GCACTTCCGGTTTTGTGAAGAAGTAAAAAATTGGATCGATTCGTGGATAG
 H  F  R  F  C  E  E  I  K  N  W  I  D  S  W  I  A
CCTCAAAAGATGACCAGTGTTTTCGACGCGGGATTCGTACGCTACCCGAA
  S  K  Y  V  L  C  F  R  R  G  V  R  T  L  P  E
AGATGGGAGAAAGTAGTGGCCAGCGATGGACAATACTTTGAATCATAAAT
R  W  E  K  V  V  A  S  D  G  Q  Y  F  E  S  *
GTATAACCAGTTTTTTacAAATTTCGAATTTCGGAAAAAACGGCGGAAGC
AAAGCTTGTACACCATA
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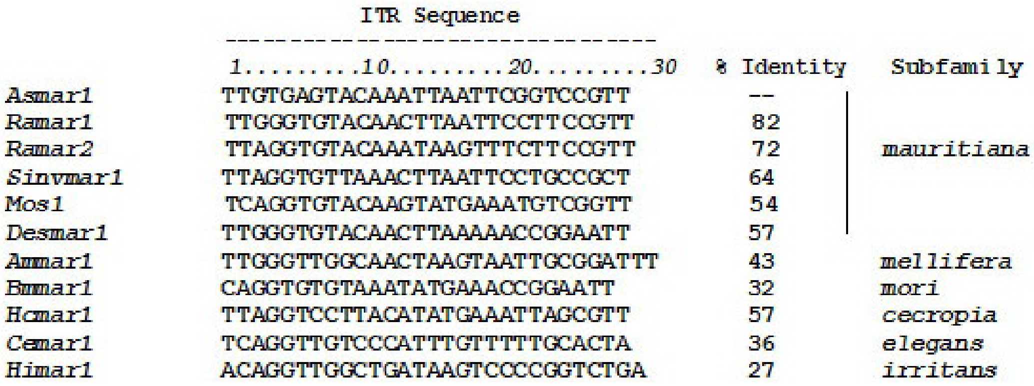
Figure 1. Nucleotide sequence and conceptual translation of the consensus *Asmar1* element inserted at a duplicated TA dinucleotide site. The inverted terminal repeats (ITRs) and the positions of two conserved motifs described by Robertson (1993) are underlined. The aspartic acids (D) of the D,D(34)D catalytic triad are in red underlined and the catalytic domain in blue.

for the binding of transposase protein in the transposition mechanism. The binding domain of the ITR sequence of the Mos1 *mariner* transposase was defined by Augé-Gouillou et al. (2001) analyzing the interaction between the transposase and the ITR sequence. The transposase of MLEs specifically bind as a dimer in the inverted terminal repeat sequence of transposon that encodes it. Two binding motifs were localized in the ITR sequence (Bigot et al., 2005). These motifs are involved in the binding of *mariner* transposase in ITR. The ITR sequence found for *Asmar1* is imperfect 5'-TTGTGAGTACAAATTAATTCGGTCCGTT-3'. Thus, in the *A. s. rubropilosa* the transposase is probably non-functional, not only due to stop codons within the ORF, but also imperfect ITR sequences.

A comparison of the terminal repeats showed that there is a high degree of conservation among the sequences of different species. The *Asmar1* ITR sequence shares extensive identity with the inverted repeats of *mauritiana* subfamily members (Figure 2). High identity (64%) is observed between *Asmar1* from *A. s. rubropilosa* and *Snvmar1* from the fire ant *Solenopsis invicta* (Krieger and Ross, 2003). This is evidence of the relationship of these *mariner* elements within *A. s. rubropilosa* as well as its relationship to *mariner* elements found in other taxa. Besides, it is possible to observe that *Asmar1* ITR shares 57-27% identity with different subfamilies.



	ITR Sequence		
	1.........10.........20.........30	% Identity	Subfamily
Asmar1	TTGTGAGTACAAATTAATTCGGTCCGTT	--	mauritiana
Ramar1	TTGGGTGTACAACTTAATTCCTTCCGTT	82	
Ramar2	TTAGGTGTACAAATAAGTTTCTTCCGTT	72	
Sinvmar1	TTAGGTGTTAAACTTAATTCCTGCCGCT	64	
Mos1	TCAGGTGTACAAGTATGAAATGTCGGTT	54	
Desmar1	TTGGGTGTACAACTTAAAAACCGGAATT	57	
Ammar1	TTGGGTTGGCAACTAAGTAATTGCGGATTT	43	mellifera
Bmmar1	CAGGTGTGTAAATATGAAACCGGAATT	32	mori
Hcmar1	TTAGGTCCTTACATATGAAATTAGCGTT	57	cecropia
Cemar1	TCAGGTTGTCCCATTTGTTTTTGCACTA	36	elegans
Himar1	ACAGGTTGGCTGATAAGTCCCCGGTCTGA	27	irritans

Figure 2. Comparison and % identity of inverted terminal repeats (ITR) sequences among *Asmar1* from *Atta sexdens rubropilosa* and other elements. The elements represented are *Ramar1* and *Ramar2* from *Rhynchosciara americana*, *Sinvmar1* from *Solenopsis invicta*, *Mos1* from *Drosophila mauritiana*, *Desmar1* from *Mayetiola destructor*, *Ammar1* from *Apis mellifera*, *Hcmar1* from *Hyalophora cecropia*, *Cemar1* from *Caenorhabditis elegans*, *Himar1* from *Haematobia irritans*, *Bmmar1* from *Bombyx mori*.

Figure 3 shows a comparison among ITR sequences of *Asmar1*, *Ramar1* and *Ramar2*. These ITR sequences share a high identity (82-72%), including six continuous nucleotides (5'-GTACAA) in the 5'-extremity and the six late nucleotides (TCCGTT-3') of the sequence.

However, the presence of an imperfect ITR sequence, generated from mutations may have been the starting point for the inactivation of this element in *A. s. rubropilosa*. *Asmar1*, no longer able to undergo transposition, may have accumulated new mutations, creating a totally defective element. Some studies show important characteristics about the ITR sequences, such as conservation of a palindrome sequence and mirror motifs (Bigot et al., 2005), and a possible function, initially proposed by Pietrokrovski and Henikoff (1997) and later confirmed by Augé-Gouillou et al. (2001), where the ITR sequence could be a region involved in the *mariner* transposase binding by HTH motif present in the N-terminal, although the conservation and evolution of ITR sequences in the *mariner* elements represent a puzzle to be solved.

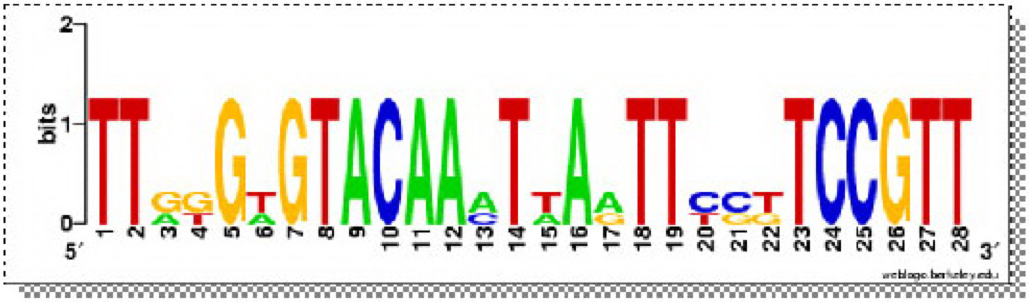


Figure 3. Comparison of inverted terminal repeat (ITR) sequences among *Asmar1* from *Atta sexdens rubropilosa* and *Ramar1* and *Ramar2* from *Rhynchosciara americana.* The logo was drawn in weblogo.berkeley.edu.

A TA dinucleotide immediately flanks the ITR sequence, as is typical for *mariner* insertion events. This finding suggests that the *Asmar1* element has a transposition mechanism similar to other *mariner* elements. The TA dinucleotide represents the target site of the element, which would then be duplicated upon insertion in the genome.

A phylogenetic tree based on transposase sequences was constructed to compare and investigate the phylogenetic distribution and evolutionary status of the known full-length *mariners*. The alignment was generated by the use of ClustalX with default parameters and the tree was elaborated by neighbor joining algorithm and constructed with the TreeView 1.6.6 software (Saitou and Nei, 1987; Page, 1996). The protein sequences used were downloaded from GenBank and the accession Nos. are: *A. s. rubropilosa Asmar1* (JF717775), *R. americana Ramar1* (DQ784570), *R. americana Ramar2* (DQ784571), *D. erecta Demar1* (U08094), *Apis mellifera Ammar1* (U19902), *Ceratitis capitata Ccmar1* (AAB17945), *Caenorhabditis elegans Cemar1* (NP_497296), *C. elegans Cemar2* (NP_497120), *Mayetiola destructor Desmar1* (AAA66077), *D. mauritiana Mos1* (AAA28678), *Haematobia irritans Himar1* (U11645), *Chrysoperla plorabunda Cpmar1* (AAA28265), *Mantispa pulchella Mpmar1* (U11649), *Homo sapiens Hsmar2* (AAC52011), *O. atropalpus Atmar1* (AAL16723), *Hyalophora cecropia Hcmar1* (M63844). A *Bmmar1* sequence from *B. mori* (AAB47739) was used as an out-group (Shao and Tu, 2001). The tree obtained was classified into six subfamilies based on their branching pattern (Figure 4). The grouping of *Asmar1* within the *mauritiana* subfamily of *mariner* elements was strongly supported in bootstrap analysis and amino acid identity and similarity with its sister clade.

Figure 5 shows an alignment of *Asmar1* (Genbank accession No. JF717775) consensus with the *Ramar1* element of *R. americana* (Genbank accession No. DQ784570), *Mboumar* element of *M. bouvieri* (Genbank accession No. AJ781769.1) and *Desmar1* element of *M. destructor* (Genbank accession No. AAA66077). The *Asmar1* and *Mboumar* consensus transposase sequences share 44% amino acid identity and 58% conservative replacements, while *Desmar1* transposase shares 45 and 60% amino acid identity and conservative replacements.

The *Ramar1* element appears to be the closest *mariner* to *Asmar1* with 46 and 62% amino acid identity and conservative replacements, respectively.

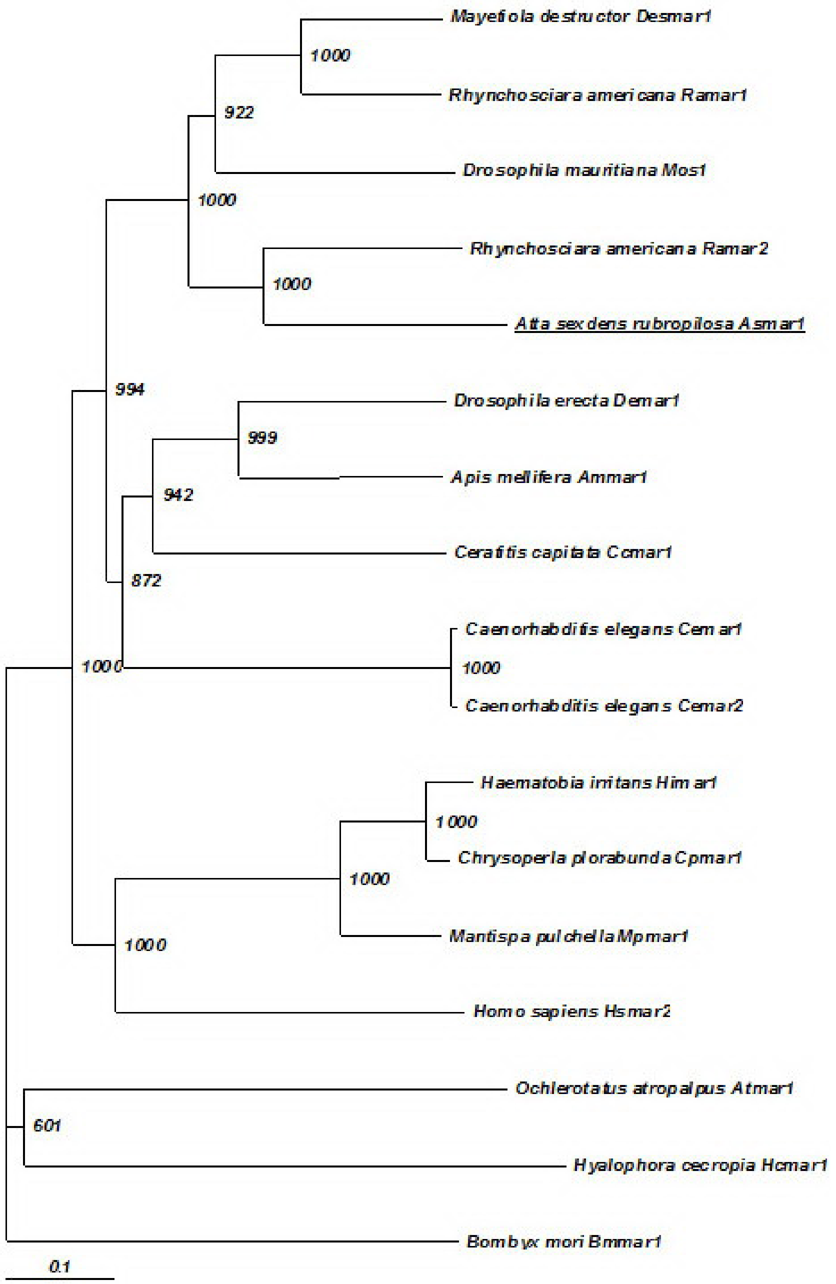


Figure 4. Phylogenetic relationship among the consensus *Asmar1* and other *mariner* elements based on their transposase amino acid sequences, using *Bmmar1* as outgroup.

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Asmar1   MSNFVLT---QHLRD--FDFLLLKKSAAEAHRMLVEVYGNTAPTGKSCREWFRRFKDEISALKTSLALDSQKIPKTKNDI  75
Ramar1   MSSFVAN--KHHLREVLIFCFHWKKSAAEAHQMLVEVYGDSAPSERFCREWFGRFKSGDFSVKDKERPGQPKKFEDE-EL  77
Mos1     MSSFVPN--KEQTRTVLIFCFHLKKTAAESHRMLVEAFGEQVPTVKKCERWFQRFKSGDFDVDDKEHGKPPKRYEDA-EL  77
Desmar1  MENFENWRKRRHLREVLLGHFFAKKTAAESHRLLVEVYGEHALAKTQCFEWFQRFKSGDFDTEDKERPGQPKKFEDE-EL  79

Asmar1   TRRRSESNARGACRIIGD-NSSRICTIESHEVMGMIEKQGNWVPMNLNRETLKGDFSLANSFKD-NREKVFC---IGLDE  150
Ramar1   ETLLEQDSCQTQTELAKSLGVTQQAISKRLKAAGYIQKQGNYVPYELKERDVERRFCMSEMLLERHKRKSFLHRIVTGDE  157
Mos1     QALLDEDDAQTQKQLAEQLEVSQQAVSNRLREMGKIQKVGRWVPHELNERQMERRKNTCEILLSRYKRKSFLHRIVTGDE  157
Desmar1  EALLDEDCQQTQEELAKSLGVTQQAISKRLKAAGYIQKQGNWVPHELKPRDVERRFCMSEMLLQRHKKKSFLSRIITGDE  159

Asmar1   MWIFYDNPKKKKYYAKPDQSLPSISTSTPNIHDSKIMLCIWWD-KDLVYYELLKPGDSITGDRYRLQLIRLSRVLQEKWP  229
Ramar1   KLIHYDNPKRKRSYVKPGQ--PGTSTSKPNIHGAKVMLCIWWDQKGLIHYELLKPGQTINGDFYRQQWIRLKQAVAEKRP  235
Mos1     KWIFFVSPKRKKSYVDPGQ--PATSTARPNRFGKKTMLCVWWDQSGVIYYELLKRGETVNTARYQQQLINLNRALQRKRP  235
Desmar1  KWIHYDNSKRKKSYVKRGG--RAKSTPKSNLHGAKVMLCIWWDQRGVLYYELLEPGQTITGDLYRTQLIRLKQALAEKRP  237

Asmar1   EYEQRH--VILQHDNARPHVAKVVKTYLETLKWEVLPHPPYSPDVAPSDYHLFRSMAHGLADQHFRFCEEIKNWIDSWIA  307
Ramar1   DYATRHESIIFHHDNARPHAAVQVKNYLKNSGWEILVHPPYSPDLAPSDYHLFRSMQNALSGIRFTSEQGIKSWLNSFLA  315
Mos1     EYQKRQHRVIFLHDNAPSHTARAVRDTLETLNWEVLPHAAYSPDLAPSDYHLFASMGHALAEQRFDSYESVKKWLDEWFA  315
Desmar1  EYAKRHGAVIFHHDNARPHVALPVKNYLENSGWEVLPHPPYSPDLAPSDYHLFRSMQNDLAGKRFTSEQGIRKWLDSFLA  317

Asmar1   SKYVLCFRRGVRTLPERWEKVVASDGQYFES  338
Ramar1   SKDERFFHDGIRKLPERWEKVVASDGQYF--  344
Mos1     AKDDEFYWRGIHKLPERWEKCVASDGKYLE-  345
Desmar1  AKPAKFFEKGIHELSERWEKVIASDGQYFE-  347
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Figure 5. Alignment of the conceptual translation of the consensus *Asmar1* transposase sequence with those of *Rhynchosciara americana Ramar1*, *Messor bouvieri Mboumar* and *Mayetiola destructor Desmar1* elements.

Concluding remarks

Leaf-cutter ant colonies of *Atta* spp are responsible for the largest herbivory impacts in most habitats of the New World tropics (Wilson, 1980). They may account for the destruction of up to 17% of the total leaf production in tropical rainforests (Begon, 1996). The present study provides the first evidence of a full-length *mariner* element in the *A. s. rubropilosa* genome. This transposable element, although non-functional, shows the presence of the *mariner* element family in the *A. s. rubropilosa* genome. The high identity among these elements of different model systems led to the amplification of the *Asmar1* element. Thus, it is possible to relate this fact with the hypothesis of horizontal transfer, which provides that the *mariner* transposable elements would be inherited from related species, although similarity has already been observed between *mariner* elements of distant species. These results serve as a step toward understanding the dynamics of MLE distribution in *Atta sexdens rubropilosa*. Further studies will be important to better characterize the mobile elements in the different castes and to establish its possible association with some relevant cellular function.

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