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Genetic variation of the viviparid snail, *Sinotaia quadrata* (Gastropod: Viviparidae), in Taiwan

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ABSTRACT

Allozyme electrophoresis was used to assess the genetic variation and population structure of a Taiwanese viviparid snail, *Sinotaia quadrata*. Five of 17 loci were polymorphic, but a deficiency of heterzygotes for all loci was observed. Values for Nei's genetic distances among the six populations were small, with a mean value of 0.0061. The phenogram constructed using the UPGMA method revealed that the six groups of viviparids could be clustered into northern and southern–eastern groups. The fixation index (*Fst*) was low (mean = 0.056), and the effective number of migrants was high (*Nm* = 6.5846). However, no correlation between genetic distance and geographical distance was detected (r^2 = 0.0636, *p* = 0.364). Gene flow probably due to aquaculture activities has resulted in high genetic similarity among populations of *S. quadrata*.

Key words: Viviparid, *Sinotaia quadrata*, Allozyme, Genetic variation, Phylogeography.

INTRODUCTION

Population genetics is concerned with the distribution of genetic variability within and among populations (Avise, 2000). Two competing hypotheses, vicariance and dispersal, attempt to account for the current distribution patterns of spatially disjunct taxa (Ronquist, 1997). Under the dispersal view, taxa occupying the present distribution ranges originated by active or passive dispersal from their ancestral origins. Under the vicariance interpretation, the distribution of organisms may have occurred due to separation by environmental events (Briggs, 1974). These two hypotheses can be examined by genetic population structure using molecular evidence (reviewed in Avis, 2000). The distribution patterns of aquatic organisms are related to physical subdivisions within water bodies. For example, the genetic structure of freshwater fish in Taiwan suggests the importance of Pleistocene glacial events in shaping their distribution in Taiwan (Wang *et al*., 1999; Wang *et al*., 2000). The geographic events are also related to the zoogeographic provinces of the island of Taiwan; they can be differentiated by the multispecies distribution patterns of freshwater fish fauna (Tzeng, 1986). In contrast to fishes, freshwater viviparid snails, which possess both characters of low mobility as adults and brooding in the larval stage, have a low dispersal ability (Pace,1973; Calow and Calow, 1983). In addition, the possibility of gene flow is increased because this

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viviparid, a common aquaculture species, has frequently been transported by humans.

Different dispersal abilities derived from various life histories might be reflected in studies of the population structure. Although research on population genetics of fish has been undertaken, to date, similar investigations using aquatic invertebrates with low mobility as the study materials are few in Taiwan.

This is a study of the genetic structure of a Taiwanese freshwater snail, *Sinotaia quadrata*, that is commonly distributed in lakes, ponds, rice paddies, irrigation canals, and streams (Pace, 1973). *Sinotaia quadrata* has developed as a dominant by-product of corbicula cultures for food purposes (Chiu *et al*., 2002a). Chiu (2002b) used allozymes to examine the genetic variation of *Cipangopaludina* spp. in Taiwan and detected a very low genetic difference within the species. Allozyme electrophoresis has been successfully used to detect genetic variations within and among European viviparids at the species level (Katoh and Foltz, 1994; Falniowski *et al*., 1996; Chiu *et al*., 2002b). In this study, we used allozymes as genetic markers for investigating the degree of geographic divergence among six populations of *S. quadrata*. We estimated gene frequencies of enzyme loci in six populations located in Taiwan. Using *F* statistics to estimate the degree of genetic divergence among populations, we then calculated genetic distances among populations and examined their correlations with linear geographic distances. Finally, we summarize the results by depicting the biogeographical pattern of *S. quadrata*.

MATERIALS AND METHODS

Distribution, habitat characteristics, and sample collection

Snails were collected at six sampling locations in Taiwan from various habitats including ponds, drainage canals, lakes, and rivers. Habitat information and localities are listed in Table 1. In 1998, 30 mature individuals were collected from each locality. In total, 136 adult *Sinotaia quadrata* were collected and kept frozen at –80 °C for electrophoresis.

Eletrophoretic procedures

Procedures for tissue extraction by horizontal starch-gel electrophoresis were modified from Chiu *et al*. (2002b). Foot tissue of 0.2-0.5 g was homogenized with an equal volume of extraction buffer, containing 10 mM Tris-HC1 (pH 7. 0), 1 mM EDTA, and 0.05 mM NADP (Pasteur *et al.,* 1998) in an ice bath. Homogenates were centrifuged at 17,000 *g* for 40 min at 4 °C, and the supernatants were stored at –70 °C until used for electrophoresis.

Horizontal starch-gel electrophoresis was carried out with Tris-citrate pH 8.0 (Selander *et al.,* 1971) and CAAPM buffer systems (Clayton and Tretiak, 1972), followed by staining of the 17 loci (Table 2). Detailed enzyme-staining recipes followed those of Richardson and Bavoerstack (1986) and Murphy *et al*. (1996). Multiple loci encoding the same enzyme (allozymes) were labeled with consecutive numbers so that the most-anodal end was designated as "1". The electrophoretic bands corresponding to multiple alleles at each locus were assigned consecutive numbers according to their relative electrophoretic mobility, with the dominant allele designated as 100.

Statistical analyses

Allelic frequencies were calculated using the BIOSYS-I computer package (Swofford and Selander, 1989). In order to quantify the genetic variation of specimens from each locality, the population genetic variability was determined using the mean number of alleles per locus, the mean effective number of alleles per locus (Hartle and Clark, 1989), the percentage of polymorphic loci at the 0.95 criterion, and the average observed

Table 1. Collection sites, habitat descriptions, and allelic frequencies at five polymorphism loci for six samples of *Sinotaia quadrata*. (*, ** significant deviation from the Hardy-Weinberg proportion at $p < 0.05$ and $p < 0.01$, respectively).

Locality		Dahu 121°35' E 25°05' N	Dahanshi 121°25' E 25°00' N	Jubei 121°00' E 24°52' N	Puli 120°28' E 23°25' N	Juchi 121°05' E 23°50' N	Shoufeng 121°00' E 24°52' N
Habitat		lake	river	pond	irrigation canal	irrigation canal	pond
No. of snails		30	30	30	30	30	30
Locus	Allele						
AAT-1	100	0.733	0.867	0.750	0.700	0.633	0.650
	79	0.267	0.133	0.250	0.300	0.367	0.350
		**	**	*	*	**	**
AAT-3	100	1.000	1.000	0.917	1.000	1.000	1.000
	92	0	0	0.083	0	0	0
				*			
AK	111	0.350	0.317	0.133	0.567	0.567	0.650
	100	0.650	0.683	0.867	0.433	0.433	0.350
		**		*		**	
EST-1	100	0.900	1.000	0.900	0.933	0.95	0.883
	94	0.100	0	0.100	0.067	0.05	0.117
						**	**
EST-2	120	0	0.033	0	0.017	0	0.050
	100	1.000	0.967	1.000	0.983	1.000	0.950
			**				**

and expected heterozygosities per locus, according to Nei (1978). Chi-square goodness-of-fit tests were computed to determine if there were significant deviations from the Hardy-Weinberg equilibrium between the observed and expected heterozygosities. To determine genetic relationships among populations, Nei's (1978) unbiased genetic distances (D) were calculated, and a phenogram was constructed by the UPGMA method using PHYLIP 3.5 (Felsenstein, 1993). The fixation index (*Fst*) of Wright (1978) was utilized as a measure to indicate the degree of genetic divergence, found at a locus among local populations. Additionally, we calculated the effective number of migrants (*Nm*) to estimate gene flow (Slatkin and Barton, 1978) among *S. quadrata* populations.

RESULTS

Genetic variation

Seventeen loci were observed from ten enzymes (Table 2). Numbers of loci for each enzyme ranged from three to one. Twelve of the 17 loci were monomorphic (AAT-2, ARK-1, ARK-2, GAPD, GPI, IDH1, IDH-2, MDH–1, MDH–2, MPI-1, MPI-2, and 6PGDH). The remaining 5 loci of AAT-1, AAT-3, AK, EST-1, and EST-

Table 2. Enzymes, enzyme abbreviations, enzyme commission numbers (E.C.), number of loci, and the most-effective buffer systems resolved for *Sinotaia quadrata*.

Enzyme	Abbreviation	E.C. no.	No. of loci	Buffer system
Aspartate aminotransferase	AAT	2.6.1.1	3	CAAPM 6.0
Adenylate kinase	AK	2.7.4.3	1	CAAPM 6.0
Arginine kinase	ARK	2.7.3.3	2	CAAPM 6.0
Esterase	EST	3.1.1.	2	CAAPM 6.0
á-Glycerophosphate dehydrogenase	GAPDH	1.2.1.12	1	TC 8.0
Glucose-6-phosphate	GPI	5.3.1.9	1	TC 8.0
Isocitrate dehydrogenase	IDH	1.1.1.42	2	TC 8.0
Malate dehydrogenase	MDH	1.1.1.37	2	TC 8.0
Mannose-6-phosphate isomerase	MPI	5.3.1.8	2	TC 8.0
Phosphogluconate dehydrogenase	6PGDH	1.1.1.44	1	TC 8.0

2 shown in Table 1 were polymorphic. There were deviations from the Hardy-Weinberg equilibrium at the AAT-1 locus in samples from all locations; at the AAT-2 locus in the sample from Jubei; and at the AK locus in samples from Jubei, Juchi, and Dahu. EST-1 in samples from Juchi and Shoufeng, and EST-2 in samples from Shoufeng and Dahu also deviated from the Hardy-Weinberg equilibrium (Table 1).

Indices of genetic variability are given in Table 3. Percentage of polymorphic loci ranged from 17.65% (Juchi, Dahu, and Dahanshi) to 29.41% (Shoufeng); the mean number of alleles per locus ranged from 1.176 (Dahu) to 1.294 (Shoufeng). The mean heterozygosity per locus ranged from 0.026 (Juchi and Dahanshi) to 0. 057 (Puli), indicating a general deficiency of heterzygotes (Table 3).

Genetic distances and the phenogram

Genetic distances among the six populations of *S. quadrata* ranged from 0.0003 between Puli and Juchi, to 0.0182 between Jubei and Shoufeng, with a mean of 0.0061 (Table 4). The assumed genetic relationships were based upon a phenogram drawn with the commonly used UPGMA method. The UPGMA phenogram of *S. quadrata* mainly consisted of two clusters: 1) northern and 2) southern – eastern, with samples from northern locations of Jubei, Dahu, and Dahanshi separated from those of Shoufeng, Juchi, and Puli (Fig. 1). In the first cluster, samples from Dahu and Dahanshi constitute a subcluster, which then clusters with Jubei. In the second cluster, Juchi and Puli constitute a subcluster, which then clusters with Shoufeng.

Relationships between genetic distance (vertical axis) and geographic distance

(horizontal axis) among populations are shown in Fig. 2. The result indicates no correlation between genetic distance and geographical distance ($r^2 = 0.0636$, $p = 0.364$).

Genetic differentiation in *S. quadrata*

The fixation index (*Fst*) was calculated according to Wright (1978) as shown in Table 5. A fixation index (*Fst*) of 1 indicates that there is a characteristic allele of a definite locus among one or more populations. In our study, the fixation index of the 12 monomorphic loci, AAT-2, ARK-1, ARK-2, GAPD, GPI, IDH1, IDH-2, MDH–1, MDH–2, MPI-1, MPI-2, and 6PGDH, were zero. There is evidence that the higher fixation index is, the more advanced the divergence of the locus. The most advanced locus was the AK locus which had an *Fst* value of 0.131. The *Fst* value of the other four loci ranged from 0.023 to 0.070, all of which were lower than 0.1. The average value of *Fst* was 0.056 (Table 5). *Nm* ranged from 1.655 to 10.605 with an average of 6.5846 which suggests a high level of gene flow among populations ($Nm > 1$) (Table 5) (Slatkin and Barton, 1978).

DISCUSSION

Genetic variation of *Sinotaia quadrata*

The slight genetic difference among populations of *S. quadrata* we studied is similar to that shown in the confamily *Cipangopaludina chinensis* (Chiu *et al*., 2002b) indicating high gene flow among populations. However, the phenogram based on Nei' s genetic distances showed that the two geographical clusters were separated by a very small genetic distance.

Indices of genetic variability revealed low genetic variations within populations. The indices of genetic variability, the percentage of polymorphic loci, the mean number of alleles per locus, and the mean heterozygosity were slightly higher than those of *Cipangopaludina chinensis* as examined by Chiu *et al*. (2002b). A general deficiency of heterzygotes was also indicated (Table 3). Bottleneck events or the founder effect might account for the low genetic variation. For example, the low genetic variabilities of primary freshwater fish are due to the founder effect and bottleneck events during the recent glacial epochs (Wang *et al*. 1999).

Genetic relationship among populations of *S. quadrata*

Nei' s genetic distances showed small divergences among populations (0.0003-0.0182) which were considerably smaller than those for *Viviparus georgianus* (0.00-0.06) (Katoh and Foltz, 1994) and *V. contectus* (0.00-0.04) (Falniowski *et al*., 1996). Small genetic distances were also found among Taiwanese populations of *Cipangopaludina chinensis* (0.002-0.006) (Chiu, 2002 b). The genetic distances among populations of *S. quadrata* in Taiwan are smaller than those reported for other species of viviparids.

This distribution pattern is consistent with that of freshwater fishes. (Wang *et al*. 1999; Wang *et al*. 2000). According to the phenogram, two groups, i.e., northern and southern – eastern, were clustered together. Samples of Dahu and Dahanshi are closely related, because Dahu and Dahanshi are located in the same drainage area of the Taipei Basin. Jubei is located in the drainage area of the Touchien River. The remaining the three populations form a sister group to the northern group. Samples from Puli (central area) and Juchi (southern area) were clustered and had the smallest genetic distance in this study (0. 0003). Puli and Juchi are located in the Choshui River and Pajang River drainage areas, respectively, and both are located in the same biogeographical province (Wang *et al*., 1999). This result is consistent with that of Wang *et al*. (1999) and Wang *et al*. (2000). Specimens from Shoufeng were clustered with those from Puli and Juchi and possessed very small genetic distances

Table 3. Estimates of genetic variability calculated for each of the six populations of *Sinotaia quadrata*; standard errors are in parentheses.

Locality	Dahu	Dahanshi	Jubei	Puli	Juchi	Shoufeng
No. of snails	30	30	30	30	30	30
Percent of polymorphic loci (95%)	17.65%	17.65%	23.53%	23.53%	17.65%	29.41%
Mean no. of alleles per locus	1.176	1.177	1.235	1.235	1.177	1.294
	(0.393)	(0.393)	(0.437)	(0.437)	(0.393)	(0.470)
Mean effective no. of alleles per locus	1.100	1.067	1.077	1.110	1.114	1.124
	(0.249)	(0.194)	(0.164)	(0.282)	(0.304)	(0.276)
Mean observed heterozygosity	0.029	0.026	0.035	0.057	0.026	0.043
	(0.067)	(0.089)	(0.070)	(0.141)	(0.066)	(0.103)
Mean expected heterozygosity	0.061	0.044	0.056	0.064	0.063	0.076
	(0.146)	(0.118)	(0.113)	(0.154)	(0.161)	(0.156)

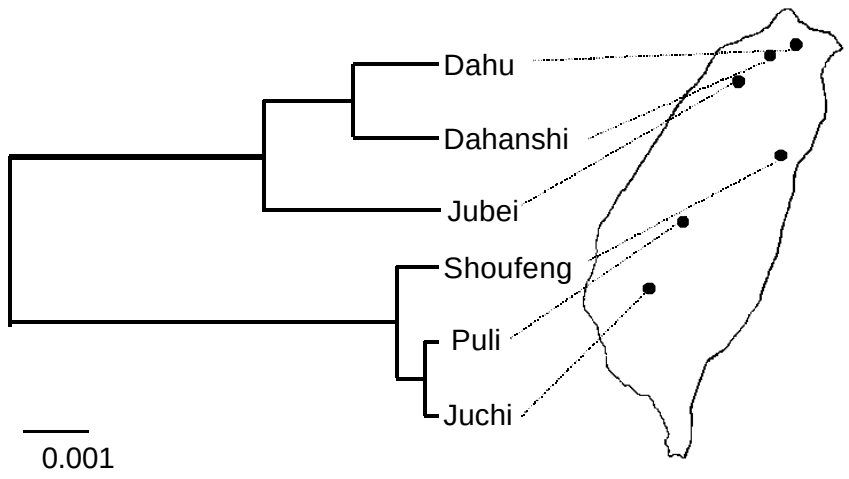

Figure 1. UPGMA phenogram of Nei' s (1972) genetic distances (D), among six populations of *Sinotaia quadrata*.

Table 4. Nei' s (1972) genetic distances among six populations of *Sinotaia quadrata*.

	Dahu	Dahanshi	Jubei	Puli	Juchi	Shoufeng
Dahu	-					
Dahanshi	0.0018	-				
Jubei	0.0034	0.0040	-			
Puli	0.0031	0.0059	0.0125	-		
Juchi	0.0037	0.0075	0.0133	0.0003	-	
Shoufeng	0.0064	0.0108	0.0182	0.0009	0.0009	-

Table 5. Fixation index of six populations of *Sinotaia quadrata.*

Locus	*Fis*	*Fit*	*Fst*	*Nm*
AAT-1	0.515	0.530	0.029	8.258
AAT-3	0.346	0.392	0.070	3.300
AK	0.309	0.400	0.131	1.655
EST-1	0.236	0.254	0.023	10.605
EST-2	0.653	0.662	0.027	9.105
Average	0.411	0.447	0.056	6.585

(0.0009 and 0.0009). This result does not support the concept that the Central Mountain Range was an important barrier restricting gene flow between western and eastern populations as has been postulated for many primary freshwater fishes (Tzeng, 1986; Wang *et al*. 1999). The origin of the population in eastern Taiwan is still controversial. According to the record of Pace (1973), *S. quadrata* was absent from eastern Taiwan. However, we collected specimens from Shoufeng, near corbicula farms. We suspect that this population may have been carried by humans to eastern Taiwan for aquaculture purposes.

Gene flow among populations

Small genetic distances are considered to be correlated with high gene flow among populations. Values of *Fst* range from 1 to 0. An *Fst* of 1 indicates an absolute subdivision among populations; and an *Fst* of 0 indicates no subdivision at all among populations. In our study, *Fst* averaged 0.056 and indicated little subdivision among populations. The estimated gene flow (*Nm*) ranged from 1.655 to 10.605 with average of 6.585 which is much higher than 1. High values of *Nm* indicate a high level of gene flow among populations (Slatkin and Barton, 1978).

We plotted the genetic and geographical distances among populations (Fig. 2). The results indicate no significant correlation between genetic and geographical distances. The strong gene flow among *S. quadrata* populations does not reflect the geographic distances. This result is counter to the one-dimensional stepping stone model (Kimura and Weiss,1964), which only allows for migration to adjacent populations, and in which genetic divergence is positively correlated to geographical distance.

Patterns of biogeography of *S. quadrata*

The genetic structure of *Sinotaia quadrata* in Taiwan is in agreement with the biogeography of two freshwater cyprinids, *Zacco pachycephalus* and *Acrossocheilus paradoxus*, the latter having been affected by Pleistocene glaciation events (Wang *et al*., 1999; Wang *et al*., 2000). The viviparids studied in the present work, once assumed to be isolated populations, show high similarity among the populations. This was the result of a recent event of strong gene flow which may have been driven by human activity for commercial purposes.

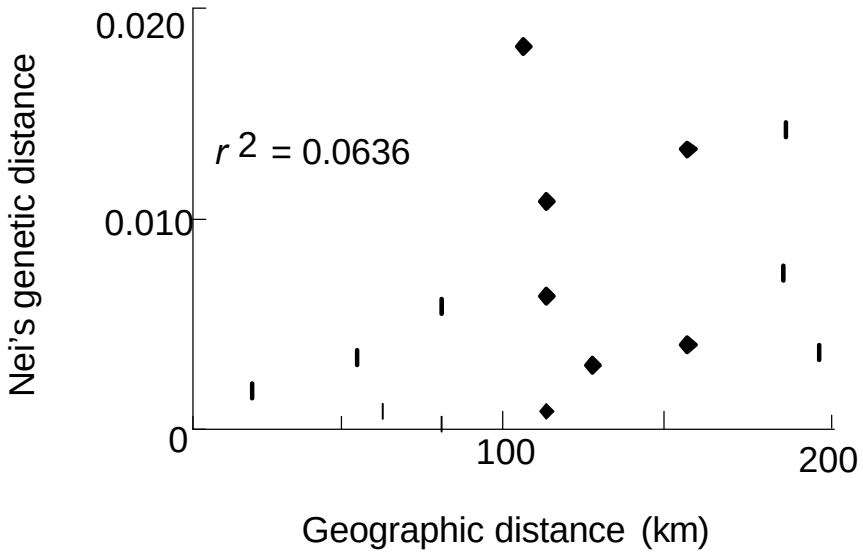

Figure 2. Relationships between Nei's genetic distances and geographical distances separating *Sinotaia quadrata* populations.

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台灣產石田螺 (*Sinotaia quadrata*; Gastropod: Viviparidae) 的遺傳變異

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本文以同功酶水平電泳對台灣地區石田螺進行遺傳變異及親緣地理學的研究。17個基因座中共偵測到五個多型性的基因座，並且普遍有異型結合子缺乏的情形。雖然，六個族群間的遺傳距離相當低(平均值 0.0061)，但是，由遺傳距離所建構的 UPGMA 圖所可以分為兩大群，北部群及南部-東部群。族群間表現了相當低的固定指數 (fixation index) (平均 Fst = 0.056)及高的有效遷移族群 (平均 Nm = 6.5846)，證明族群間有高度的基因交流。然而，遺傳距離與地理距離並無顯著相關(r^2 = 0.0636, p = 0.364)，這個族群間的高相似度可能是由於近代人為養殖活動的攜帶抵消了地理事件所造成遺傳結構所致。

關 鍵 字: 田螺、石田螺、同功酶、遺傳變異、親緣地理學