

Genetic Evidence to Clarify the Systematic Status of the Genera *Zacco* and *Candidia* (Cypriniformes: Cyprinidae)

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Hurng-Yi Wang, Sin-Che Lee and Ming-Jenn Yu (1997) Genetic evidence to clarify the systematic status of the genera *Zacco* and *Candidia* (Cypriniformes: Cyprinidae). *Zoological Studies* **36**(3): 170-177. Genetic relationships among species of the genera *Zacco* and *Candidia* were analyzed using allozyme data from sampled specimens collected from 6 rivers in Taiwan. A total of 78 alleles were resolved for 26 loci from 13 enzyme systems. Nei's genetic distance between 2 congeneric species (*Zacco pachycephalus* and *Z. platypus*) was 0.285, which is within the range for the same genus. A slightly larger mouth cleft, smaller lateral line scales, and fixed alleles at *mMDH*100*, *ME-1*100*, *PGI-B*100*, *PGM-1*100*, and *PGM-2*100* in *Zacco pachycephalus* can be used to distinguish it from *Z. platypus*. Comparison with *Aphyocypris kikuchii*, *Candidia* are 2 distinct genera. In addition, a barbel at mouth corner, and fixed alleles at *sAAT-1*120*, *CK-A*93*, *FH-1*80*, *FH-2*82*, *G*₆*PDH-1*80*, *IDHP-1*113*, *IDHP-3*120*, *ME-1*103*, *ME-2*50*, *PGM-1*120*, and *PGM-2*120* in *Candidia* can also be used to distinguish it from the genus *Zacco*. The colonization and speciation event of the genus *Zacco* in Taiwan was discussed in detail.

Key words: Allozyme comparisons, Zacco and Candidia, River habitats, Taiwan.

Species of the genera Zacco Jordan and Evermann 1902, and Candidia Jordan and Richardson 1909 (Cyprinidae: Rasborinae) are common minnows in western Taiwan rivers. Several species of the genus Zacco occur in Japan, Korea, China, and Taiwan (Banarescu 1968), while the genus Candidia containing only 1 species is unique to Taiwan. Some external features of these 2 general are similar, such as in an elongated body, medium or small-sized scales, a lateral line profile running along the lower flank of the body, the origin of the dorsal fin inserted opposite to the base of the ventral fin, maxillae reaching or behind the front margin of the orbit, tubercles present on both sides of the snout, and elongated anal fin rays appearing only in mature males (Regan 1908, Banarescu 1968). However, the single species of the genus Candidia differs from species of the genus Zacco by having barbels at the mouth corner, and a longitudinal stripe on the body sides, and by the

anterior 4 branched anal rays not extending to the caudal base in sexually mature males.

According to recent studies, the genus Zacco in Taiwan contain 2 valid species, Z. pachycephalus and Z. platypus (Shen et al. 1993). Zacco species which appear in older literature, such as Zacco evolans, would be a junior synonym of Z. pachycephalus (Oshima 1919). The record of Z. temmincki in Taiwan by Oshima (1919) and the subsequent record by Chen and Yu (1986) were misidentifications of Z. pachycephalus. Actually, Z. temmincki (Temminck and Schlegel 1846) is only found in Korea, Japan, and Mainland China. The distributions of the 2 previously recognized Zacco species in Taiwan are different. Z. platypus is restricted to northern Taiwan, while Z. pachycephalus is distributed throughtout Taiwan except on the eastern side. The recent occurrence on the latter species in eastern Taiwan is a result of artificial introduction from release of fish fry.

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The distribution pattern of *Candidia barbatus* is similar to that of *Z. pachycephalus*, also having the same problem of fry release in eastern Taiwan by the local government agents. Since *Z. pachycephalus* lives sympatrically with *C. barbatus* and have close resemblances of some external features as stated above, some authors have discussed placing *C. barbatus* under the genus *Zacco* (Banarescu 1968, Shen et al. 1993). Therefore, it is still unclear whether *C. barbatus* belongs with the *Zacco* species or it is in a separate genus. In this paper we use allozyme electrophoresis and choose *Aphyocypris kikuchii* as an outgroup to clarify the taxonomic status of the genera *Zacco* and *Candidia*.

MATERIALS AND METHODS

A total of 66 Zacco platypus (56.9 to 89.6 mm in standard length, SL), 146 Z. pachycephalus (54.3 to 156.9 mm in SL), 87 Candidia barbatus (63.7 to 144.5 mm in SL), and 18 Aphyocypris kikuchii (38.9 to 58.6 mm in SL) were collected during 1991 to

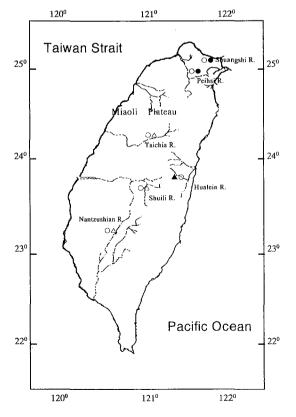


Fig. 1. Map of Taiwan showing the location of sampling sites. *Zacco pachycephalus* (\bigcirc) , *Z. platypus* (), *Candidia barbatus* (\triangle) , and *Aphyocypris kikuchii* (\blacktriangle) .

1994 from 6 rivers: Hualien River, Nantzushian River, Peihsi River, Shuangshi River, Shuili River, and Tachia River (Fig. 1).

Tissues from eyes, heart, liver, and skeletal muscle were homogenized in 2-3 volumes of extraction buffer (0.1 M Tris-HCl, 1 mM EDTA (Na₂), and 0.05 mM NADP⁺, pH 7.0; Shaklee and Keenan 1986). The homogenates were centrifuged at 17 000 g for 40 min, and the clear supernatants were stored at -70° C until electrophoresis.

The tissue extracts were then applied on a 12% starch gel for horizontal electrophoresis. The buffer solutions used were those of Sung et. al. (1993). Staining methods and recipes were adopted from Shaklee and Keenan 1986, Pasteur et al. 1988, Murphy et al. 1990, and Sung et al. 1993. Locus nomenclature follows that of Shaklee et al. (1990). Alleles at any locus were given according to the proportion of their relative mobility to the most common allele which is designated as 100.

The BIOSYS-1 vers. 1.7 (Swofford and Selander 1989) computer program was used to estimate genetic variability (heterozygosity, and percent of polymorphic loci under the 0.95 criterion, P_{95}), and Nei's (1972) and modified Roger's genetic distance (Wright 1978) between all pairwise combinations of taxa.

RESULTS

Genetic data were obtained from electrophoresis on 26 loci with 78 alleles encoded for 13 enzymes from 4 species, among which, 19 loci showed clearly interspecific differences (Table 1). Genetic variabilities, expressed by mean heterozygosity (H) and percentages of polymorphic loci (P₉₅), of these species are $\underline{H} = 0.03$, $\underline{P}_{95} = 15.4\%$ in Z. pachycephalus; $\underline{H} = 0.024$, $\underline{P}_{95} = 11.5\%$ in Z. *platypus*; $\underline{H} = 0.021$, $\underline{P}_{95} = 8.0\%$ in *C. barbatus*; and H = 0.051, P₉₅ = 17.4% in *A. kikuchii*. Some fixed allele frequency differences shown in Table 1 can be used to distinguish these species. First, at the generic level, genetic distances (D) between Candidia and Zacco (0.951-1.115) as well as between Zacco and Aphyocypris (1.045 - 1.061) are almost the same (Table 2). An obviously complete substitution of alleles between Zacco and Candidia can also be well recognized from the following loci: Candidia has fixed alleles at sAAT-1*120, FH-1*80, FH-2*82, G₆PDH*80, IDHP-1*113, IDHP-3*120, and ME-2*50, while both Zacco species lack above alleles. Second, at the specific level within Zacco itself, Nei's genetic distance (D) between **Table 1.** Allelic frequency of 23 comparable loci among 4 species, *Zacco pachycephalus*, *Z. platypus*, *Candidia barbatus*, and *Aphyocypris kikuchii*. Six monomorphic loci, including *CK-B*, *LDH-B*, *LDH-C*, and *XDH*, are excluded from this table

Locus	allele	Z. pachycephalus	Z. platypus	C. barbatus	A. kikuchii
sAAT-1	100	0.975	0.923	0.000	0.000
	113	0.025	0.077	0.000	0.000
	120	0.000	0.000	1.000	0.000
	142	0.000	0.000	0.000	1.000
sAAT-2	20	0.000	0.000	0.000	0.167
	-100	1.000	1.000	1.000	0.833
CK-A	75	0.000	1.000	0.000	0.000
	93	0.000	0.000	1.000	0.000
	100	0.993	0.000	0.000	0.000
	112	0.000	0.000	0.000	1.000
	120	0.007	0.000	0.000	0.000
CK-C	97	0.152	0.000	1.000	0.000
	100	0.848	1.000	0.000	1.000
FH-1	80	0.000	0.000	1.000	ns
	100	1.000	1.000	0.000	ns
FH-2	82	0.000	0.000	1.000	ns
	100	1.000	1.000	0.000	ns
G ₆ PDH	80	0.000	0.000	1.000	0.000
-	100	1.000	1.000	0.000	1.000
IDHP-1	68	0.000	0.000	0.000	0.028
	87	0.000	0.000	0.000	0.972
	100	1.000	0.985	0.000	0.000
	113	0.000	0.000	1.000	0.000
	120	0.000	0.015	0.000	0.000
IDHP-2	75	0.000	0.000	0.176	ns
	100	1.000	1.000	0.000	ns
	115	0.000	0.000	0.824	ns
IDHP-3	86	0.000	0.000	0.000	0.278
	98	0.000	0.000	0.000	0.722
	100	1.000	1.000	0.000	0.000
	120	0.000	0.000	1.000	0.000
LDH-A	100	1.000	1.000	1.000	0.000
	110	0.000	0.000	0.000	1.000
sMDH-A	100	1.000	1.000	0.929	1.000
SMDITA	120	0.000	0.000	0.071	0.000
sMDH-B	65	0.010	0.000	0.000	0.000
UNDIT D	100	0.990	1.000	0.000	1.000
	130	0.000	0.000	1.000	0.000
mMDH	100	1.000	0.000	0.000	0.000
mmun	153	0.000	0.000	0.000	1.000
	153 200	0.000		1.000	0.000
			1.000		
ME-1	100 101	1.000	0.000	0.000	0.000
	101	0.000	0.000	0.000	1.000
	103	0.000	0.000	1.000	0.000
	107	0.000	1.000	0.000	0.000
ME-2	50	0.000	0.000	1.000	0.000
	100	1.000	1.000	0.000	0.000

Locus	allele	Z. pachycephalus	Z. platypus	C. barbatus	A. kikuchii
ME-2	120	0.000	0.000	0.000	0.917
	145	0.000	0.000	0.000	0.083
MPI-1	95	0.028	0.000	0.000	0.000
	100	0.706	0.937	1.000	0.000
	105	0.266	0.069	0.000	0.000
	110	0.000	0.000	0.000	1.000
PGDH-1	100	0.787	0.962	1.000	0.000
	110	0.000	0.000	0.000	1.000
	125	0.213	0.038	0.000	0.000
PGI-A	22	0.000	0.000	0.000	0.889
	72	0.000	0.000	0.000	0.111
	-40	0.023	0.938	1.000	0.000
	-100	0.926	0.062	0.000	0.000
	-140	0.051	0.000	0.000	0.000
PGI-B	75	0.000	1.000	0.000	0.083
	100	1.000	0.000	0.000	0.417
	115	0.000	0.000	0.435	0.000
	125	0.000	0.000	0.224	0.500
	135	0.000	0.000	0.341	0.000
PGM-1	75	0.000	1.000	0.000	0.000
	100	1.000	0.000	0.000	0.000
	102	0.000	0.000	0.000	1.000
	120	0.000	0.000	1.000	0.000
PGM-2	75	0.000	1.000	0.000	0.000
	100	1.000	0.000	0.000	0.000
	102	0.000	0.000	0.000	1.000
	120	0.000	0.000	1.000	0.000

Table 1. (Co	ont.)
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ns: not scorable.

Table 2. Nei's (1972) genetic distance (below diagonal) and modified Roger's genetic distance (above diagonal) among *Zacco pachycephalus*, *Z. platypus*, *Candidia barbatus*, and *Aphyocypris kikuchii*

Species	Z. pachycephalus	Z. platypus	C. barbatus	A. kikuchii
Z. pachycephalus		0.328	0.817	0.782
Z. platypus	0.285	_	0.806	0.790
C. barbatus	1.115	0.951		0.857
A. kikuchii	1.045	1.061	1.521	

Z. pachycephalus and *Z. platypus* is 0.285 (or I = 0.752). *Z. platypus* has fixed alleles at *mMDH*200*, *ME-1*107*, *PGI-B*80*, *PGM-1*75*, and *PGM-2*75*, while *Z. pachycephalus* has fixed alleles at *mMDH*100*, *ME-1*100*, *PGI-B*100*, *PGM-1*100*, and *PGM-2*100*. In the Shuanghsi River where 2 *Zacco* species live sympatrically, 2 F_1 natural hybrids have occurred, judging from the occurrence

of intermediate zymograms at the following 5 loci shown in Fig. 2: the one between alleles ME-1*107and ME-1*100; mMDH*200 and mMDH*100; PGI-B*100 and PGI-B*80; PGM-1*100 and PGM-1*75; and PGM-2*100 and PGM-2*75. Morphologically, the 2 F₁ hybrids resemble *Z*. *pachycephalus* in having a wider mouth cleft and smaller scale size than in *Z. platypus*.

DISCUSSION

The genetic distance of 0.285 between Z. pachycephalus and Z. platypus is beyond the range of the populational level of variation (Shaklee et al. 1982) but it fits well within the same genus. Some external differences including lateral line scales, the size of mouth cleft, and the shape of jaws can further distinguish these as 2 valid species. When fish species share a common spawning ground, the incidence of yielding natural hybrids between any 2 closely-related species is expected (Hubbs 1955). The occurrence of 2 F_1 hybrids between Z. platypus and Z. pachycephalus from the Shuangshi and Peihsi Rivers is an example. The habitat of these 2 species are sympatric in northern Taiwan and both have the same spawning season which commences in early spring and ends in late summer (Liu 1984, Wang et al. 1995). This would facilitate the production of natural hybrids. Successive generations of hybridization would lead to continuous intergradation of phenotypes and fusion of the participating species (Sakai and Hamada 1985). If this happens, the pooled gene frequency of these 2 species would approach the Hardy-Weinberg equilibrium, because of high gene flow. The pooled allozyme data for these 2 species in the same collection site reveal a great departure

from the Hardy-Weinberg equilibrium, however, indicating the existence of a reproductive isolating mechanism between them.

Though Z. platypus was reported to be distributed throughout western Taiwan from the Kaoping River in the south the Lanyang River in the north (Oshima 1923, Liang 1984, Tzeng 1986), in fact, we confirmed that the species is not found outside the northern part of Taiwan during our recent investigation. Several other reports are in agreement with this result (Lee 1995, Fang et al. 1996). After close examination of Z. platypus specimens described by Liang (1984), we have determined that they are a misidentification of Z. pachycephalus. For these reasons, we consider that the previous report on the distribution of Z. platypus from regions other than northern Taiwan is in error due to the misidentification of Z. pachycephalus.

A new species *Z. taiwanesis* from the Choshui River described by Chen (1982) is considered to be a synonym of *Z. pachycephalus*. The species characters designated including a smaller head and more anteriorly positioned dorsal fin origin can be considered within the range of intrapopulational variation. The above 2 morpho-types of *Zacco* species collected during this study period showed the same allozyme patterns.

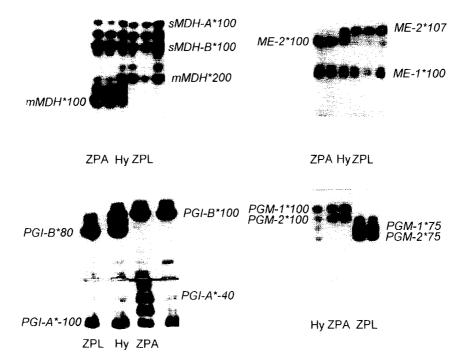
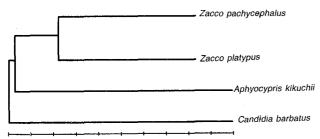


Fig. 2. Electrophoresis patterns of malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucose isomerase (PGI), and phosphoglucomutase (PGM) in *Z. pachycephalus* (ZPA), *Z. platypus* (ZPL), and their hybrid (Hy).

Zacco temmincki is distributed in Japan, Korea, and southeastern China (Banarescu 1968, Hosoya 1993). There is a previous record of so-called Z. temmincki in Taiwan by Oshima (1919). However, Z. temmincki was not found during this study. The color pattern and lateral line scale counts in Oshima's Z. temmincki are more likely those of Z. pachycephalus rather than Z. temmincki of Japan and Korea. It is assumed that Z. temmincki of Oshima (1919) was actually a misidentified Z. pachycephalus. Therefore, we neither agree with Banarescu (1968) who claimed that there is only 1 species of Zacco (Z. pachycephalus), nor with that of Oshima (1919) who recorded the occurrence of Z. temmincki in Taiwan. There are 2 species of Zacco in Taiwan: Z. platypus and Z. pachycephalus.

Both Zacco and Candidia were previously placed in the genus Opsariichthys (Güther 1868, Regan 1908). However, as mentioned above, both were also recognized as valid genera (Jordan and Evermann 1902, Jordan and Richardson 1909). C. barbatus is externally similar to Z. pachycephalus except for the barbels (Regan 1908), which misled Banarescu (1968) to place this species under the genus Zacco. However, genetic distance between the genera Zacco and Candidia is much higher than that set for the interspecific level(Shaklee et al. 1982). The distance Wagner tree shows that the relationships between Candida and Zacco is the same as between Aphyocypris and Zacco (Fig. 3). In addition, the lack of an elongated anal fin, and the possession of reddish spots below the eyes and at the anterior bases of the pectoral and ventral fins in mature males of C. barbatus indicate that it should not be a member of the genus Zacco.

The speciation that took place in genera *Zacco* and *Candidia* in Korea and Japan was discussed by Ming (1991) and Okazaki et al. (1991). Based on allozyme analyses, they confirmed that 3 pre-



0.00 0.04 0.09 0.13 0.17 0.22 0.26 0.30 0.34 0.39 0.43

Fig. 3. Distance Wagner tree illustrating relationships among species, reconstructed from the added lengths of horizontal branches for modified Roger's genetic distance among taxa.

sumptive valid species exist for the Z. temmincki complex, provisionally designated types A, B, and C, respectively. Types A and B are found in Japan, with types B and C in Korea. Ming (1991) concluded that the genera Zacco and Candidia were separated from one another in the early Pliocene (about 5 Mya), with 1 lineage of the Z. platypus/ pachycephalus group and the other with the Z. temmincki/Candidia group. The latter laterally branched in the late Pliocene. According to morphological descriptions of Hosoya (1993), Z. temmincki Type A is more closely related to C. barbatus than to the other 2 types of Zacco with both elongated anal fin not reaching the caudal base even in sexually mature males, and the anterior bases of the pectoral and ventral fins being red instead of yellowish as in the other Zacco species. Therefore, we suggest that the recent split in the late Pliocene took place with 1 branch of Z. temmincki B and C types and the other with C. barbatus and Z. temmincki A type. The Z. temmincki/Candidia group differs from the Z. platypus/ pachycephalus group by having a distinct lateral band on the body sides instead of having 10 more cross bars as in the latter group. We suggest that the taxonomic status of the Z. temmincki complex should be reconsidered.

The distribution pattern of the genus Zacco in Taiwan was probably influenced by geohistorical events. About 1.5-1 Mya, Taiwan was connected to the Asian continent with the rise of the Central Mountain Range and the regression of sea levels (Lin 1963). Because the distribution of the genus Zacco is restricted to western Taiwan, the time of colonization of this genus in Taiwan might not be earlier than the rise of Central Mountain Range. Therefore, the 1st invasion of the genus Zacco in Taiwan might have taken place at that time. The speciation event of Z. platypus and Z. pachycephalus might also have occurred simultaneously. The divergent time of about 1.3-1.4 Mya between these 2 species, estimated by genetic distance, supports this hypothesis. The early colonization by a Zacco population in Taiwan eventually evolved to the endemic species Zacco pachycephalus.

After several periods of separation and reconnection, Taiwan was reconnected to the continent with the formation of the Miaoli Plateau about 240 000-150 000 years ago. We suggest that the 2nd invasion of genus *Zacco* might have taken place at that time. Because of the limitation of the Miaoli Plateau, *Z. platypus* was restricted to northern Taiwan. This may explain why *Z. platypus* is widely distributed in mainland China, but is restricted to the northern part of the island of Taiwan.

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以遺傳學之證據釐清鱲屬與馬口魚屬之分類地位

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以同功酶的資料分析採自臺灣六條河川中的繼屬與馬口魚屬魚類。在13 個酵素系統中共得到26 個基因 座,78 個對偶基因。繼屬的二個種間(粗首鑞與平領鑞)的 Nei's 遺傳距離為 0.285,相當於屬內的分化程 度。粗首繼具有較大的口裂,較多的側線鱗片數,以及在 mMDH*100, ME-1*100, PGI-B*100, PGM-1*100,與 PGM-2*100等對偶基因上與平領鑞有所區別。在屬間方面,若與菊池式細繼比較,馬口魚 顯然與鱲屬的二種魚類關係較遠,因此它們應為不同屬。馬口魚的嘴角有口鬚,並且在 sAAT-1*120, CK-A*93, FH-1*80, FH-2*82, G₆PDH-1*80, IDHP-1*113, IDHP-3*120, ME-1*103, ME-2*50, PGM-1*120,與 PGM-2*120 等對偶基因上可明顯與繼屬魚類有別。文中並討論繼屬在臺灣的起源以及可能的種化時間。

關鍵詞:同功酶比較, 繼屬與馬口魚屬, 河川棲地, 臺灣。

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