Phylogenetic Analysis Reveals the Overlapping Distribution of the Indian and Southeast Asian Clades of Oecophylla smaragdina (Fabricius) (Hymenoptera, Formicidae) in Central Bangladesh

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https://doi.org/10.5109/1854016

出版情報：九州大学大学院農学研究院紀要. 62 (2), pp.429-434, 2017-09-08. Faculty of Agriculture, Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., **62** (2), 429–434 (2017)

Phylogenetic Analysis Reveals the Overlapping Distribution of the Indian and Southeast Asian Clades of *Oecophylla smaragdina* (Fabricius) (Hymenoptera, Formicidae) in Central Bangladesh

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(*Received April 28, 2017 and accepted May 10, 2017*)

Oecophylla smaragdina, the weaver ant species is widely distributed from India through Southeast Asia to Northern Australia including many tropical Western Pacific Islands. In the previous phylogeographic study, the populations was divided into 7 groups, of which Indian populations are the sister group to other 6 Southeast Asian groups. Central Bangladesh populations of weaver ant have been reported Southeast Asian groups in spite of its geographical proximity however, a recent phylogenetic study of *O. smaragdina* revealed that the western Bangladesh population belongs to Indian clade. The purpose of the present study was to analyze the phylogeographic distribution of Southeast Asian and Indian clades of weaver ant in Bangladesh along with the haplotype diversity of these two clades. Adult *Oecophylla smaragdina* workers were collected from 71 colonies at 67 localities in 38 districts belonging to 7 divisions of Bangladesh during 2013 to 2016 to infer the phylogenetic position. Their haplotype and phylogenetic relationships were determined by analyzing 2 mitochondrial loci: *Cytochrome b* Oxidase subunit 2 (*Cytb*) consisting of 580 bp and *Cytochrome c oxidase subunit I* (*COI*) consisting of 725 bp. Bayesian analysis inferred that the western parts of Bangladesh were occupied by mitochondrial Indian haplotype, whereas the eastern parts were dominated by the haplotypes of SE Asian clade. The central parts consisted of the mixture of both Indian and SE Asian clades. This study suggested that the Indian and Souheast Asian clades of *O. smaragdina* expanded their distribution northward after glaciation and the two clades supposedly encountered and overlapped in central Bangladesh.

Key words: COI, Cytb, geographical distribution, mitochondrial DNA, *Oecophylla smaragdina*

INTRODUCTION

The weaver ant, *Oecophylla* (Hymenoptera, Formicidae) are conspicuous arboreal ants consisting of two species, *O. smaragdina* and *O. longinoda*. Both species are distributed in tropical and subtropical Asia and Africa, respectively. Workers show polymorphic characters with diversified organizing behavior in the colony. Workers construct pendulous bag–like nests from cluster of green leaves which are bound together with silk produced by their mature (Chapuisat & Keller, 2002). *Oecophylla* ants are hosts to a variety of inquilines, such as spiders, which mimic the colony odor to escape detection (Schlüns *et al*., 2009). *Oecophylla smaragdina* and *O. longinoda* are very similar in morphology and behavior (Bolton, 1995). Most of the modern flora and fauna in this continent were profoundly influenced by Pleistocene glaciation (Seal *et al*., 2015). The distribution of weaver ant might also been affected by the same phenomenon during this period. According to the fossil records, *Oecophylla* might have originated in the early Paleogene (ca. 60 Ma) in the Palaearctic region, and dispersed during the climatic changes of the Eocene–Oligocene transition at ca. 43 Ma (Dlussky *et al*., 2008). Recently, Blaimer *et al*. (2015) estimated the divergence time of the genus *Oecophylla* based on the fossil records and ultra conserved elements (UCEs). They estimated that *Oecophylla* crown group evolved during Oligocene at ca. < 30 Ma and stem–group evolved during early Eocene at ca. 50 Ma.

Azuma *et al*. (2006) proposed an outline of the phylogeography of *O. smaragdina* and categorized the sampled populations into 7 major clades: group 1 from India; group 2 from Southeast Asian mainland including the Indochinese and Malayan Peninsulas, as well as the Greater Sunda Islands; group 3 from the Philippines; group 4 from Flores; group 5 from Sulawesi; group 6 from Halmahera; group 7 from Australia and New Guinea. Hereafter we refer their group 1 as the Indian clade and group 2 as Southeast Asian clade. Asaka (2010) extended the survey of *O. smaragdina* to South Asia, and collected several samples from India and Sri Lanka. Her phylogenetic analysis showed that all analyzed samples belonged to Indian clade with low sequence divergence.

Azuma *et al*. (2006) revealed the identity of Bangladesh populations as Southeast Asian type in spite of geographical proximity to India. They hypothesized the existence of an Indian refuge for the independence of group 1 from group 2, and concluded that if the Indian population originated from the Indian refuge and Bangladesh population originated from the Indochina refuge, deep genetic gap might be occurred. However, recent phylogeographic study (Rahman *et al*., 2016) identified the western Bangladeshi populations as Indian type. A recent study emphasized the site records for *O. smaragdina* in Bangladesh (Wetterer, 2017). Similar trends were also observed in the case of Asian elephants, where two highly divergent mtDNA of Asian elephants

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overlapped geographically due to glaciation during Pleistocene (Vidya *et al*., 2009).

The purpose of the present study is to examine the phylogenetic study of weaver ant populations from northern, eastern and central part of Bangladesh for covering its distribution range in the country. The previous sampling by Azuma *et al*. (2006) was limited to only one site of Nurbag, Gazipur, located at the central part of Bangladesh, distinguished as Southeast Asian clades. However, *O. smaragdina* from the western parts of Bangladesh were identified as Indian clade. This result suggests the importance of phylogenetic study of central and eastern Bangladeshi populations to identify the nature of distribution.

MATERIALS AND METHODS

Sampling and preparation of specimens

In 2013 to 2016 we collected adult *Oecophylla smaragdina* workers from 71 colonies at 67 localities in 38 districts belonging to 7 divisions of Bangladesh (Fig. 1). The specimens were preserved in 99% ethanol prior to DNA extraction.

Molecular data collection

Genomic DNA was extracted from the legs of specimens that were preserved in alcohol by using *QIAGEN DNeasy Blood and Tissue kit* (Qiagen, Maryland, USA). Amplification of both mitochondrial and nuclear DNA was done by polymerase chain reaction (PCR). The primers used for amplification are identical to primers reported by Crozier *et al*. (1994), Lunt *et al*. (1996), Azuma *et al*. (2002), and Azuma *et al*. (2006). For, mitochondrial DNA analysis, Primers for the *Cytb* gene fragment were Cb1 (5‘TATGTACTACCATGAGGACAAATATC’3) and tRs (5’TATTTCTTTATTATGTTTTCAAAAC’3). For the COI gene fragment, COI 1–3 (5’ATAATTTTTTTTATAGTTATACC’3) and COI 2–4 (5’TCCTAAAAAATGTTGAGGAAA’3) were used as forward and reverse primers, respectively by Crozier and Crozier (1993). The thermal cycling parameters for *Cytb* and *COI* basically followed the protocols established by Crozier and Crozier (1993) and Sameshima *et al*. (1999), including 95°C for 5 min for initial denaturation, 35 cycles of dissociation (92°C, 1 min), annealing (50°C for *Cytb* and 54°C for *COI*, 1 min), and extension (70°C, 2 min). Illustra ExoProStar was followed according to the instruction of the manufacturer GE Healthcare. For cycle sequencing, ABI PRISM Big Dye Terminator v3.1 cycle sequencing kits from Applied Biosystems were used in an automated sequencer. Sequencing reactions were performed by using ABI 3100 Avant DNA Sequencer (Applied Biosystems).

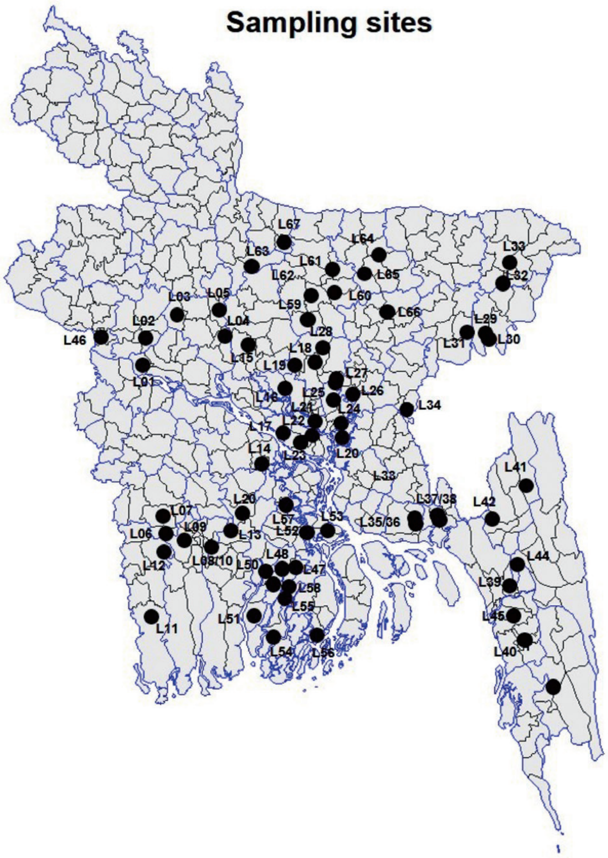

Fig. 1. The sampling sites of *Oecophylla smaragdina* in Bangladesh. Locality codes correspond to those in Table 1.

Phylogenetic inference

For the phylogenetic analysis of *O. smaragdina* populations, 51 samples for *Cytb* and 58 samples for *COI* genes have been used with 507 bp and 639 bp, respectively. In addition, sequence data of both *COI* and *Cytb* were used from Azuma *et al*. (2002), Azuma *et al*. (2006) and Asaka (2010). The sequence data of both *COI* and *Cytb* of *Oecophylla longinoda* from Cameroon were used as outgroup in this analysis. The sequencing analysis was done by using Vector NTI Advance ver. 11.5 software. The sequences of *Cytb* and *COI* were aligned by using MEGA 6.0 software (Tamura *et al*., 2013). Phylogenetic trees were inferred from 106 concatenated matrix sequences of both COI and Cytb genes, conducted by MrBayes 3.1.2 with 1,000,000 generations. For the selection of best– fit model, MrModeltest 2.3 was performed with PAUP*4.0b10. The substitution model, GTR + I + G was used in mitochondrial *COI* and *Cytb* genes were used the alignment was partitioned into 1^{st}, 2^{nd} and 3^{rd} nucleotide positions. The nucleotide sequences for both *Cytb* and *COI* were deposited in the GenBank with accession number (Table 1).

RESULTS AND DISCUSSION

We recognized 175 variable characters, of which 132 characters were parsimony informative. The Bayesian analysis of the mitochondrial concatenated matrix dataset showed that the Bangladeshi *O. smaraggina* samples were nested into two distinct clades (posterior probability > 90%) (Fig. 2). Bangladeshi 34 weaver ant sam-

Table 1. Detailed locality information with GenBank accession number of sequencing data

Locality code	Locality Name	No. of colonies	Upazila	District	Division	Collection Date	Accession number	
							COI	*Cytb*
L01	Ishwardi	1	Ishwardi	Pabna	Rajshahi	18 Mar. 2014	KX385842	KX430217
L02	Bonpara	1	Baraigram	Natore	Rajshahi	19 Mar. 2014	KX385843	KX430218
L03	Tarash	1	Tarash	Sirajganj	Rajshahi	18 Mar. 2014	KX385841	KX430216
L04	Chauhali	1	Belkuchi	Sirajganj	Rajshahi	19 Mar. 2014	KX389168	KX398946
L05	w side of Jamuna Bridge	1	Sirajganj sadar	Sirajganj	Rajshahi	18 Mar. 2014	KX385840	KX430215
L06	Panjia	1	Keshabpur	Jessore	Khulna	04 Mar. 2014	KX371575	KX398943
L07	Manirampur	1	Manirampur	Jessore	Khulna	14 Sep. 2013	KX355139	KX430212
L08	Khulna Univ. Campus	1	Batiaghata	Khulna	Khulna	03 Mar. 2014	KX379493	KX398942
L08	Khulna Univ. Campus	1	Batiaghata	Khulna	Khulna	03 Mar. 2014	KX379494	KX430213
L09	Chuknagar	1	Dumuria	Khulna	Khulna	04 Mar. 2014	KX385837	KX398944
L10	Batiaghata	1	Batiaghata	Khulna	Khulna	15 Sep. 2013	KX389167	
L11	Atulia	1	Shyamnagar	Satkhira	Khulna	24 Mar. 2014	KX385844	KX398947
L12	Modonpur	1	Tala	Satkhira	Khulna	25 Mar. 2014	KX385845	KX430219
L13	Mollarhat Bazar	1	Mollarhat	Bagerhat	Khulna	29 Oct. 2014		KX430220
L14	Bhanga	1	Bhanga	Faridpur	Dhaka	09 Nov. 2014	KX389172	
L15	Elenga	1	Kalihati	Tangail	Dhaka	18 Mar. 2014	KX385839	KX398945
L16	Kumrail	1	Dharmrai	Dhaka	Dhaka	19 Oct. 2014	KX389169	
L17	Thanamore	1	Dohar	Dhaka	Dhaka	21 Oct. 2014	KX389170	
L18	Bhawal National park	1	Joydebpur	Gazipur	Dhaka	17 Mar. 2014	KX385838	KX430214
L19	Nurbag	1	Kaliakoir	Gazipur	Dhaka	22 Oct. 2014	KX389171	KX430221
L20	Pachuria	1	Gopalganj sadar	Gopalganj	Dhaka	29 Oct. 2014	KY618816	
L21	Ruhitpur	1	Keraniganj	Dhaka	Dhaka	21 Oct. 2014		KY562567
L22	Nimtali	1	Shirajdikhan	Munshiganj	Dhaka	21 Oct. 2014	KY628426	
L23	Bejgaon	1	Sreenagar	Munshiganj	Dhaka	21 Oct. 2014		KY583087
L24	Shiddhirganj	1	Narayanganj	Narayanganj	Dhaka	21 Oct. 2014		KY562571
L25	Vulta	1	Rupganj	Narayanganj	Dhaka	20 Oct. 2014		KY562573
L26	Panchdona	1	Norsingi	Norsingdi	Dhaka	20 Oct. 2014	KY657490	KY562569
L27	Charpara	1	Kaliganj	Gazipur	Dhaka	20 Oct. 2014	KY628425	
L28	Rajbari	1	Sreepur	Gazipur	Dhaka	20 Oct. 2014		KY562568
L29	Tea Resort Center	1	Sreemangal	Moulovibazar	Sylhet	14 Nov. 2014	KY618809	KY583084
L30	Lauchara National Park	1	Sreemangal	Moulovibazar	Sylhet	15 Nov. 2014	KY618815	KY583085
L31	Bahubal	1	Bahubal	Habiganj	Sylhet	14 Nov. 2014	KY618818	KY583083
L32	Tarau	1	Balaganj	Sylhet	Sylhet	15 Nov. 2014	KY618817	
L33	Doradarpur	1	Dakhin surma	Sylhet	Sylhet	15 Nov. 2014	KY618810	KY657484
L34	Mondabag	1	Kasba	Bramhanbaria	Chittagong	10 Aug. 2015	KY608802	KY657492
L35	Sebarhat	1	Senbag	Noakhali	Chittagong	13 Aug. 2015	KY608803	KY550396
L36	Senbag Upazilla Hospital	1	Senbag	Noakhali	Chittagong	13 Aug. 2015		KY657493
L37	Mohipal	1	Feni Sadar	Feni	Chittagong	14 Aug. 2015	KY618811	KY550397
L38	Mohipal Primary School	1	Feni Sadar	Feni	Chittagong	14 Aug. 2015	KY628427	KY550398
L39	Raujan Bazar	1	Raujan	Chittagong	Chittagong	16 Aug. 2015		KY550399
L40	Satkania	1	Satkania	Chittagong	Chittagong	16 Aug. 2015	KY657489	KY550400
L41	Dighinala HRC	1	Dighinala	Khagrachari	Chittagong	12 Aug. 2015	KY608804	KY550401
L42	Matiranga Dhibi	1	Matiranga	Khagrachari	Chittagong	18 Aug. 2015	KY608805	KY550402
L43	Rumakarai	1	Ruma	Bandarban	Chittagong	20 Aug. 2015	KY657488	KY550403
L44	Kawkhali Bazar	1	Kawkhali	Rangamati	Chittagong	21 Aug. 2015	KY583089	
L45	Potia	1	Potia	Chittagong	Chittagong	07 Sep. 2015		KY562572
L46	Thanapara Sardah	1	Charghat	Rajshahi	Rajshahi	23 Nov. 2015	KY628429	

(Table 1. Continuation)

Locality code	Locality Name	No. of colonies	Upazila	District	Division	Collection Date	Accession number	
							COI	*Cytb*
L47	Nalchiti primary sc. field	1	Nalchiti	Jhalokati	Barisal	15 Feb. 2016	KY618814	KY657585
L48	BRAC More	1	Jhalokati Sadar	Jhalokati	Barisal	15 Feb. 2016	KY657491	KY550389
L49	Bagharibazar	1	Rajapur	Jhalokati	Barisal	16 Feb. 2016	KY618813	KY550388
L50	Kawkhali Upz P chottor	1	Kawkhali	Pirojpur	Barisal	16 Feb. 2016	KY583090	KY550390
L51	Shakharikati	1	Mathbaria	Pirojpur	Barisal	16 Feb. 2016	KY583091	KY550391
L52	Rupatoli	1	Barisal Sadar	Barisal	Barisal	17 Feb. 2016		KY550395
L53	Patarhat	1	Mehendiganj	Barisal	Barisal	18 Feb. 2016	KY583092	KY550392
L54	Barguna Sadar Bus Stand	1	Barguna Sadar	Barguna	Barisal	08 Feb. 2016		KY550393
L55	PSTU	1	Dumki	Patuakhali	Barisal	11 Feb. 2016		KY550394
L56	Panpatti	1	Golachipa	Patuakhali	Barisal	20 Feb. 2016	KY583093	KY583088
L57	Agailjhara uni P office	1	Agailjhara	Barisal	Barisal	10 Feb. 2016	KY628430	
L58	Mohespur	1	Bakerganj	Barisal	Barisal	10 Feb. 2016	KY618812	KY657486
L59	Bhaluka Bazar	1	Bhaluka	Mymensingh	Mymensing	12 Nov. 2016	KY657499	
L60	Trishal primary school	1	Trishal	Mymensingh	Mymensingh	12 Nov. 2016	KY657500	
L61	BAU campus	2	BAU sadar	Mymensingh	Mymensingh	13 Nov. 2016	KY657501 KY657502	
L62	Nandail	1	Muktagacha	Mymensingh	Mymensingh	30 Oct. 2016	KY657503	KY657505
L63	Sarishabari highschool	2	Sarishabari	Jamalpur	Mymensingh	02 Nov. 2016	KY657504	KY657506/ KY657507
L64	Sadar Hospital and pri sch	2	Netrokona sadar	Netrokona	Mymensingh	03 Nov. 2016	KY657494/ KY657495	
L65	Gauripur Upz complex	1	Gauripur	Mymensingh	Mymensingh	10 Nov. 2016	KY657496	
L66	Dighir par	2	Hosenpur	Kishorganj	Mymensingh	01 Nov. 2016	KY657497	
L67	Sadar Thana more	1	Sherpur sadar	Sherpur	Mymensingh	03 Nov. 2016	KY657498	

ples were nested with Indian clade of *O. smaragdina*, whereas 37 samples were nested with the Southeast Asian clades. Therefore, the occurrence of both the Indian and SE Asian types was found within Bangladesh.

Based on the phylogenetic tree obtained, the Bangladeshi populations showed the overlapping distribution of the Indian and SE Asian clades of *O. smaragdina* (Fig. 3). While the western part of Bangladesh was mainly occupied by Indian clades, the Eastern part is dominated by SE Asian clade. The mixture of two clades was found in the central parts of Bangladesh. According to those results, Bangladesh can be considered as a transitional zone of both the two clades.

Divergence time of the ant genus *Oecophylla* is thought to be a significant factor of such distribution. Diversification within groups in this continent was recorded from the Middle Pliocene to Early Pleistocene (Azuma *et al.*, 2002). After this period, world has encountered a significant climatic change. It might also affect the distribution of *Oecophylla* in different parts of the world. Lokkers (1986) suggested two limiting factors, low temperature and humidity for distribution range of *Oecophylla* in Australia. During Last Glacial Maximum (LGM), the tropic region shifted southward and it retained northward after glaciation. This study suggested that the Indian and Souheast Asian clades of *O. smaragdina* expanded their distribution northward along suitable regions with high temperature and humidity, then the two clades supposedly encountered and overlapped in central Bangladesh.

AUTHOR CONTRIBUTIONS

MMR, SH, and KO conceived and designed the experiments. MMR and SH performed the experiments. MMR analyzed the data. MMR, SH, and KO contributed reagents, materials and analysis. MMR and SH wrote the paper.

ACKNOWLEDGEMENT

We are thankful to the authority of Bangabandhu Sheikh Mujibur Rahman Agricultural University (BSMRAU), Bangladesh, Mr. Shovon Kumar Paul, Bangladesh Tea Research Institute, Sreemangal, Sylhet, Mr Shibly Noman, Agriculture Officer, Khagrachari, Chittagong for helping us to collect samples. We express our sincere gratitude to Dr. Masaru Matsumoto, Institute of Tropical Agriculture of Kyushu University, for his technical support. We are grateful to Dr. Noriko Azuma and Ms. Yukiko Asaka, Sapporo, Japan for their valuable advice and suggestions. We are also thankful to Dr. Akinori Ozaki, Institute of Tropical Agriculture for providing facilities during sampling in Bangladesh. This

Fig. 2. Bayesian phylogenetic tree (1146 bp) as inferred from the mitochondrial gene fragments of the *COI* (639 bp) and the *Cytb* (507 bp) genes (substitution model: GTR + I + G 1000000 generations used in MrBayes 3.1.2 MrModeltest 2.3,PAUP*4.0b10). Taxon name with red triangle shape indicating the samples from Bangladesh.

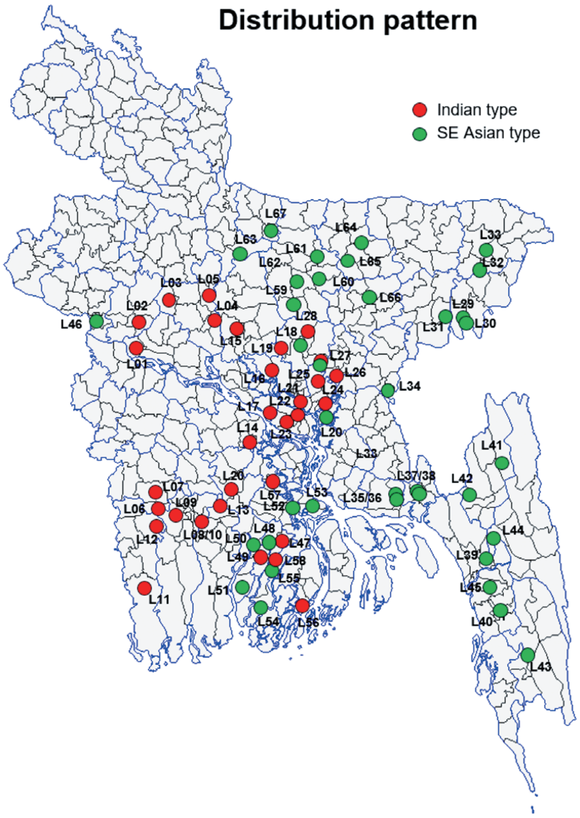

Fig. 3. Distribution pattern of Indian and SE Asian clades of *Oecophylla* in Bangladesh.

work was supported in part by JSPS KAKENHI (Grant–in–Aid for Scientific Research (B)) Grant Number 26304014, MEXT, Japan.

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