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Population Genetics of the Violet Vinegar Crab (*Episesarma versicolor*) Along the Andaman Sea Coast of Thailand

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Verakiat Supmee, Lertluk Ngernsiri, Ajaraporn Sriboonlert, Passorn Wonnapinij, and Pradit Sangthong (2012) Population genetics of the violet vinegar crab (*Episesarma versicolor*) along the Andaman Sea coast of Thailand. *Zoological Studies* **51**(7): 1040-1050. *Episesarma versicolor* is an important commercial fishery product in Southeast Asia. In Thailand, this species is currently being overexploited. In order to provide necessary information for constructing a species management plan, we performed a population genetic analysis of this species living on the Andaman Sea coast of Thailand. Intraspecific variation was determined from complete sequences of the mitochondrial (mt)DNA control region (CR) with a size of 790-798 bp. MtDNA CR sequences of 72 individuals from 5 west coastal areas of southern Thailand, including Satun, Trang, Krabi, Phang Nga, and Ranong, were analyzed. In total, 62 haplotypes with 58 rare haplotypes were identified. Estimated values of haplotype and nucleotide diversities were 0.978 and 0.007, respectively. Neutrality tests (Tajima's *D* and Fu's F_S statistics) showed that Andaman populations of *E. versicolor* had experienced expansion. However, the analysis of mismatch distribution rejected the sudden expansion model, corresponding to the results of the raggedness indices test and the complex network topology of a minimum spanning network (MSN). The MSN showed 2 major lineages including clade I, a common lineage of *E. versicolor* living on the Andaman coast, and clade II, a Krabi-specific lineage. Estimated values of τ, θ_0, and θ_1, and the MSN topology revealed the direction of expansion as northward along the Andaman coast. The approximate time of the expansion was 10,000 yr ago which was during the post late-glacial period of the Holocene Epoch. An AMOVA analysis showed that most of the genetic variation was due to variations within populations. It also showed a lack of variation among populations. The analysis of pairwise differences (F_{ST}) also showed no statistically significant difference between all possible regional combinations. Based on these results, an absence of a population structure of *E. versicolor* on the Andaman Sea coast was possibly caused either by a high level of gene flow due to the high dispersal ability of this species or expansion experienced throughout its demographic history. Both the historical demography and genetic features of *E. versicolor* on the Andaman Sea coast revealed by this study are necessary information contributing to efficient strategies to conserve this species in Thailand. http://zoolstud.sinica.edu.tw/Journals/51.7/1040.pdf

Key words: Mitochondrial DNA, Control region, Demographic history, Expansion dating, Mangrove crab.

Episesarma versicolor, the violet vinegar crab, is a grapsoid crab belonging to the family Grapsidae. This species generally lives in tropical mangrove swamps. *Episesarma versicolor* is

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an important fishery product and protein source for people living in Southeast Asia, China, and Australia (Carpenter and Niem 1998). In Thailand, *E. versicolor* is generally preserved with salt or fish sauce. This preserved form is an ingredient of many Thai dishes, including papaya salad and pickled crab. Approximately 18,000 tons of *E. versicolor* is annually consumed domestically in Thailand (Tiensongrassamee 2009). *E. versicolor* has a crucial role as a decomposer in mangrove ecosystems by degrading organic matter. Furthermore, its fecal material potentially contributes to secondary production via a coprophagous food chain (Gillikin and Schubart 2004).

In Thailand, *E. versicolor* is mainly found in mangrove swamps located along the Andaman Sea coast (Naiyanetr 2007), from Ranong to Satun Provinces. This mangrove swamp has a total area of 1764.86 km^2 and covers 900 km of the Andaman Sea coast. This area is considered the largest mangrove swamp in Thailand (Juntarashote 2003). It is a major habitat of this species and a main fishery area for local people. The area was reported to have topographic and hydrographic variations (Aungtonya et al. 2000, Plathong and Plathong 2008). These factors may affect genetic variations of this species; however, its genetic features have not yet been reported. Due to dramatic decreases in *Episesarma* populations, especially the population of *E. versicolor*, caused by overexploitation for commercial purposes (Tiensongrassamee 2009), an effective sustainable management strategy is needed. This plan needs to be based on detailed information regarding genetic features and the historical demography of the species.

In this study, we hypothesized that a large number of fragmented mangrove swamps observed along the Andaman Sea coast of Thailand generate genetic variations of *E. versicolor* populations living in this area. In order to obtain information about genetic features of *E. versicolor* within and among fragmented habitats in this area, both the population genetic structure and historical demographics were studied. Since the mitochondrial genome is exclusively maternally inherited with a relatively rapid evolutionary rate and a lack of recombination (Avise 2000), genetic variations within this species were identified by examining the complete sequence of the mitochondrial (mt)DNA control region (CR).

MATERIALS AND METHODS

Sample collection

Seventy-two individuals of *Episesarma versicolor* were collected from 5 mangrove swamps located along the Andaman Sea coast, including Satun (St), Trang (Tg), Krabi (Kb), Phang Nga (Pn), and Ranong (Rn), as shown in figure 1, with the information about these samples reported in table 1. These samples were caught fresh and immediately stored on ice before being transferred to the laboratory and kept at -20°C for further analysis.

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from *E. versicolor* muscle tissue of the 1st or 2nd walking

Fig. 1. Collecting localities for *Episesarma versicolor* on the west coast of southern Thailand along the Andaman Sea. Locality abbreviations are given in parentheses: Satun (St); Trang (Tg); Krabi (Kb); Phang Nga (Pn); Ranong (Rn).

legs using a Genomic DNA Mini Kit (Geneaid, Taiwan) according to the manufacturer's protocol. A complete nucleotide sequence of the mtDNA CR from each specimen was amplified using 2 pairs of overlapping primers.

The 1st primer pair, EVcr_p2H1 5'-AAAACTA TATATTCACACGATGTTCA and EVcr_L1 5'-ACCC ATTAGCTTTAAATTTAGC, was used to amplify the 5' fragment of the mtDNA CR. The 2nd primer pair, EVcr_pLfH1 5'-AAACCTAAGCCAAAATTAAAC and EVcr_p1L1 5'-AAATCAAAATATAATTATTGACCC, was used to amplify the 3' fragment of the mtDNA CR. Each PCR was conducted in a total volume of 50 μl consisting of 5 μl of 10x *Taq* buffer, 5 μl of 25 mM $MgCl_2$, 4 μl of 2 mM dNTPs mix, 2 μl each of 10 μM forward and reverse primers, 0.5 μl of 2.5 units *Taq* DNA polymerase (Fermentas, Lithuania), 5 μl of total DNA (50-100 ng), and 26.5 μl of ultrapure water. The PCRs were performed using the following conditions in a thermocycler (Bio-Rad, USA); initialization at 94°C for 2 min; 35 cycles of 94°C for 30 s, 46°C for 30 s, and 72°C for 1 min; with a final extension at 72°C for 5 min. The PCR products were purified using a Gel/PCR DNA fragment extraction kit (Geneaid) and sequenced by Macrogen (South Korea).

Data analysis and genetic variation study

All amplified partial sequences of each specimen were assembled using CAP3 (Huang and Madan 1999) to construct a complete sequence of the mtDNA CR. Multiple sequence alignments were performed using ClustalW vers. 1.83 (Thompson et al. 1994). All ambiguous positions of the aligned sequences were manually adjusted. Standard indices of genetic diversity including the nucleotide diversity (π) (Nei and Tajima 1981), haplotype diversity (h) (Nei 1987), and mean number of nucleotide differences among all haplotypes were estimated using DnaSP vers. 5.00 (Librado and Rozas 2009).

Population genetic structure and historical demographic analyses

The population genetic structure of *E. versicolor* was primarily determined based on the geographic structure which was divided by either administrative district or latitude. Based on administrative districts, this species was separated into 5 groups: St, Tg, Kb, Pn, and Rn. Based on latitude, this species was separated into 2 groups: a northern group including the Pn and Rn populations and a southern one including the St, Tg, and Kb populations. A hierarchical analysis of molecular variance (AMOVA) was performed with ARLEQUIN vers. 3.5 (Excoffier and Lischer 2010) to compare levels of genetic diversity within and among putative populations. The associated *F*-statistic analogs, including Φ_{CT}, Φ_{SC}, and Φ_{ST}, were estimated at different hierarchical levels. The significance of the Φ-statistic was tested using 10,000 permutations. In addition, genetic distances between all possible combinations of populations (pairwise F_{ST}) were estimated. The

Table 1. Collecting localities, codes of collecting sites, number of individuals per sampling site (*N*), and summary statistics of genetic variability for *Episesarma versicolor* along the Andaman Sea coast (standard deviations in parentheses)

Locality	Code	N	No. of haplotypes	No. of polymorphic sites	Haplotype diversity (h)	Nucleotide diversity (π)
Satun	St	15	14	21	0.924 (0.053)	0.006 (0.001)
Trang	Tg	11	8	13	0.927 (0.066)	0.006 (0.001)
Krabi	Kb	18	18	40	1.000 (0.019)	0.010 (0.001)
Phang Nga	Pn	16	16	36	1.000 (0.022)	0.008 (0.001)
Ranong	Rn	12	12	19	0.985 (0.040)	0.006 (0.001)
Total		72	62	57	0.978 (0.011)	0.007 (0.001)

significance of the pairwise differentiation was tested with 10,000 permutations. The historical demography of *E. versicolor* was examined using 3 different approaches. In the 1st approach, selective neutrality for each sampling locality and for the entire Andaman population were tested using Tajima's *D* (Tajima 1989) and Fu's F_S (Fu 1997) statistics based on 10,000 replicates. Second, a minimum spanning network (MSN) based on the mean number of pairwise differences between all haplotypes of the CR was constructed using ARLEQUIN. Finally, both observed and expected mismatch distributions under the sudden expansion model were estimated. The fit between them was tested using the Harpending raggedness index (Harpending 1994) and the sum of squared deviations (SSD) of the test of goodness-of-fit with 10,000 bootstrap replicates, as implemented in ARLEQUIN. Mutation parameters before and after population growth, θ_0 and θ_1, were estimated. θ_0 and θ_1 were defined as $2Nu$ for mitochondrial loci (Rogers and Harpending 1992), where *N* is the effective female population size. The τ parameter was estimated. The time since population expansion (*T*) was calculated as $T = \tau/2u$ (Rogers and Harpending 1992), where $2u = \mu \times$ generation time × number of bases sequence, where μ is the mutation rate.

RESULTS

CR variation

Sizes of the mtDNA CR complete sequence amplified from each *Episesarma versicolor* individual were in the range of 790-798 bp. The alignment results showed that out of 787 aligned sites, 730 sites were monomorphic, and 57 were polymorphic. Among the 57 polymorphic sites, 33 sites were singleton and 24 sites were parsimoniously informative sites. In total, 62 haplotypes were identified, consisting of 3 shared (VD03, VD06, and VD07), 1 population-specific (VD01), and 58 rare haplotypes (Table 2). The dominant haplotype (VD03) was shared by 4 populations: the St, Tg, Pn, and Rn populations. The VD06 haplotype was shared by the Tg and Rn populations. The VD07 haplotype was shared by the Tg, Kb, and Pn populations. The VD01 haplotype was only found in the Kb population. The number of haplotypes, the number of polymorphic sites, nucleotide diversity (π), and haplotype diversity (*h*) of each population are shown in table 1. The range of haplotype diversity was 0.924-1.000, and that of nucleotide diversity was 0.006-0.010. The overall haplotype diversity was 0.978 ± 0.011, and nucleotide diversity was 0.007 ± 0.001.

Population genetic structure

The AMOVA test results showed that most of the genetic variations of *E. versicolor* were within-population variations. The *F*-statistic analysis showed no significance in either putative structure (Table 3) of single groups or 2-separated population groups, indicating a lack of genetic structure in *E. versicolor* across the Andaman Sea habitat. Pairwise F_{ST} values were negative for all possible population combinations, confirming the lack of population genetic structure of this species across the Andaman Sea coast. These pairwise F_{ST} values are presented in table 4.

Table 2. Haplotype distributions of *Episesarma versicolor* from 5 localities along the Andaman Sea coast. Stations codes are given in table 1

Haplotype	St	Tg	Kb	Pn	Rn	Total
VD01	-	2	-	-	-	2
VD02	-	1	-	-	-	1
VD03	2	3	-	1	1	7
VD04	-	1	-	-	-	1
VD05	-	1	-	-	-	1
VD06	-	1	-	-	1	2
VD07	-	1	1	1	-	3
VD08	-	1	-	-	-	1
VD09	-	-	1	-	-	1

Table 2. (continued)

Haplotype	St	Tg	Kb	Pn	Rn	Total
VD10	-	-	1	-	-	1
VD11	-	-	1	-	-	1
VD12	-	-	1	-	-	1
VD13	-	-	1	-	-	1
VD14	-	-	1	-	-	1
VD15	-	-	1	-	-	1
VD16	-	-	1	-	-	1
VD17	-	-	1	-	-	1
VD18	-	-	1	-	-	1
VD19	-	-	1	-	-	1
VD20	-	-	1	-	-	1
VD21	-	-	1	-	-	1
VD22	-	-	1	-	-	1
VD23	-	-	1	-	-	1
VD24	-	-	1	-	-	1
VD25	-	-	1	-	-	1
VD26	-	-	-	1	-	1
VD27	-	-	-	1	-	1
VD28	-	-	-	1	-	1
VD29	-	-	-	1	-	1
VD30	-	-	-	1	-	1
VD31	-	-	-	1	-	1
VD32	-	-	-	1	-	1
VD33	-	-	-	1	-	1
VD34	-	-	-	1	-	1
VD35	-	-	-	1	-	1
VD36	-	-	-	1	-	1
VD37	-	-	-	1	-	1
VD38	-	-	-	1	-	1
VD39	-	-	-	1	-	1
VD40	-	-	-	-	1	1
VD41	-	-	-	-	1	1
VD42	-	-	-	-	1	1
VD43	-	-	-	-	1	1
VD44	-	-	-	-	1	1
VD45	-	-	-	-	1	1
VD46	-	-	-	-	1	1
VD47	-	-	-	-	1	1
VD48	-	-	-	-	1	1
VD49	-	-	-	-	1	1
VD50	1	-	-	-	-	1
VD51	1	-	-	-	-	1
VD52	1	-	-	-	-	1
VD53	1	-	-	-	-	1
VD54	1	-	-	-	-	1
VD55	1	-	-	-	-	1
VD56	1	-	-	-	-	1
VD57	1	-	-	-	-	1
VD58	1	-	-	-	-	1
VD59	1	-	-	-	-	1
VD60	1	-	-	-	-	1
VD61	1	-	-	-	-	1
VD62	1	-	-	-	-	1
Total	15	11	18	16	12	72

Demographic history

Two methods of neutrality tests, Tajima's *D* and Fu's F_S statistics, were applied to examine the historical demography of this species for each population and for all populations pooled together. Results of these analyses are shown in table 5. Tajima's *D* statistics of the 4 populations of St, Kb, Pn, and Rn populations, were statistically non-significantly negative, whereas this statistic for the Tg population was statistically non-significantly positive. However, when all populations were pooled together, the *D* statistic was statistically significant. Fu's F_S statistics of all 5 populations were negative, but only 4 populations (St, Kb, Pn, and Rn) were statistically significant. The F_S statistic of the pooled population was a statistically significant negative value. According to the measured SSD from the goodness-of-fit test, the mismatch distribution observed from the pooled population did not fit a sudden expansion model, although those of each population could not reject the model. The Harpending raggedness indices were non-significant low values (Table 5). The MSN displayed a complex network topology, including both distantly related haplotypes and separated haplotype lineages (Fig. 2). Two major clades of haplotypes were identified. Clade I was composed of 42 haplotypes from all populations, except the Kb population. Every clade I haplotype was centered on haplotype VD03 which was a common haplotype of this clade and all populations living on the Andaman Sea coast. Clade II was composed of 20 haplotypes: 1 shared haplotype

Table 3. Hierarchical analysis of molecular variance of *Episesarma versicolor*

Source of variation	*d.f.*	Sum of squares	Variance components	Percentage of variation	*p* value
1) Single region					
Among populations	4	9.396	-0.056 Va	-1.80	Φ_{ST} = -0.018 (p = 0.837)
Within populations	67	210.590	3.143 Vb	101.80	
Total	71	219.986	3.088		
2) Upper and lower regions					
Among groups	1	3.499	0.046 Va	1.48	Φ_{CT} = 0.148 (p = 0.201)
Among populations within groups	3	5.897	-0.083 Vb	-2.68	Φ_{SC} = -0.027 (p = 0.952)
Within populations	67	210.590	3.143 Vc	101.20	Φ_{ST} = -0.012 (p = 0.832)
Total	71	219.590	3.106		

Table 4. Population pairwise F_{ST} values (p values in parentheses). Station codes are given in table 1

	St	Tg	Kb	Pn	Rn
St	-				
Tg	-0.019 (0.501)	-			
Kb	-0.025 (0.853)	-0.032 (0.892)	-		
Pn	-0.024 (0.700)	-0.005 (0.408)	-0.006 (0.483)	-	
Rn	-0.026 (0.634)	-0.007 (0.389)	-0.005 (0.415)	-0.029 (0.856)	-

(VD07), 1 haplotype from the Tg population (VD05), 1 haplotype from the Rn population (VD45), and 17 unique haplotypes from the Kb population. The topology of clade II clearly showed that the central haplotype was VD07, which is a single shared haplotype of the clade. Interestingly, every haplotype from Kb specifically belonged to clade II. The closest connection between these 2 clades was a single mutation step that distinguished between VD03 and VD07. The estimated θ_1 was higher than θ_0 for every sampling location, especially northern Andaman populations (Table 5). The initiation time of this species' population expansion across the Andaman Sea coast was approximately 10,000 years ago. This initiation time was estimated from the mutation rate of 19% per million years with a generation time of 1 year. Due to a lack of fossil records of grapsoid crabs, this mutation rate of the mtDNA CR was estimated from fossil records of a closely related shrimp, *Farfantepenaeus aztecus* and *Litopenaeus setiferus* (McMillen-Jackson and Bert 2003).

DISCUSSION

Mangrove swamps along the Andaman Sea coast are considered the largest mangrove ecosystems in Thailand and provide appropriate habitat for several faunas, including *Episesarma versicolor* (Juntarashote 2003, Thampanya et al. 2006, Panjarat 2008). Specimens of this species used in this study were collected from 5 locations throughout the area, thus supporting the Andaman Sea coastline being the main natural habitat of *E. versicolor* (Chuensri 1982, Naiyanetr 2007).

A pattern of genetic diversity within the Andaman population of *E. versicolor* presented a high value of haplotype diversity but a low level of nucleotide diversity. This pattern was reported as a typical character of genetic variations of crustacean species (Kong et al. 2010, Chu et al. 2012). Regarding the population genetic theory, this pattern can be generated by an accumulation of new mutations in a rapidly expanding population (Watterson 1984). The result of this study is consistent with the theory which states the recent population expansion of *E. versicolor* along the Andaman Sea coast occurred approximately 10,000 yr ago. Both Tajima's D and Fu's F_S statistics of the pooled population were negative and statistically significantly deviated from a neutral state. In the case of Tajima's *D* test, the statistically significant negative value might have been caused by purifying selection, the presence of slightly deleterious mutations, or a population expansion (Yang 2006). On the other hand, the statistically significant negative value of Fu's F_S statistics indicated population expansion, because this test is a powerful statistical test for detecting demographic expansion, especially from non-recombinant genetic data (Ramírez-Soriano et al. 2008). However, the fit of the sudden expansion model to the demographic history of the Andaman *E. versicolor* population was rejected by a goodness-of-fit test. The result of the statistical test was supported by the complex topology of the MSN. This network showed that southern populations, including the St, Tn, and Kb populations, consisted of long haplotype lineages, presenting multiple mutational steps from the common haplotype. In contrast, most haplotypes of the northern populations, including the Pn, Ng, and Rn populations, were directly connected to the common haplotype by a single or only a few mutational steps. These results indicated that the southern populations have a longer demographic history than northern populations. The different time periods of the demographic history between the southern and northern populations, for which

Table 5. Parameter indices of the mismatch distribution analysis. Station codes are given in table 1

Locality	Tajima's *D*	Fu's F_S	τ	θ_0	θ_1	SSD	Raggedness
St	-0.493	-8.364*	9.539	0.002	10.147	0.034	0.039
Tg	0.321	-1.594	8.027	0.000	9.204	0.031	0.058
Kb	-1.141	-11.982*	3.289	5.838	99,999.00	0.012	0.017
Pn	-1.292	-10.792*	1.365	6.813	99,999.00	0.045	0.093
Rn	-0.906	-8.114*	2.500	3.045	99,999.00	0.021	0.051
Total	-1.765*	-25.196*	1.652	0.000	99,999.00	0.147*	0.015

* $p < 0.05$.

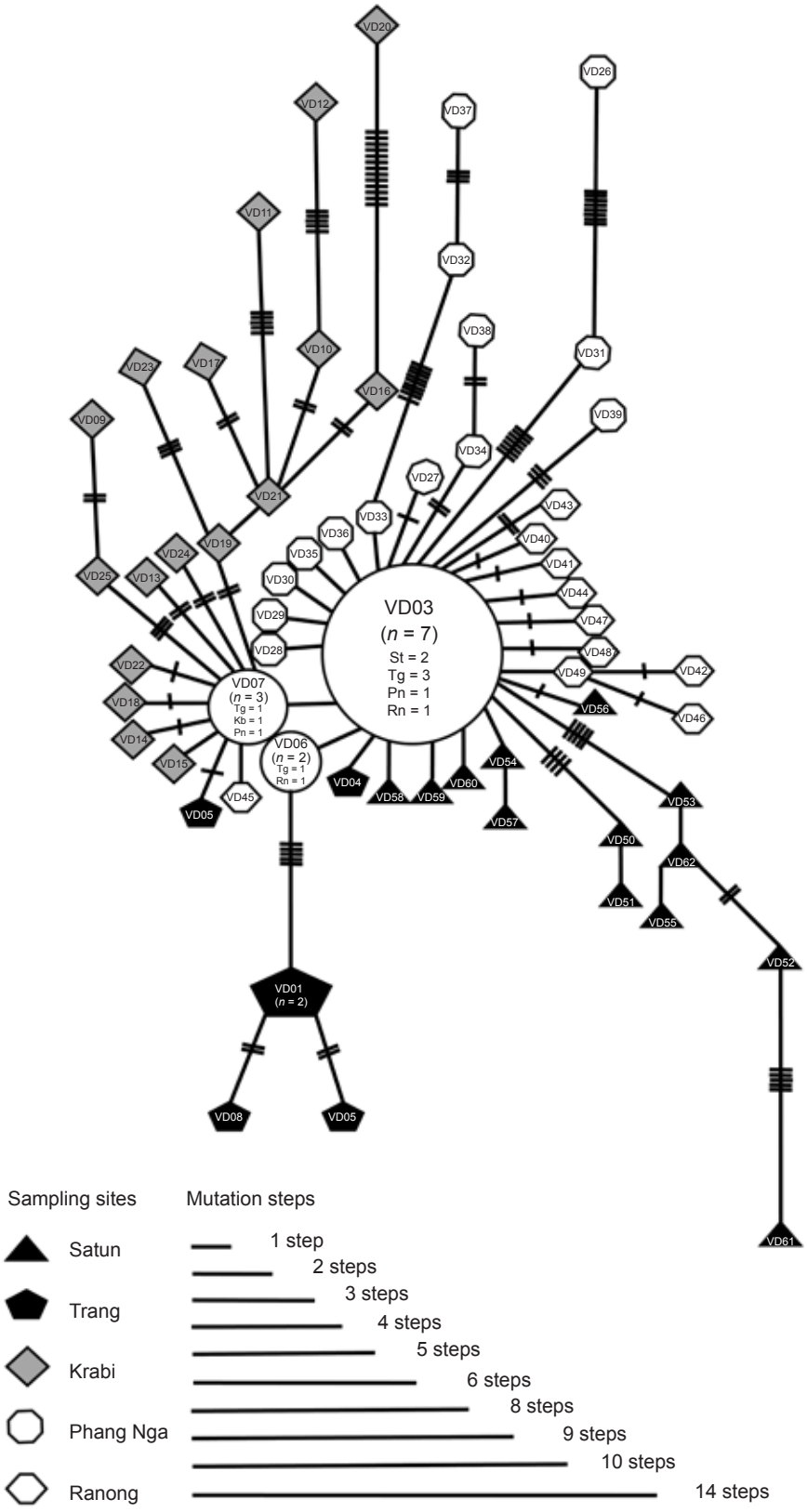

Fig. 2. Minimum spanning network of 62 mitochondrial haplotypes of *Episesarma versicolor*. Sizes of the circles are proportional to the frequency of the haplotypes. Vertical bars on the line indicate the number of substitutions separating 2 haplotypes. A lack of vertical bars on the line connecting haplotypes indicates that a single substitution separates the 2 haplotypes.

the time period of the southern populations is longer than that of the northern populations, also indicated that the direction of expansion was northward along the Andaman Sea coast. τ values also confirmed the direction of the population expansion by presenting a decreasing south-to-north pattern. In addition, there is a vast difference in θ_1 values between the southern and northern populations, and northern populations have a larger value than southern populations. This result indicated that the effective female population size has dramatically increased particularly in northern habitats. Results of the mismatch distribution analyses indicated the northward expansion of *E. versicolor* along the Andaman Sea coast. The demography of *E. versicolor* from the Andaman Sea displayed an uncommon pattern of demographic history for marine species which are usually described as a sudden demographic expansion (McMillen-Jackson and Bert 2003, Sotelo et al. 2009). The pattern of *E. versicolor*'s demography along the Andaman coast may have developed under the influence of geographic events since the early period of dispersal.

The expansion of the *E. versicolor* population along the Andaman Sea coast was estimated to have occurred around 10,000 yr ago, during the early Holocene epoch (Gradstein et al. 2004). This period was in the post-glacial period when the sea level had risen, remained at a high level until the middle Holocene Epoch, then fallen from the mid- to the late Holocene Epoch (Scoffin and Tissier 1998, Horton et al. 2005, Woodroffe and Horton 2005). These changes in sea levels resulted in a progradation of mangroves across the bays (Tanabe et al. 2003, Rhodes et al. 2011). Therefore, populations of *E. versicolor* possibly expanded concomitantly with habitat expansion. The estimated time of the population expansion obtained in this study supported diversification of marine species in Southeast Asia having been generated by environmental factors during 2.4 million to 10,000 years ago (McMillan and Palumbi 1995, Panithanarak et al. 2010). Changes in sea levels during the Pleistocene and Miocene periods, after approximately 1.81 mya (Gradstein et al. 2004) affected the diversification of *E. versicolor* on the Andaman Sea coast and also diversification of other species: for example, other marine species and freshwater decapod species living along the Atlantic-Mediterranean transition area (Garcia-Merchan et al. 2012), fiddler crabs in the northern Gulf of Mexico (Thurman 2003), Mud crab, *Scylla paramamosain*, living along the Chinese coasts of the South China and East China Seas (He et al. 2010), and freshwater white-clawed crayfish (*Austropotamobius italicus italicus*) of the Iberian Peninsula (Pedraza-Lara et al. 2010).

Both the AMOVA and pairwise F_{ST} results showed a lack of population genetic structure of *E. versicolor* along the Andaman coastline of Thailand. These results suggest that there is only 1 population of *E. versicolor* across 900 km of the Andaman coastline. The lack of genetic variation was also reported in populations of other mangrove crabs, *Ucides cordatus* (Oliveira-Neto et al. 2007), *S. serrate* (Fratini et al. 2010), *Neosarmatium meinerti* (Ragionieri et al. 2010), and *Uca annulipes* (Silva et al. 2010). There are 2 main factors which maintain genetic homogeneity between long-distance and separated habitat populations: a high level of gene flow and having experienced demographic expansion. Both *N. meinerti* and *Uca annulipes* populations were maintained on the East African coast as a single population by high levels of gene flow across a 3000-4000-km coastline (Ragionieri et al. 2010, Silva et al. 2010). There are 2 main factors providing gene flow between populations: biological factors and oceanographic factors (Bucklin et al. 1997, Demarchi et al. 2010). In the case of mangrove crabs, biological factors are the larval and adult behaviors, e.g., larval exportation behavior during ebb tides (Drake et al. 1998, Paula et al. 2007). The experienced demographic expansion could also have generated a single population. If the species experienced a recent population bottleneck, this mechanism will generate a single population; for example, the population of *U. cordatus* living along the Brazilian coast (Oliveira-Neto et al. 2007) and *S. serrata* living in the western Indian Ocean (Fratini et al. 2010). According to the evidence of gene flow among the Andaman Sea habitats of crustaceans (Wanna et al. 2004) and molecular evidence indicating the expansion experience discussed above, both gene flow and historical demography should have contributed to the genetic features of *E. versicolor* on the Andaman Sea coast.

CONCLUSIONS

In this study, 72 nucleotide sequences of the mtDNA CR with a size of approximately 800 bp were analyzed to determine genetic variation and historical demography of *Episesarma versicolor* living along the Andaman Sea coast of Thailand. The statistical results of multiple tests indicated

a lack of population structure and the northward direction of population expansion of this species in this area. Our findings suggest that local populations are demographically related and have substantially exchanged both larvae and post-larvae individuals among various habitats. These results should provide necessary information for constructing effective sustainable management strategies that will help recolonize this species across the Andaman east coast and reduce overexploitation of this species in this area.

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