# Systematic Studies of the Genus Cobitis (Pisces: Cobitidae) in Korea IV. Introgressive Hybridization between Two Spined Loach Subspecies of the Genus Cobitis

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Since early 1930' Cobitis taenia striata were introduced to the Dongjin in Chollabukdo, where it hybridized with an endemic subspecies C. tlutheri. Protein electrophoresis revealed high levels of hybridization with intensive backcrossing occupied approximately 20 kilometers of the river. This is roughly one-half of teh historic range of the endemic species. The average frequency of introduced alleles of three diagnostic loci ranged 0.03-0.46 among 11 sites in teh sympatric area. Clinal patterns in allele frequencies suggest C. t. striata were introduced in an upper reaches of the Dongjin and downstream dispersal of the introduced alleles followed. There is little linkagedisequilibrium between the diagnostic loci, suggesting the nuclear genomes of teh two subspecies are randomly associated. The evidence presented here and previously supports recognition of C. t. striata and C. t. lutheri as the typical subspecies.

KEY WORDS: Hybridization, Introgression, Electrophoresis, Cobitidae, Cobitis taenia lutheri, Cobitis taenia striata.

Hybrids have always been of intense interest to the biologist, particularly they are sometimes seen as antithetical to the biological species concept of reproductively isolated entities (Ferguson, 1980). On the systematic level, narrow zones of the hybridization pose a problem in defining species limits. Extensive interbreeding of allopatric populations in contact zone is generally accepted as conspecific (Yang and Selander, 1968). Hybrids are frequently morphologically intermediate between parental species, but morphological characters are usually polygenically controlled and often have environmentally observed variability. If they are formed between similar or sibling species,

C. t. striata and C. t. lutheri were classified as

where seperation of the parental species may be difficult(Hunt and Selander, 1973; Moran, 1979; Learly et al., 1984), then identification of the hybrid can present problems to the systematist. In a few cases the hybrid may be morphologically indistinguishable from one of the parents (Ferguson, 1980; Gyllensten et al., 1985). Consequently protein differences between parental types are extremely valuable in detecting hybridization and introgression. Genotype proportions and frequency of markers in the parental types provide information about past and current patterns of successful mating in the genetic composition of the populations (Avise and Saunder, 1974; Wake et al., 1980; Dowling and Moore, 1984).

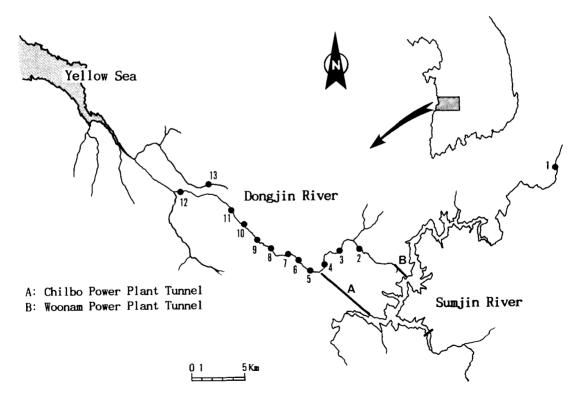
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subspecies of C. taenia by their distinct differences in body color pattern and allopatric distribution (Kim, 1980). In 1931 and 1945, two power plants were constructed at the upstream of the Dongjin that used water diverted from the Sumjin to generate electricity. As a result several fish species native to the Sumjin were introduced to the Dongjin. Kim and Lee (1984) reported a possibility of intergradation between the endemic spotted spine loach, C. t. lutheri and an introduced population of the stripped spine loach, C. t. striata. Most subspecies with substantial genetic difference have been described (Avise and Smith, 1974; Learly et al., 1983). Many of these have come into secondary contact due to human activities. This provide a valuable opportunity to examine the differences between subspecies that had substantial genetic divergence before secondary contact. Studying hybridization with introduced organisms allow assessments of evolutionary dynamics in the early stages of secondary contact between previously allopatric forms (Echelle and Connor, 1989).

In this paper, we report the results of an electrophoretic and morphological survey to examine the extent of hybridization and to clarify the taxonomic status between *C. t. lutheri* and *C. t. striata*. The results show introgressive hybridization has developed by secondary contact between these subspecies throughout approximately 20 kilometers of historical range of the *C. t. lutheri* in the past sixty years after the construction of power plants.

# **Materials and Methods**

A total of 664 specimens was collected from 13 different sites in the Dongjin and the Sumjin between April to August of 1984 (Fig. 1). Reference populations of Cobitis taenia striata (site 1) and C. t. lutheri (site 13) were obtained



**Fig. 1.** A map showing the collection sites for the study of hybridization between *C. t. triata* (1) and *C. t. lutheri* (13) in the Dongjin. Numbers refer to the collection sites listed in table 1.

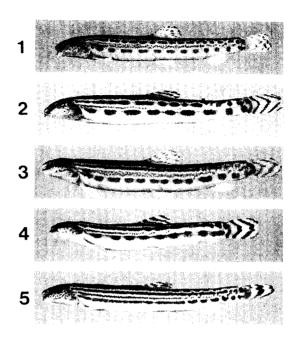
from well-seperated locations. All specimens were immediately frozen on dry ice after collection, transported to the laboratory, and stored at -70°C. The muscle was excised from each specimen, homogenized in distilled water and centrifuged at 18,000 rpm for 30 minutes to obtain extracts of water soluble proteins. After the muscle excision each specimen's sex, standard length and band types were recorded and then tagged for preservation.

Analysis of morphological variation in a sympatric area was based on 18 external body proportions obtained from eight morphological characters. The characters used were standard length (SL), head length (HL), body depth (BD), length from the origin of the dorsal fin to the end of the snout (OD), caudal peduncle length (CPL), caudal peduncle depth (CPD), snout length (SnL) and the eve diameter (ED). Detrminations were made using Kim's (1980) description. Color pattern analysis was done only on females due to C. t. lutheri males' variable color patterns during breeding season. A color pattern hybrid index (CHI) was devised based on the color pattern of body side. A range from one (pure C. t. striata with three striated lateral bands) to five (pure C. t. lutheri with two spotted lateral bands) was established (Fig. 2) as color pattern hybrid indices. Linear discriminant function analysis of body proportions using the SPSS program of Nie et al. (1975) was done on an MV-8,000 computer using the entire set of independent variables.

Muscle extracts were subjected to horizontal starch gel electrophoresis and the results were interpreted following Selander *et al.* (1971) and Wake *et al.* (1981). The amount of linkage disequilibrium between each pair of diagnostic loci from which all genotypes were determined were estimated using Hartl's procedure (1980).

# Result

To identify diagnostic loci of the two subspecies, 27 variable loci from 12 enzymic and non-enzymic proteins were examined. Only three of seven loci showing fixed or nearly fixed differences between two subapecies in allele frequencies were



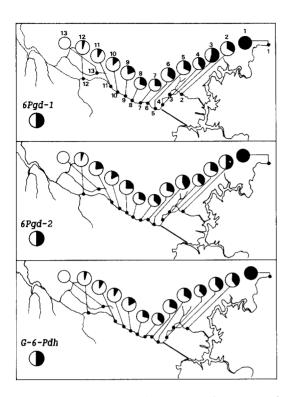
**Fig. 2.** Representative specimens of female spined loach from the reference samples of *C. t. lutheri* (1), *C. t. striata* (5) and their hybrids (2-4).

used: 6Pgd-1, 6Pgd-2, and G-6-Pdh. The other four (Ald, Gdh-1, Gdh-2, and Pgi-1) were excepted due to occasional scoring difficulties when determining their individual genotypes.

Except the two reference populations singlelocus analysis from the Dongjin was done on the alleles of C. t. striata and C. t. lutheri for all three diagnostic loci (Table 1). A typical clinal patterns of change for the frequency of introduced C. t. striata alleles was observed (Fig. 3). The Baegsangyo population (site 13) showed no evidence of influence from C. t. striata. The frequency of Striata alleles at site twelve averaged 0.03 (Table 2). Traveling upstream the frequency of Striata alleles continued to increase, reaching a peak of 0.52 for 6Pgd-1 at site three. The three diagnostic loci showed similar clinal patterns throughout the sympatric zone. Four unique alleles (6Pgd-1a, 6Pgd-1d, 6Pgd-2a, G-6-Pdha) were found with frequencies ranging 0.01-0.08 (Table 1). This occurence of rare alleles in the hybridization zone is difficult to account for in terms of parental population introgression because they are not present in samples taken from either

**Table 1.** Genotypic arrays for three diagnostic loci in reference samples of *C. t. striata* (site 1) and *C. t. lutheri* (site 13) and for hybrids from the Dongjin, Chollabuk-do (site 2-12). Locality numbers as in Figure 1. Alleles are given letters in alphabetic order of decreasing anodal mobility.

Collection sites	N	Locus				
Conection sites	14	6Pgd-1	6Pgd-2	G-6-Pdh		
C. t. striata						
1. Kwanchon	15	15 bb	15 bb	15 bb		
Hybrids						
2. Sanoe	24	3 bb	2 aa	5 bb		
		15 bc	9 bb	11 bc		
		6 cc	6 bc	8 cc		
			7 cc			
3. Sinbae	32	1 ab	6 bb	10 bb		
		9 bb	9 bc	4 bc		
		14 bc	17 cc	18 cc		
		8 cc				
<ol><li>Haengdan</li></ol>	15	2 bb	4 bb	4 bb		
		9 bc	5 bc	5 bc		
		4 cc	6 cc	6 сс		
<ol><li>Chilbo</li></ol>	68	1 ab	15 bb	1 ab		
		10 bb	25 bc	9 bb		
		29 bc	28 cc	25 bc		
		28 cc		33 сс		
6. Siseon	83	1 ab	12 bb	7 bb		
		14 ხხ	28 bc	31 bc		
		36 bc	43 cc	<b>4</b> 5 cc		
		32 cc				
7. Sansong	26	1 ab	7 bb	9 bb		
		1 ac	5 bc	17 bc		
		2 bb	14 cc			
		10 bc				
		12 cc				
8. Doogok	33	2 bb	5 bb	4 bb		
		14 bc	7 bc	8 bc		
		16 cc	21 cc	21 cc		
9. Samri	100	1 ac	8 bb	10 bb		
		6 bb	30 bc	13 bc		
		28 bc	62 cc	77 cc		
		65 cc				
10. Sinki	73	1 ac	4 bb	3 bb		
		5 bb	14 bc	10 bc		
		8 bc	55 cc	60 сс		
		58 cc				
11 17	7.4	1 cd				
11. Keosan	74	1 ac	7 bb	1 bb		
		18 bc	21 bc	10 bc		
10 6:	116	55 cc	46 cc	63 cc		
12. Sintaein	116	3 bc	4 bb	1 bb		
		111 cc	8 bc	2 bc		
		2 dd	104 bc	113 сс		
C. t. lutheri						
<ol><li>13. Baegsangyo</li></ol>	17	17 cc	17 cc	17 cc		



**Fig. 3.** Clinal variations of major allele frequencies of three diagnostic loci at sampling sites in the Dongjin. The solid circles represent *C. t. striata* alleles and open circles represent *C. t. lutheri* alleles.

site one or thirteen. Therefore these alleles were not used in estimating the genetic contribution of each subspecies to the total population.

A composite genetic hybrid index (GHI) of +1 for alleles typical to C. t. Striata and -1 for C. t. lutheri based on the three diagnostic loci gives a genotypic distribution of +6 to -6 (Table 2).  $F_{\parallel}$  and certain  $F_{\parallel}$  or later generational crosses scored zero. Electrophoretic hybrids were found at all sympatric areas except the reference ones (sites 1 and 13). The scores showed a modal shift conforming to changes in allele frequencies. At low stream locations in the Dongjin (sites 10 to 12) the mode shifted toward C. t. lutheri, at sites 2 to 4 it shifted toward C. t. striata and it was intermediate at all other sites.

Standardized linkage disequilibrium values (D') are represented in Table 3. All combinations showed generally low disequilibrium values suggesting no linkage, but significant positive

linkage disequilibrium (P<0.05) was detected in eleven of the thirty-three gene pair combinations.

Color pattern and discriminant function analysis were done on the hybrids. The mean CHI scores showed clinal variation like GHI cline (Table 4) while discriminant function analysis showed no genotype differences in seven groups. Genetically pure females showed almost complete separation but  $F_1$  hybrid females overlapped with C. t.lutheri (Fig. 4a). Backcross or F2 individuals were scattered over the F<sub>1</sub> and both parental clusters (Fig. 4b). CHI and GHI indices were compared for all the adult females collected from the Dongjin (Fig. 5) and an asymmetrical relationship was found. Seventy-nine percent of C. t. lutheri were morphologically and genetically pure (19 of 24) while only 55 percent (18 of 33) of C. t. striata were. Some individuals morphologically similar to C. t striata were genetically more similar to C. t. lutheri and vice versa. Using morphological criteria two of nineteen genetically intermediate individuals (class zero) were scored as pure C. t. striata. None however scored as pure C. t. lutheri.

### Discussion

We confirmed the hybridization between C. t. striata which introduced from the Sumiin and C. t. lutheri the endemic in the Dongjin using the analysis of starch gel electrophoresis. Our electrophoretic analysis showed that only 4 percent of the individuals from locality 2 can even conceivably be pure (using samples from localities 1 and 13 as standards), and there is a possibility that this figure is too high because of our inability to seperate some backcrosses from parental phenotypes. Only a few potential F<sub>1</sub>'s were found. And a few electromorphic phenotypes were found which were not expected from backcrosses. These results suggest that almost free interbreeding between the two subspecies is likely and that a substantial amount of hybridization and backcrossing have probably occured.

The presence of four unique alleles only in the hybrid zone is particulary interesting, in as much as they were not detected in either of our parental

**Table 2.** Genetic hybrid index scores and frequency of Striata alleles in *Cobitis* fishes collected from the Sumjin and the Dongjin of Chollabuk-do. Scores of +6 corresponds to pure C. t. striata genotype; a score of -6 corresponds to pure C. t. lutheri genotype.

	N	+6	+4	+2	0	-2	-4	-6	Mean	Freq.of Striata alleles
C. t. striata										
1. Kwanchon	15	15							+6.00	1.000
Hybrids										
2. Sanoe	22	1	1	2	10	5	3		-0.36	.458
3. Sinbae	30	3	1	5	3	9	4	5	-1.07	.417
4. Haengdan	15	2		2	2	7	3		-0.80	.433
5. Chilbo	69	3	1	7	13	26	11	8	-1.57	.361
6. Sisungyo	83	2	2	9	16	21	18	15	-1.64	.327
7. Sansung	24		1	1	6	7	7	2	-2.00	.333
8. Doogok	32			4	3	12	7	6	-2.50	.273
9. Samli	99		1	1	10	26	28	33	-3.59	.198
10. Singi	71			1	4	10	18	38	-4.48	.132
11. Geosangyo	73			2	2	14	22	33	-4.25	.151
12. Sintaein	114				1	5	10	98	-5.60	.031
C. t. lutheri										
13. Baegsangyo	17							17	-6.00	.000

Table 3. Linkage disequilibrium values (D' × 1000) in spined loach collected from the Dongjin river, Chollabuk-do.

	Collection sites										
	2	3	4	5	6	7	8	9	10	11	12
6Pgd-1x6Pgd-2	4.1	91.6	78.9	42.3	73.5	36.6	-4.4	16.0	5.1	38.1	8.0
6Pgd-1xG-6-pdh	100.3	64.5	112.3	89.4	107.7	69.4	52.7	30.4	27.1	24.0	-0.2
G-6-Pdhx6Pgd-2	-18.6	72.9	45.5	66.6	50.3	46.6	57.1	20.6	22.1	6.7	30.8

types. However, this is not uncommon phenomena in hybrid zones. Unique alleles in hybridizing taxa were reported in mammals (Hunt and Selander, 1973; Greenbaum, 1981), chorus frogs (Gartside, 1980) and salamanders (Sage and Selander, 1979; Wake et al., 1980). Two explanations have been proposed to explain their presence: either this is a consequence of higher mutation rates in hybrid genomes (Thomson and Woodruff, 1978), or they were formed by intragenic recombination between different alleles carried by the parent populations (Watt, 1972; Golding and Strobeck, 1983). Whatever their origin they apparently suggest hybridization can introduce genetic variations into a population

(Futuyama, 1990). At all sites with adequetely large samples, deficiences of heterozygotes were observed in *6Pgd-1,2* and *G-6-Pdh* using the Hardy-Weinberg expectation. These deficiences may be result of a partial assortative mating, genetic drift or selection against (Mayr, 1963; Crow and Kimura, 1970). General hybrid proportions ranging from 19-88% with a mean value of 71.5% makes the Wahlund assortative mating effect and genetic drift more likely than selection against (for example, pure individuals might migrate into the hybrid zone area (Crow and Kimura, 1970)). Linkage disequilibrium analysis also support this possibility. The lack of concordance among samples where pairs of loci

	N		Color pattern hybrid Index (CHI)					
		1	2	3	4	5	mean	
2. Sanoe	11		1	2	4	4	4.00	
3. Sinbae	29		7	11	5	6	3.34	
4. Haengdan	4	1			3		3.25	
5. Chilbo	31	2	4	14	7	4	3.23	
6. Siseon	26	3	2	16	5		2.88	
7. Sansong	9			7	2		3.22	
8. Doogok	9			1	4	4	3.33	
9. Samri	33	2	9	14	4	4	2.97	
10. Sinki	13	3	5	5			2.15	
11. Koesan	31	6	7	15	1	2	2.55	
12. Sintaein	19	8	6	4		1	1.78	
	215	25	42	92	35	21		

**Table 4.** The lateral color pattern distribution of females at each localities by CHI. Score of 1 corresponds to pure *C. t. lutheri* color pattern; a score of 5 corresponds to pure *C. t. striata*.

show evidence of linkage disequilibrium suggests these instances reflect variation in the rate of decay due to genetic drift. This was more noticeable near power plants (sites 2, 5, and 6) and pure *C. t. lutheri* (site 12).

Morphological analysis shows complex variation in character introgression possibly because many gene loci play concordant roles in the phenotype expression. This would give a wide array of phenotypes when hybridization in successive generations occurs. With morphologically similar species this leads to continuous intergradation of phenotypes and the fusion of the two (Dowling and Moore, 1984). C. t. striata and C. t. lutheri exemplify this situation. The asymmetry between color pattern and genetic hybrid indices suggests C. t. striata has a more canalized phenotype than does C. t. lutheri (Fig. 5).

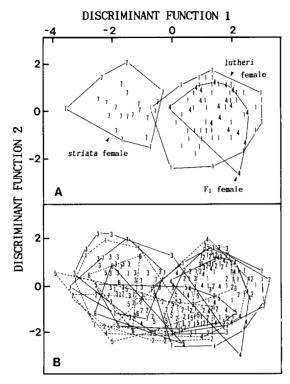
In taxonomic view, Kim and Lee (1988) concluded that *C. t. striata* and *C. t. lutheri* are separate species for several reasons: the different laminar circularis and suborbital spine shapes, restricted seasonal variation in male *C. t. lutheri* color patterns, habitat segregation in sympatric areas, etc. However this does not agree with previous reports and our present data. Morphological similarities among three subspecies of *C. taenia* including *striata* and *lutheri* are well documented (Kim, 1980). It was difficult identifying individuals collected from the Dongjin

as either  $C.\ t.$  striata or  $C.\ t.$  lutheri due to their highly variable color patterns (Kim and Lee, 1984) caused in part by geographic and seasonal variations. Fish frequently crossbreed but usually only sterile  $F_1$  individuals result and little or no evidence shows backcrossing with the parent species. Despite the high rate of crossbreeding in fish-particularly fresh water fish-introgression rarely occurs (Mayr, 1963). Therefore, the abundant  $F_1$  and backcross hybrids are the result of the conspecifisity of their parent's taxa. Our data suggests  $C.\ t.$  striata is introgressive with respect to  $C.\ t.$  lutheri. Despite a small deficiency of total heterozygotes based on Hardy-Weinberg expectations, the degree of hybrids was very high.

In conclusion, we prefer to recognize *C. t. striata* and *C. t. lutheri* as typical subspecies based on our present data and previous elctrophoretic (Park, 1988), karyotypic (Lee, 1989) and taxonomic (Kim and Lee, 1984) data.

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**Fig. 4.** Plots of the first and second discriminant functions for the individuals of 7 groups classified by GHI. Numbers refer to the group numbers listed in Table 2. A: Comparison of females among C.t.striata, C.t. lutheri and their  $F_1$  hybrids. B: Plots of all individuals with their GHI, line represents females (solid line) and males (dot line).

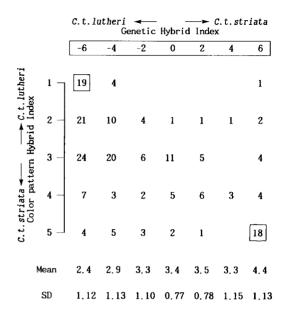
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**Fig. 5.** Comparison of scorings using genetic and color pattern hybrid indices for female individuals collected from the Dongjin. Individual scorings that are potentially pure *C. t. lutheri* and *C. t. striata* are inclosed in boxes. All other individuals are considered hybrids.

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한국산 기름종개속 어류(Pisces: Cobitidae)의 계통분류학적 연구 IV. 줄종개와 점줄종개의 잡종에 관한 연구 김재흡·양서영(인하대학교 이과대학 생물학과)

줄종개 C. t. striata 와 점줄종개 C. t. lutheri는 allopatric subspecies이나 발전 및 관개용수를 위한 섬진강의 유로변경에 의해 동진강에서 2차 접촉하게 되었다. 상기의결과로 발생될 잡종여부를 구명하기 위하여 전기영동을 실시하여 G-6-pdh, 6Pgd-1, 및 6Pgd-2 등 3개의 유전적 표식인자를 찾아내고, 이를 이용 두 아종사이의  $F_1$  및  $F_2$  잡종혹은 backcross 개체를 구별하였다. 유전적 표식인자에 의해 각 개체들을 7개 집단으로 재분리 분석하였다. 동진강의 공서지역 11개 지점에서 유전적 표식인자의 줄종개 대립인자 평균빈도가 0.03-0.46으로 하류에서 상류로 갈수록 점차 증가하는 cline 현상을 보여 줄종개의 유입을 나타내었다. 공서지역에서 채집된 개체들은 형질유입효과에 의한 형태변이가 매우 다양하여 형태에 의한 종분류는 불가능하였다. 줄종개와 점줄종개 표식인자간 linkage disequilibrium이 거의 나타나지 않아 유전자의 교환이 자유로이 일어남을 알수 있었다. 본 연구결과 줄종개와 점줄종개는 분포와 형태적으로는 차이가 있으나 생식적 격리가 이루어지지 않은 전형적인 아종으로 분류함이 타당하다고 사료된다.