Detection of Heterozygosity and Allelic Frequency of Indian and Southeast Asian Types of *Oecophylla smaragdina* (Fabricius) (Hymenoptera, Formicidae) in Bangladesh using Microsatellite Markers

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**Abstract**

**Background:** The two types of Asian weaver ant species, *Oecophylla smaragdina*, Indian types and Southeast (SE) Asian types can co-occur in the same habitat. Previous study on mtDNA based phylogenesis of *O. smaragdina* in Bangladesh has revealed the presence of the mixture of both Indian and SE Asian type of *O. smaragdina*. However, the nuclear DNA based study showed some inconsistency leading the chance of hybridization as colonies encountered from two localities contained *O. smaragdina* workers from more than one type as identified via longwave length rhodopsin (LWRh) and mitochondrial COI and Cytb gene analysis. The purpose of present study was to detect hybridization status and to find out the identical allele for Indian and SE Asian type of *O. smaragdina* from different colonies.

**Method:** A total of seven *O. smaragdina* colonies had been collected from Bangladesh during 2013 to December 2016. Microsatellite analysis were performed for Gene mapping and heterozygosity study with 11 microsatellite loci through electropherogram study generated by peak scanner software.

**Result:** Among 11 microsatellite loci, two loci, MS 8.24 and MS 6.45 provided the identical allele position for Indian and SE Asian types while no allelic position were identified with nine microsatellite loci. The results inferred that weaver ant of both Indian and SE Asian type engage in bidirectional interspecific gene flow. The strong possibility of hybridization between these two types is inferred, which indicates that barriers to hybridization do not exist or can be completely overcome. This is unexpected, given that they are non-sister species and broadly sympatric in nature. These findings also indicate the possible occurrence of hybrid-hybrid crosses in some localities of weaver ant, a phenomenon rarely observed in ants.

**Key words:** Heterozygosity, Identical allele, Microsatellite markers, Mitochondrial DNA, Nuclear DNA, *Oecophylla smaragdina*.

**Introduction**

The weaver ant species, *Oecophylla smaragdina*, is widely distributed from India through Southeast Asia to northern Australia including many tropical western Pacific islands (Wetterer, 2017). The ant is arboreal, observed in natural forests, fruit orchards and homestead woodlands and is one of the important biological control agents (Dlusky, 2008). The phylogenetic study of *O. smaragdina* based on mitochondrial Cytb and CO1 genes identified two major types where Indian types occurred mainly in India and Sri Lanka while the Southeast Asian (SE Asian) types have been observed in most of the SE Asian countries including Bangladesh (Azuma et al. 2006, 2002). However, recent phylogenetic study revealed the occurrence and dominance of Indian type in the western part (Rahman et al. 2017a) and SE Asian types in the eastern part and overlapping population of *O. smaragdina* in the central part of Bangladesh (Rahman et al. 2017b) that can lead the chance of hybridization. Recently, for inferring the evidence of hybridization a comprehensive view of evolutionary history by analyzing nuclear and mitochondrial DNA between species level phylogeny in Hymenoptera was found effective and has been used extensively (Roos et al. 2011; Ascher et al. 2001; Cameron and Williams, 2003). Azuma et al. (2006) through long wavelength rhodopsin (LWRh) analysis categorized the Indian and SE Asian type of *O. smaragdina* population as Srmagadina B and Srmagadina A and suggested that SE Asian are derived and monophyletic while the Indian type is the ancestral. Discordant genetic
relationships usually occurred from mitochondrial introgression or the incomplete lineage sorting (Eto et al. 2013) which was observed from the two types of weaver ants in Bangladesh (Rahman et al. 2020). The occurred discordancy can partially reveal the hybrid phenomenon but cannot fully detect the hybridization status of the colony by revealing the identical alleles.

Microsatellite markers, also known as simple sequence repeats (SSRs) is very useful for revealing the heterozygosity and finding the identical alleles with combination of mitochondrial and nuclear DNA results. It’s a nuclear DNA marker and combines all the alleles from each parental species for F1 detection and can be used to identify the polymorphism by detecting heterozygosity and with high rate of mutation (Lodkale and Lushai, 1998; Hancock, 1999). The microsatellite markers consist of short but repeated units of around two to six base pairs in length and include both coding and non-coding regions of up to 200 bp (Beukeboom and Zwaan, 2005). By combining the alleles from each parental species in all loci, microsatellites can indicate F1 hybrids as microsatellite is considered as nuclear DNA marker, although the event of backcrossing has the significant effect on detection of hybridization (Goodman et al. 1999). Through mtDNA, only the maternal identity can be traced without the detection of hybrid. Therefore, Hybridization can be revealed through the inconsistency result of mt DNA and nuclear DNA analysis along with backcrossing with the parental species (Mardulyn and Cameron, 1999). However, by only microsatellite study, hybridization can be undetected if backcrossing occurred repeatedly because back crossing sometimes causes the complete elimination of the nuclear genome of the maternal species from hybrid (Schlick-Steiner et al. 2011).

Mallet (2005) reported that hybridization often takes place among the closely related species because of insufficient evolution of reproductive barriers. This may lead to inconsistent between nDNA and mtDNA types within the cell of a hybrid and thus, the occurrence of both Indian and SE Asia types, created the possibility of a hybrid colony of *O. smaragdina*, especially in the overlapping zone in Bangladesh. In the present context, four possible combinations can happened within the cell if the crossing between the male and female Indian and SE Asian types occurred. The occurrence of either Indian or SE Asian in both mtDNA and nDNA is consistent, *i.e.*, both the mtDNA and nDNA are Indian type or both are the SE Asian type. The inconsistency might be found out if the nDNA are Indian type and mtDNA are SE Asian type or the vice-versa (Fig 1a). In the case, where mtDNA are SE Asian type, the crossing might to be expected between the male of Indian type and female of SE Asian type and mtDNA are maternally inherited. Through, comparing the results of the nucleotide sequences obtained from nDNA analysis by LW Rh and mtDNA and nDNA inconsistency was observed (Rahman et al. 2020) and it partially reveals the hybrid phenomenon but cannot fully detect the hybridization status of the colony. In addition, in the diploid cell, the nucleus can contain both the Indian and SE Asian types. However, the crossing pattern of occurring either the male or female from Indian or SE Asian type can be detected through mtDNA analysis (Fig 1b). Microsatellite markers could identify the heterozygosity in the above-mentioned condition. The detailed explanation about the justification of choosing nuclear DNA and microsatellite analysis for revealing the hybridization status were described in Fig 1 Therefore, the purpose of this study was to facilitate further confirmation of heterozygosity along with the actual hybrid condition within the diploid nucleus by detecting identical allele between Indian and SE Asian types within the colony.

**MATERIALS AND METHODS**

**Localities of *O. smaragdina* sampling in Bangladesh**

A total of seven *O. smaragdina* colonies had been collected from seven localities belonging to eight divisions of Bangladesh during 2013 to December 2016. The detailed locality information is presented in Fig 2 and Table 1.

**Sample preparation**

The samples of *O. smaragdina* collected from Bangladesh were preserved in 99% ethanol prior to DNA extraction. All the molecular analysis and sequencing were done in the laboratory Institute of Tropical Agriculture of Kyushu University, Japan.

**DNA extraction**

For molecular analyses, specimens were randomly chosen from seven colonies of seven different localities. Ten individuals from each colony were selected randomly for extraction of DNA. For the convenient discussion, we grouped sample no. 133 to 142 from L3, 143 to 152 from L4, 153 to 160 from L2, 163 to 170 from L7, 173 to 180 from L1, 181 to 188 from L5 and 189 to 195 from L6. Genomic DNA was extracted from the fore, middle and hind legs of specimens that were preserved in alcohol by using QIAGEN DNeasy Blood and Tissue kit (Qiagen, Maryland, USA) following manufacturer’s instruction. Samples were vortexed by adding 180 µl tissue lysis buffer (Buffer-ATL) and 20 µl proteinase K. Buffer-AL (lysis buffer) of 200 µl were added to the samples and were incubated at 55°C for 48 hours. The contaminant of DNA was washed out using two wash buffers (Buffer- AW1 and Buffer- AW2). The unbound proteins were removed by the elution buffer (Buffer- AE). Extracted DNA were purified using DNA purification buffer (Buffer- AL). All centrifugation steps were completed at room temperature as mentioned by Crozier et al. (1993) and Crozier et al. (1994). The colony mates of the specimens used for DNA analysis were preserved in the laboratory of Institute of Tropical Agriculture, Kyushu University after DNA extraction.

**Primers and PCR status followed for microsatellite study**

The primers used in PCR and with its corresponding loci information are given in Table 2. PCR was performed in a 15 µl reaction volume containing 1 µl x reaction buffer (10XEx7Eq buffer), 1 µl x dNTP with 1.8 mM MgCl2, 1 µl of...
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...each primer, 0.1 μl of Ex Taq DNA polymerase (TAKARA, USA) and about 1 μl template DNA. Forward primers were 5'-end labeled with 6-FAM fluorescent dye. Cycling parameters were followed as mentioned by Azuma et al. (2004). Fragments were run on an ABI PRISM 310 genetic analyzer (Applied Biosystems). For gene mapping by fragment analysis and data processing, Peak Scanner software v 1.0 (Applied Biosystems) was used. For identifying the heterozygosity by the observation of number of peaks by sharing the locus number were determined by electropherogram study given in Fig 3. This figure is the representative method of the total study.

**RESULTS AND DISCUSSION**

In this study, 11 microsatellite primers (MS 2.2.2, MS 2.3, MS 5.10, MS 2.14, MS 3.2, MS 6.45, MS 6.29, MS 5.2, MS 7.1, MS 8.24 and MS 6.47) (Azuma *et al.* 2004) were used. However, we failed to analyze the samples using MS 5.2 microsatellite primer. The results of heterozygosity study using each microsatellite primer were presented in Table 3.

**Use of different microsatellite primers for detecting heterozygosity and allelic frequency**

**Microsatellite primer MS 5.10**

With this primer, we analyzed a total of 68 samples from seven localities. Among them, all the samples from the locality L4, L46, L27, L67, L50 and L66 were sharing both the loci 98 and 99 while the samples from locality 13 were sharing both the loci 96 and 97 (Table 3). L13 was identified as Indian type of *Oecophylla smaragdina* by both mitochondrial and nuclear DNA analysis. However, L34, L46, L67, L50 was determined as SE Asian type and L27 and L66 was characterized as Indian type. So, in this case for the primer MS 5.10, we failed to distinguish identical alleles.

**Fig 1a:** Consistent and inconsistent status of mitochondrial and nuclear DNA in cell.

**Fig 1b:** Heterozygous status of the cell nucleus.
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**Table 1:** Detailed locality information of weaver ant sampling in Bangladesh for microsatellite study.

| Locality No. | Locality Name          | Upazila   | District | Division | Collection Date | GPS Coordination |
|--------------|------------------------|-----------|----------|-----------|-----------------|------------------|
| L13          | Mollahat Bazar         | Mollahat  | Bagerhat | Khulna    | 29 Oct. 2014    | 24°01’16.6" N 90°17’53.7" E |
| L27          | Bhawal National Park   | Joydebpur | Gazipur  | Dhaka     | 17 Mar. 2014    | 24°04’43" N 90°24’06" E  |
| L34          | Tea Resort Center      | Sreemangal Moulovibazar | Sylhet | 14 Nov. 2014 | 24°18’7.2" N 91°45’34.92" E |
| L46          | Mohipal Primary School | Feni sadar | Feni     | Chittagong | 14 Aug. 2015    | 23°1’1.10" N 91°23’50" E  |
| L50          | Matiranga Dhibi        | Matiranga | Khagrabari | Chittagong | 18 Aug. 2015    | 23°2’30.12" N 91°52’30" E  |
| L66          | Mohespur               | Bakerganj | Barisal  | Barisal   | 10 Feb. 2016    | 22°33’30" N 90°20’18" E  |
| L67          | Bhaluka Bazar          | Bhaluka   | Mymensingh | Mymensingh | 12 Nov. 2016    | 24°22’30" N 90°22’42" E  |

**Microsatellite primer MS 2.14**

This primer detected several allele positions for Indian and SE Asian types. The samples from L46, L27 shared the loci positions 231 and 234 whereas sample from L34 shared the locus 221, in addition, 1 sample from L50 shared the locus 262 with loci 231 and 234. The samples from locality L13 and L66 showed a quite different pattern of sharing allele frequencies. The samples from L13, shared the loci 245, 247, 262, 270 and 273. The samples from L66 shared the loci 238, 252 and 270 (Table 3). So, no distinguished locus position sharing by Indian and SE Asian types of samples were observed.

**Microsatellite primer MS 3.2**

For identifying the identical allele, I tested 32 samples from 4 localities. The samples from L27 and L67 shared the locus 81 while the samples from L13 shared the locus 86. The samples from locality 50 shared both locus 81 and locus 86 (Table 3).

**Microsatellite primer MS 7.1, MS 6.29 and MS 6.47**

Eight samples from each of two localities (L67 and L13) were tested by microsatellite primer MS 7.1, MS 6.29 and MS 6.47. All 08 samples shared the locus 100, locus 128 and locus 172 for MS 7.1, MS 6.47 and MS 6.29, respectively (Table 3). So, no locus was identified that can separate Indian and SE Asian type of *Oecophylla* in Bangladesh.

**Microsatellite primer MS 2.3 and MS 2.2.2**

Sixty samples from seven localities were tested each for MS 2.3 and MS 2.2.2. All the samples from MS 2.3 shared the locus 144, while two samples from L34 and L46 shared both the loci 100 and 144. In the case of MS 2.2.2, all the samples sharing the locus 103 except the samples from L13 and L66 that were sharing the locus 97. The samples from other locality that were identified as Indian type also shared the locus position 97 along with some samples from L34 which was identified as SE Asian type. So, with these two primers the identical allele position was not possible to distinguish between Indian and SE Asian types (Table 3).

**Successful detection of identical allele**

The identical allele between Indian and SE Asian types of *O. smaragdina* population in Bangladesh were possibly detected with the microsatellite primer MS 6.45 and MS 8.24. For MS 6.45, four samples from the locality L67 were analyzed and all 04 samples shared the locus 238. However, the samples from locality L13 shared the locus 244 and locus 250. As the colony of L13 locality was identified as Indian type and L67 was SE Asian type so, these locus positions was identical. Similarly, the samples with 8.24, among 08 samples, 4 samples from L67 shared the locus 277 while the rest 4 samples from locality L13 shared the locus 262 (Table 3).
In this regard, you may please reply to the reviewer comments mail.

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Table 2: List of loci used in microsatellite analysis of *O. smaragdina* in Bangladesh modified from Azuma et al. (2004).

| Locus Name | Primer Sequence (5'-3') | Repeat motif | Ta (°C) | References |
|------------|-------------------------|--------------|---------|------------|
| MS2.2.2    | F:GTCTTTAGTGTGGCCACTGCGA<br>R: GTGAATGAAAGTGTGAACCTGCTTTG  | (GCA) 6 | 48      |            |
| MS2.3      | F: TCCAGGGGTTACTCAAGGTCAAGTT<br>R: CATACACATTCTGCTGACGCTG  | (GT) 5GC(GT)5 | 48 |            |
| MS2.14     | F: TCTACGTCAGTCAACCCCAAC<br>R: GCGAGCTCTACCCCATGCTTTAG | (CGA)4CGT(CGTA)6CAA–(CGA)10TGA(CGA)3 | 52 |            |
| MS3.2      | F: GTGACATTGTGGGCGCA<br>R: CGAGGCGCAGAATTTCGTC  | (GA)6 | 52 |            |
| MS5.2      | F: AATTACGGTTCGGTCTCG<br>R: ATCGAACTTCTGCGGTTGTA  | (CT)11(CTTT)3GTTT(CTTT)2 | 48 |            |
| MS5.10     | F: GAGAGGAAAGTGCACCAATG<br>R: CGAACGCCGAAAATGTCGA  | (GA)3AA(GA)5A8(GA)4 | 52 | Azuma et al. (2004) |
| MS6.29     | F: CAATCGATGTGACCGGCT<br>R: GAACTTGTGCGGTTCTGCA  | (GA)3AA(GA)4A(GA)3 | 49 |            |
| MS6.45     | F: GTGTTGCCGCTTCG<br>R: CAGATACAGGGCCAGGT  | (GTT)3GCT(GTT)9(GCT)4(GTT)2(GCT)4 | 49 |            |
| MS6.47     | F: AGCCCTCTCTTCTCATGA<br>R: TTAATCTGCGGCCGCA  | (GA)9 | 45 |            |
| MS7.1      | F: AAAGACCGGCTGCGGAC<br>R: AGCTGCAATCCCATGCA  | (GAT)8 | 52 |            |
| MS8.24     | F: GCAGACAATGCTCTTGT<br>R: CGATGTGATTAGCCGA  | (CTT)5CTC(TCT)3–(GA)3AA(GA)11AA(TA)(GA)9 | 50 |            |

Determining heterozygosity by electropherogram study

| Microsatellite | Sample No. | Locus 97 | Locus 100 | Locus 103 |
|---------------|------------|----------|-----------|-----------|
| MS 2.2.2      | 113        | 1        | 1         |           |
|               | 114        | 1        | 1         |           |
|               | 115        | 1        | 1         |           |
|               | 116        | 1        | 1         |           |
|               | 117        | 1        | 1         |           |
|               | 118        | 1        | 1         |           |
|               | 119        | 1        | 1         |           |
|               | 140        | 1        | 1         |           |
|               | 141        | 1        | 1         |           |
|               | 142        | 1        | 1         |           |
|               | 143        | 1        | 1         |           |
|               | 144        | 1        | 1         |           |
|               | 145        | 1        | 1         |           |
|               | 146        | 1        | 1         |           |
|               | 147        | 1        | 1         |           |
|               | 148        | 1        | 1         |           |

There was not too many evidence of such heterozygous condition within the colony of *O. smaragdina* in India or any other SE Asian country and this is the first report of such mixed colony in Bangladesh as well. Similarly, Roos et al. (2011) studied tracing the evolution and hybridization of colobine monkey in the Asian continent, found several hybridization patterns by testing the mitochondrial and nuclear DNA which was found to be supported by Blaimer (2012). The observed phylogenetic incongruences resulted by hybridization among ancestral lineages most likely occurred, due to the presence of potential contact zones like today’s Bangladesh, Myanmar and the northeast of India, which is suggested as hybridization area (Karanth et al. 2008). However, several big mountains and big rivers in the border region of today’s Myanmar, India and China might have been a possible diversification hotspot (Chakraborty et al. 2007) which leads to develop such hybridization pattern.

Divergence time is also an important factor for many ant genera. *Oecophylla* is thought to be a significant factor in such distribution (Bolton, 1995). Diversification within groups in this continent was recorded from the middle Pliocene to early Pleistocene (Azuma et al. 2002). After this period, the world has encountered a significant climatic change. It might
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Also affect the distribution of *Oecophylla* in different parts of the world. During Last Glacial Maximum (LGM), the tropic region shifted southward and it retained northward after glaciation. This study suggested that the Indian and Southeast Asian clades of *O. smaragdina* expanded their distribution northward along suitable regions with high temperature and humidity and then the two clades supposedly encountered and overlapped in central Bangladesh. Similar trends were also observed in the case of study of the origin of Asian elephants (Vidy et al. 2009). They suggested a contraction-expansion scenario during climatic oscillation leads to geographical overlaps of two mtDNA clades created the allopatric population of Asian elephants in India, Sri Lanka and Myanmar. In the case of weaver ant in Bangladesh, as both the Indian and SE Asian types were dominated in Western and Eastern part of the

### Table 3: Allele record for 10 microsatellite loci in seven localities.

| Microsatellite Allele | L34 (n=8) | L46 (n=8) | L27 (n=8) | L67 (n=8) | L13 (n=8) | L50 (n=8) | L66 (n=8) |
|-----------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
|                       | SE Asian  | SE Asian  | Indian    | SE Asian  | Indian    | SE Asian  | Indian    |
| MS 2.2.2              | 97        | 3         | 4         | 8         | 1         | 8         |           |
|                       | 100       |           |           |           |           |           |           |
|                       | 103       | 8         | 8         | 4         | 8         |           |           |
|                       |           |           |           |           |           |           |           |
| % Heterozygosity      | 37.5      | 0         | 50        | 0         | 0         | 12.5      | 0         |
| MS 2.3                | 100       | 1         | 1         |           |           |           |           |
|                       | 144       | 8         | 8         | 8         | 8         | 8         | 8         |
|                       |           |           |           |           |           |           |           |
| % Heterozygosity      | 12.5      | 12.5      | 0         | 0         | 0         | 0         | 0         |
| MS 5.10               | 96        |           |           |           |           |           |           |
|                       | 97        |           |           |           |           |           |           |
|                       | 98        | 8         | 8         | 8         | 8         |           |           |
|                       | 99        | 8         | 8         | 8         | 8         | 8         |           |
| % Heterozygosity      | 100       | 100       | 100       | 100       | 100       | 100       | 100       |
| MS 2.14               | 221       | 4         |           |           |           |           |           |
|                       | 231       | 3         | 6         | 8         |           |           |           |
|                       | 234       | 5         | 8         | 5         | 8         |           |           |
|                       |           |           |           |           |           |           |           |
| % Heterozygosity      | 50        | 62.5      | 62.5      | 0         | 100       | 75        | 87.5      |
| MS 3.2                | 81        | 8         | 8         |           |           |           |           |
|                       | 86        |           |           |           |           |           |           |
| % Heterozygosity      | 0         | 0         | 0         | 87.5      |           |           |           |
| MS 6.45               | 238       | 4         |           |           |           |           |           |
|                       | 244       |           |           |           |           |           |           |
|                       | 250       |           |           |           |           |           |           |
| % Heterozygosity      | 0         | 50        |           |           |           |           |           |
| MS 6.29               | 172       | 4         | 4         |           |           |           |           |
| % Heterozygosity      | 0         | 0         |           |           |           |           |           |
| MS 7.1                | 100       | 4         | 4         |           |           |           |           |
| % Heterozygosity      | 0         | 0         |           |           |           |           |           |
| MS 8.24               | 262       | 4         |           |           |           |           |           |
|                       | 277       |           |           |           |           |           |           |
| % Heterozygosity      | 0         | 0         |           |           |           |           |           |
| MS 6.47               | 128       | 4         | 4         |           |           |           |           |
| % Heterozygosity      | 0         | 0         |           |           |           |           |           |
| MS 5.2                | Failed    |           |           |           |           |           |           |

*n* indicating the number of individuals per locality.
country, respectively and there was not such a big border of separating those two populations (Rahman et al. 2017a). The probability of the contact of both the types was considered very usual. Pusch et al. (2006) reported that ant colony with heterozygous produce hybrid workers. This type of gene introgression may increase the genetic diversity of the hybrid relative to its parental species and can lead to hybrid vigor (Helms and Keller, 2003). In this case, the O. smaragdina colony from the locality 11 and 15 in Bangladesh might have the influence of the arising of new evolutionary lineages. This hybridization therefore, can be considered as a process of the evolutionary significance of O. smaragdina in Bangladesh.

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