

ARTICLE

# Morphological differentiation among isolated populations of dwarf snakehead fish, *Channa gachua* (Hamilton, 1822) using truss network analysis

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**ABSTRACT** Truss-network analysis was applied to examine morphological differences among distinct populations of *Channa gachua* (Hamilton 1822). Ninety-eight fish individuals were collected from three-isolated habitats in north-eastern Thailand. Twenty-six truss variables were measured and then subjected to Burnaby's size adjustment for removing size-dependent effect. The transformed data were processed for univariate and multivariate statistical analyses. The multivariate ANCOVA showed highly significant differences between populations (Pillai's trace = 1.561,  $F = 10.102$ ,  $p < 0.0001$ ). The univariate ANCOVA presented the significant differences between 20 out of 26 truss variables ( $p < 0.05$ ) representing morphological characters of head, trunk and caudal peduncle areas. The variability in body shape among three populations obviously showed by the first three components of PCA accounting for 49.98% of total variances. In addition, five variables from head area and three variables from body were selected to stepwise discriminant analysis, representing the first two discriminant functions (DF1 and DF2) accounted for 72.95 and 27.95% of shape variability, respectively. A high rate of correct classification of *C. gachua* to actual sampling locations was at 93.88%. The results support the existence of local adaptation of *C. gachua* across the isolated geographical locations, and indicate the presence of three phenotypic stocks of *C. gachua* regarding their habitat locations.

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**KEY WORDS**

body shape  
*Channa gachua*  
morphometrics  
truss network analysis

## Introduction

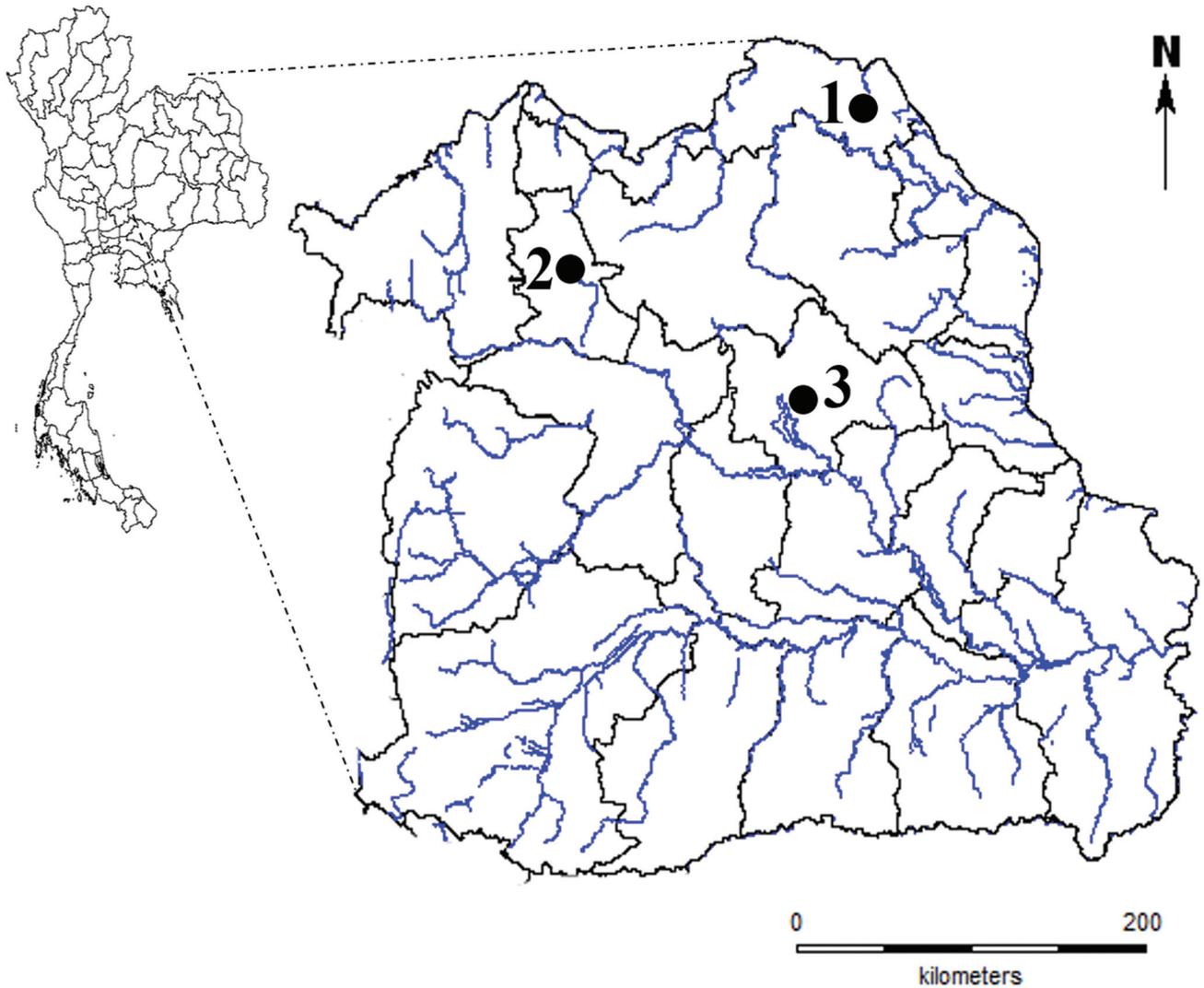
Local adaptation within a species plays a fundamental role in the improvement of survival and reproductive success (Peterson et al. 2014), the generation and maintain of species diversity (Lenormand and Thomas 2012), the range of geographical distribution (Atkins and Travis 2012) as well as the ecological and evolutionary dynamics of species interaction (Bocedi et al. 2013). Local adaptation with environmentally induced phenotypic variation is commonly observed between fish populations (Lostrom et al. 2015; Bernatchez 2016; Seebacher et al. 2017). Such variation is influenced by an assortment of environmental conditions including physico-chemical parameters of water, habitat preferences and substrate types (Sajina et al. 2011; Drinan et al. 2012; Lostrom et al. 2015). In addition, biotic factors, such as food availability, competition and predation, are also contributed to morphological variability in fish (Scharnweber et al. 2013;

Prado et al. 2016). The obtaining knowledge from the studies of morphological adaptation will lead to better understanding about ecology and evolution of the species (Agrawal 2001; Bijlsma and Loeschcke 2005; Lostrom et al. 2015), which potentially contributed to better management and conservation strategies of the fish (Schoenfuss et al. 2014).

Morphometric analysis is an integration of mathematical and statistical approaches to quantify the variation in morphological shape of an organism (Rohlf and Marcus 1993). Truss network system (TNS) is one of morphometric methods which relied on a series of measurements of across-body distances between two morphological landmarks, resulting in a uniform network covered entire body (Strauss and Bookstein 1982; Cadrin 2000). The TNS can overcome the inherent weakness of traditional measurement because of its high capability in capturing shape information with no restriction on the direction and localisation of variations (Cavalcanti et al. 1999). The analysis is also applicable to characterise and determine a various level of groups of fish including populations, stocks and assemblages (Cheng et al. 2005; Ferrito et al. 2007; McAdam et al. 2012; Mir et al. 2013; Siddik et al. 2016).

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**Figure 1.** The locations of sampling sites. Populations: 1 = CG-BK; 2 = CG-NB; 3 = CG-KS.

Dwarf snakehead, *Channa gachua* (Hamilton 1822), is the smallest size and colourful fish species of family Channidae (Courtenay and Williams 2003). The fish widely distributes in many parts of Asia from Afghanistan and Middle East Asia eastwards to Indonesia through South Asia (Ng and Lim 1990; Courtenay and Williams, 2003). It can also occupy a broad range of habitat types so that it *Channa gachua* is sometimes considered as a species complex with the vast array of morphological variation (Ng and Lim 1990; Courtenay and Williams 2003). Up to date very little information of morphological variability of *C. gachua* has been published. Hence, the present study aims to characterise the variation in morphometric characters of distinct *C. gachua* populations inhabiting in natural waters in northeast Thailand, using TNS analysis. The analysis will provide some useful information for taxonomic implication of this species.

## Materials and Methods

### Study sites and sample collection

A total of 98 specimens of *C. gachua* were collected from three geographical isolated populations in north-eastern Thailand (Fig. 1). Details of sample sizes, localities and habitat characteristics are showed in Table 1.

The fish samples were weighted, labelled and kept on ice to transport to laboratory in Department of Biology, Faculty of Science, Khon Kaen University. The fish were then stored at  $-20^{\circ}\text{C}$  prior to use, but did not stored for longer than 48 h. The precise species of the samples was identified based on Ng and Lim (1990) and Courtenay and Williams (2003).

**Table 1.** Details of, sample size (*N*), geographical locality, collecting date and ecological preferences of each sampling site.

Population	<i>N</i>	Geographical coordinates	Collecting date	Environmental conditions
1) CG-BK	31	18° 12' 41.7312" N, 103° 29' 48.4152" E	February 2010	A small and shallow waterway surrounded with rubber plantation and rice fields. Water level is less than 20 cm; habitat bottom contains small gravels and sand
2) CG-NB	31	17° 16' 57.9432" N 102° 28' 00.3432" E	February 2010	A small and shallow waterway on the mountain surrounding Deciduous Dipterocarp Forest. Water level is less than 20 cm; habitat bottom contains rock bed and sand.
3) CG-KS	36	16° 47' 11.0148" N 103° 37' 52.1256" E	March 2010	A small puddle in the rice filed which can connect to the reservoir in the raining season. Water level is around 50 cm; habitat bottom is sandy loam.

### Samples preparation and measurement

Frozen fish were thawed by soaking in water and rubbed with a cotton cloth. Each specimen was then placed on polystyrene board with the right side down. The body posture and fins were pinned at distinctive landmarks to expose the outline of the fish form. Twelve landmarks determining 26 truss distances on the body and standard length (SL) were chosen and measured (Fig. 2) using digital calliper at  $\pm 0.01$  mm. All measurements were conducted on the left side of each fish.

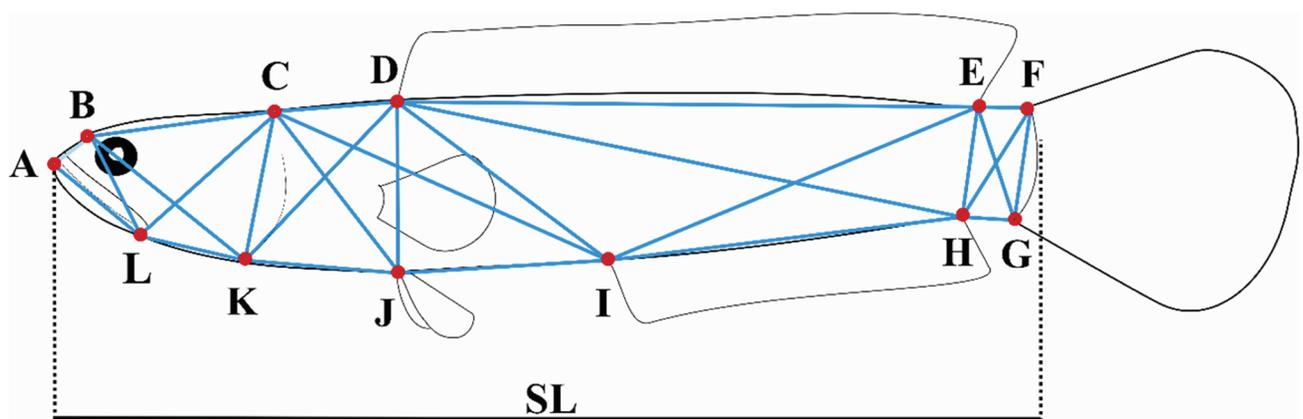
The allometric Burnaby's size adjustment method (Burnaby 1966; Elliott et al. 1995) was primary performed using program PAST version 1.3 (Hammer et al. 2001) to remove size-dependent variation from raw data which can make misinterpretation of the body shape variations (Elliott et al. 1995; Hammer et al. 2001).

### Statistical analyses

The transformed data retrieved previously was subjected to test for the significance of correlations between each of 26

transformed truss variables and the SL measurement (Poulet et al. 2004). Multivariate analysis of covariance (MANCOVA) with SL adding as a covariate was performed to account for body size differences among populations. A principal component analysis (PCA) was applied to examine the patterns of morphometric variation among populations by reducing the redundancy in the morphometric variables and extracting some of independent variables for population differentiation (Samaee and Patzner 2011; Mir et al. 2013).

A stepwise discriminant analysis (SDA) was then conducted on the transformed data to investigate the integrity of the pre-defined groups. F value criterion was used for selecting the independent variables into a model. The differences were also tested with a forward manner approach using  $F = 3.84$  for entering, and  $F = 2.71$  for removal. The Mahalanobis distance which is based on generalised squared Euclidean distance that adjusted for unequal variances was used to estimate discriminate function. Accuracy of classification was evaluated using the jackknife cross-validation (Cheng et al. 2005).



**Figure 2.** Truss and SL measurements on each *Channa gachua* specimens. A = anterior point of snout; B = posterior point of snout; C = upper-posterior point of head; D = start point of dorsal fin base; E = end point of dorsal fin base; F = upper point of caudal fin insertion; G = lower point of caudal fin insertion; H = end point of anal fin base; I = start point of anal fin base; J = point of pectoral fin insertion; K = lower posterior point of head; L = end point of mouth.

**Table 2.** Descriptive statistic and univariate analyses of covariance (ANCOVA) of each truss variable among the three population of *Channa gachua*.

Truss var.	Descriptive statistic among populations												ANCOVA results	
	CG-BK (n = 31)				CG-NB (n = 31)				CG-KS (n = 36)				F	p
	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.		
SL	140.85	20.45	104.54	180.88	102.58	21.80	58.53	146.00	73.97	12.62	53.77	127.17	111.3835	0.000001*
AB	12.57	2.87	7.89	19.45	10.13	2.18	6.58	13.91	6.11	1.07	4.73	10.48	15.5671	0.000001*
AL	23.27	8.58	13.10	42.60	12.40	2.94	7.73	16.97	7.61	1.53	5.86	13.65	12.5158	0.000015*
BL	20.26	6.47	11.60	35.42	12.47	3.17	7.52	18.37	7.62	1.57	5.47	14.45	5.1198	0.007752*
BC	22.28	3.70	16.48	30.26	18.50	4.62	9.43	29.67	13.13	2.73	8.67	23.21	1.7252	0.183733
KL	15.78	3.60	9.52	23.07	15.64	4.35	8.85	25.40	11.48	1.83	8.49	17.75	23.4432	0.000000*
BK	26.59	4.35	19.36	38.54	22.40	5.52	13.51	34.62	15.45	2.77	11.40	26.62	13.0811	0.000010*
CL	35.33	5.12	25.82	46.02	26.49	5.99	14.83	40.38	18.41	3.41	13.48	32.72	0.1527	0.888571
CK	21.82	4.05	15.75	29.99	17.33	4.39	10.08	27.47	11.15	2.39	7.15	20.92	16.6315	0.000001*
CD	16.33	5.40	9.66	29.97	10.84	2.83	6.43	18.44	7.20	1.68	4.24	12.90	1.7022	0.187837
IJ	28.02	4.74	20.09	40.62	20.58	7.37	10.98	42.03	15.58	2.59	11.46	24.83	19.6603	0.000000*
JK	16.63	3.20	10.63	23.07	9.82	2.56	4.56	15.56	6.83	1.79	3.52	12.96	12.3907	0.000017*
CI	49.35	9.55	34.76	69.22	34.47	9.98	19.16	64.39	24.56	4.39	18.47	42.27	10.6616	0.000067*
CJ	19.25	3.79	13.33	28.63	16.28	4.99	8.99	27.41	9.81	2.31	5.49	18.33	13.3878	0.000008*
DK	32.45	5.05	24.34	44.72	27.24	6.36	16.85	39.61	18.61	2.93	14.30	30.65	9.8434	0.000131*
DJ	24.77	4.10	17.82	32.37	18.94	4.70	10.84	28.44	11.95	2.76	6.92	23.62	11.4722	0.000035*
DE	82.92	12.41	58.25	104.23	57.87	12.10	31.33	81.80	44.41	7.41	32.39	74.03	48.295	0.000000*
HI	53.23	8.10	38.68	69.56	37.16	7.24	21.49	50.77	27.12	4.59	18.90	44.65	11.6786	0.000030*
DH	82.00	12.65	56.27	103.79	57.40	12.73	31.84	84.38	42.66	7.22	30.49	70.49	37.043	0.000000*
EI	59.76	8.84	44.43	78.19	42.15	7.85	23.56	55.46	31.38	5.44	22.01	53.30	14.943	0.000002*
DI	36.70	6.43	23.94	51.22	26.06	7.75	13.58	48.36	18.46	3.66	12.61	32.89	12.3275	0.000018*
EF	106.32	15.48	79.75	134.86	81.73	16.96	44.48	118.20	58.32	9.80	40.79	102.38	0.474	0.623951
GH	11.08	1.77	7.84	15.50	8.80	1.85	3.97	12.14	6.03	1.35	4.21	11.11	1.7691	0.17612
EG	17.62	3.20	12.00	24.07	13.70	3.24	8.07	20.35	9.07	1.90	5.56	16.48	12.3991	0.000017*
FH	19.98	3.53	13.76	26.62	14.86	3.23	8.22	22.80	10.46	2.16	6.65	18.38	1.2362	0.295169
EH	15.42	3.00	10.56	21.63	11.90	2.86	6.89	19.25	8.33	1.64	4.79	14.54	9.9516	0.000120*
FG	16.56	3.55	10.80	23.75	12.32	3.02	7.01	19.08	8.61	1.83	5.28	15.48	8.1013	0.000568*

**Results**

Correlation analysis of transformed truss variables with SL values indicated that the effect of body size had been successfully removed from truss-network data as none of transformed truss variables showed by the significant correlation with SL ( $r < 0.300$ ,  $p > 0.005$ , data not shown). The effect of sex on the truss measurement was not examined since *C. gachua* did not exhibit sexual dimorphism on morphometric character, except the difference of coloration between mature male and female (Lim and Ng 1990; Courtenay and Williams 2003; Ward-Campbell and Beamish 2005).

The MANCOVA on transformed truss variables showed highly significant difference of morphometric characters among populations (Pillai's trace = 1.561,  $F = 10.102$ ,  $p < 0.0001$ ). Univariate analyses revealed that 20 of 26 truss variables associated with morphological characters of head, body and caudal peduncle were differed among populations (Table 2).

In PCA, the first three principal components (PCs) accounted for 49.98% of total variance, which were 21.25%

in PC1, 17.09% in PC2, and 11.64% in PC3 (Table 3). The strong factor loadings on the PCs were determined by the value of more than 0.5.

The PC1 composed of four negatively and five positively correlated truss variables which associated with oral cavity and maxillary length (AB, AL and BK), body depth (CI, CJ DH, and DI), and dorsal fin base length (DE). The PC2 composed of nine strongly correlated truss variables which only one variable was positively correlated with PC2. These morphological variations indicated variations in head length (BC, BK and KL), head depth (CK), body depth (DJ and DK), thoracic length (JK), and caudal peduncle depth (EG and EH). The PC3 composed of three negatively and three positively correlated truss variables which associated with predorsal length (CD), abdominal length (IJ), anal fin base length (HI), body depth (CI and EI) and caudal peduncle length (GH).

Scatter plot of each individuals of *C. gachua* on the first three PCs did not show any clear separation among populations (Fig. 3), although the CG-KS population was almost separated from other two populations with positive side of PC1. While CG-BK and CG-NB were separated with positive and negative sides of PC2, respectively.

**Table 3.** Factor loadings of each truss variable on the first three principal components.

Truss variables	PC1	PC2	PC3
AB	<b>-0.72280</b>	0.06351	0.25593
AL	<b>-0.70718</b>	0.50825	0.00319
BL	<b>-0.78228</b>	0.40607	-0.10798
BC	0.09367	-0.48400	0.24717
KL	0.43702	<b>-0.59960</b>	0.03626
BK	0.23917	<b>-0.76273</b>	0.04583
CL	<b>0.53108</b>	-0.34929	-0.05214
CK	-0.16361	<b>-0.67381</b>	-0.09897
CD	0.07912	0.32240	-0.44742
IJ	0.39834	0.01498	<b>-0.60651</b>
JK	0.04924	<b>0.53886</b>	-0.12222
CI	<b>0.58869</b>	0.21011	<b>-0.71922</b>
CJ	<b>-0.57693</b>	-0.29543	0.02372
DK	0.05240	<b>-0.64423</b>	0.26995
DJ	-0.30376	-0.49763	-0.03059
DE	<b>0.84926</b>	0.32300	0.27466
HI	0.45305	0.36902	<b>0.67548</b>
DH	<b>0.84836</b>	0.29659	0.23209
EI	<b>0.53117</b>	0.34913	<b>0.65920</b>
DI	<b>0.61039</b>	-0.05212	-0.49167
EF	-0.13573	0.05017	0.22073
GH	0.12903	-0.04619	<b>0.50294</b>
EG	-0.12802	<b>-0.53017</b>	0.25887
FH	0.14532	-0.21887	-0.02974
EH	0.08067	<b>-0.48838</b>	-0.25552
FG	0.05352	-0.22683	-0.03934
Variation %	21.25	17.09	11.64

From factor loadings (Table 3) and scatter plots (Fig. 3) of PCA, the results suggested that the three populations had two different patterns of morphological variations. The CG-KS population had different variations compare with others in mouth and jaw sizes, and body length and depth. The difference between CG-BK and CG-NB populations expressed on head depth and length, body depth and caudal peduncle depth. Moreover, all of three populations had the same pattern of variations in predorsal length, abdominal length, and anal fin base length.

Stepwise discriminant analysis was performed within 26 transformed truss variables. Eight out of twenty-six truss variables were selected including the five variables from head and the three variables from body measurements. The results accounted for the first two discriminant functions (DF1 and DF2) with the percentage of shape variation at 71.57 and 28.79, respectively. The most important morphometric characters in the discrimination of each truss variables were dorsal fin base length (DE) and lower head length (KL) for the negative side of DF1, while snout length (AB) and maxillary length (AL) were highly correlated with the positive side of DF1. In contrast, the most influenced variables of the DF2 were lower head length (KL) and maxillary length (AL) for

**Table 4.** Pooled-within groups correlation (r) and standardized coefficients (Z) of each selected truss variables along the first two discriminant functions (DF).

Truss variables	DF1		DF2	
	r	Z	r	Z
DE	-0.5166	-0.6037	0.2791	0.2918
KL	-0.3258	-0.3007	-0.6544	-0.6603
AL	0.3807	0.4456	0.5324	0.5292
AB	0.4091	1.0639	-0.0239	-0.3785
IJ	-0.2147	-1.2137	0.1458	0.6321
BC	0.0101	1.2118	-0.1469	-0.4480
CI	-0.2463	1.4660	0.1365	-0.4801
CJ	0.1968	0.3733	-0.2285	-0.4519
Eigen value	4.6919		1.7394	
Wilk's lambda	0.0641		0.3650	
Variation %	72.95		27.05	

**Table 5.** Classification results of *Channa gachua* into their original groups using stepwise discriminant analysis.

Pre-defined groups	Predicted group memberships			Global accuracy
	CG-BK	CG-NB	CG-KS	
CG-BK	29 (93.55%)	2 (6.45%)	0 (0%)	93.88%
CG-NB	3 (9.68%)	28 (90.32%)	0 (0%)	
CG-KS	0 (0%)	1 (2.78%)	35 (97.22%)	

the negative and positive sides, respectively (Table 4).

For population discrimination, ninety of ninety-eight samples (93.88%) of *C. gachua* were correctly classified to actual sampling locations (Wilks' lambda = 0.06413, approx.  $F_{(16,176)} = 32.4360$ ,  $p < 0.0001$ ). The corrected classification rates of each population ranged from 90.32% to 97.22% (Table 5). Interestingly, the classification rates were highly corrected indicating more differences in morphological characteristics among populations.

The examination of the bivariate ordination of each score of all *C. gachua* specimens on the first two discriminant function axes (Fig. 4) revealed a clear separation of the CG-KS population from other populations on negative side of DF1. In addition, CG-BK population was separated from CG-NB populations by DF2, although there was some overlap in spatial distribution between two populations. These results indicated that CG-KS had smaller relative head size especially snout and maxillary lengths. The body shape of CG-KS was more elongated than those of other populations. Moreover, the CG-BK samples had smaller head size than CG-KS specimens, but had larger maxilla length, abdominal length, and dorsal fin base length than CG-NB samples.

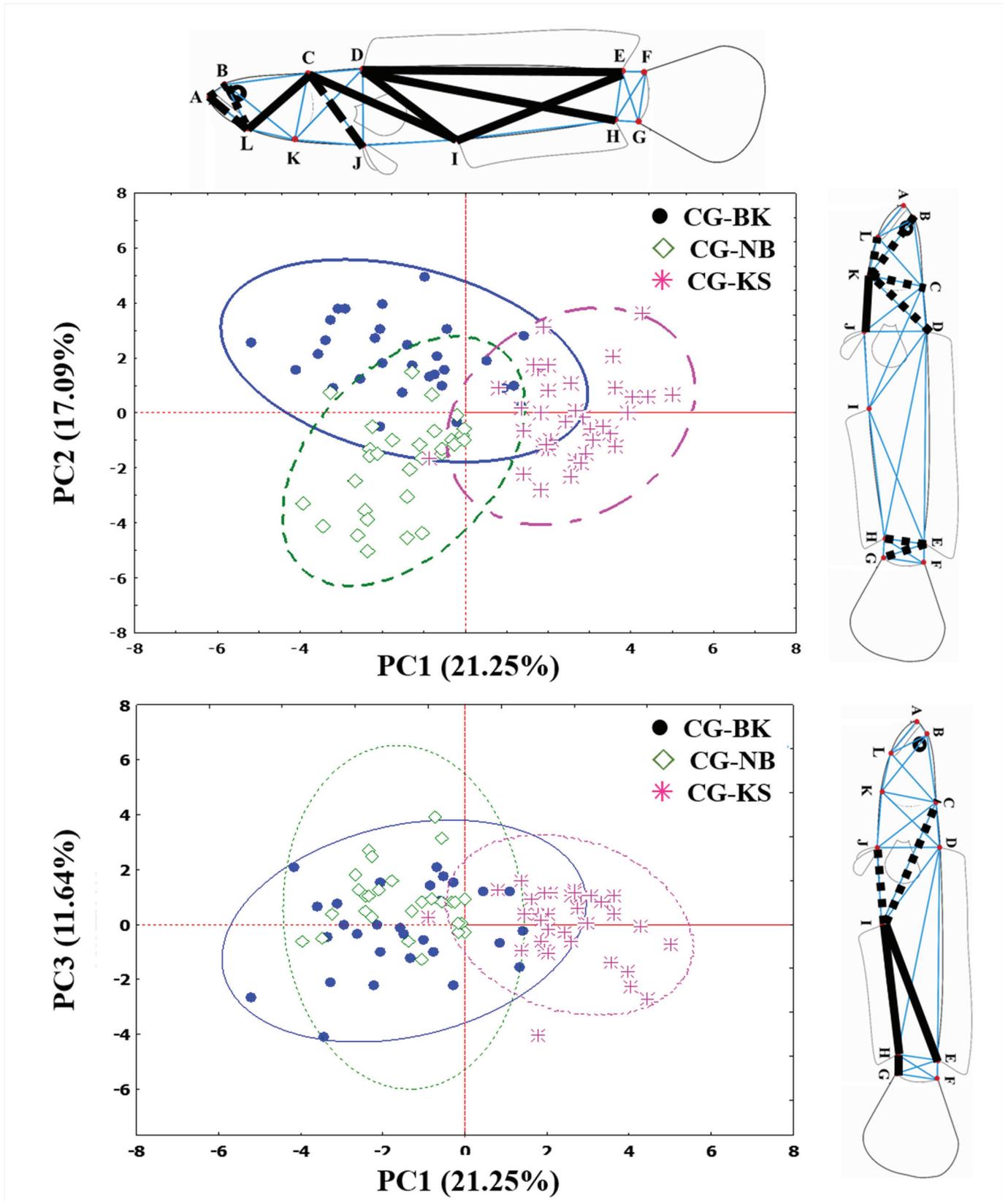


Figure 3. Scatter plots of each *Channa gachua* individual from three different localities against the first three principal component axes. Inserting images exhibit locations of measured variables which positively (bold line) and negatively (dash line) with each component.

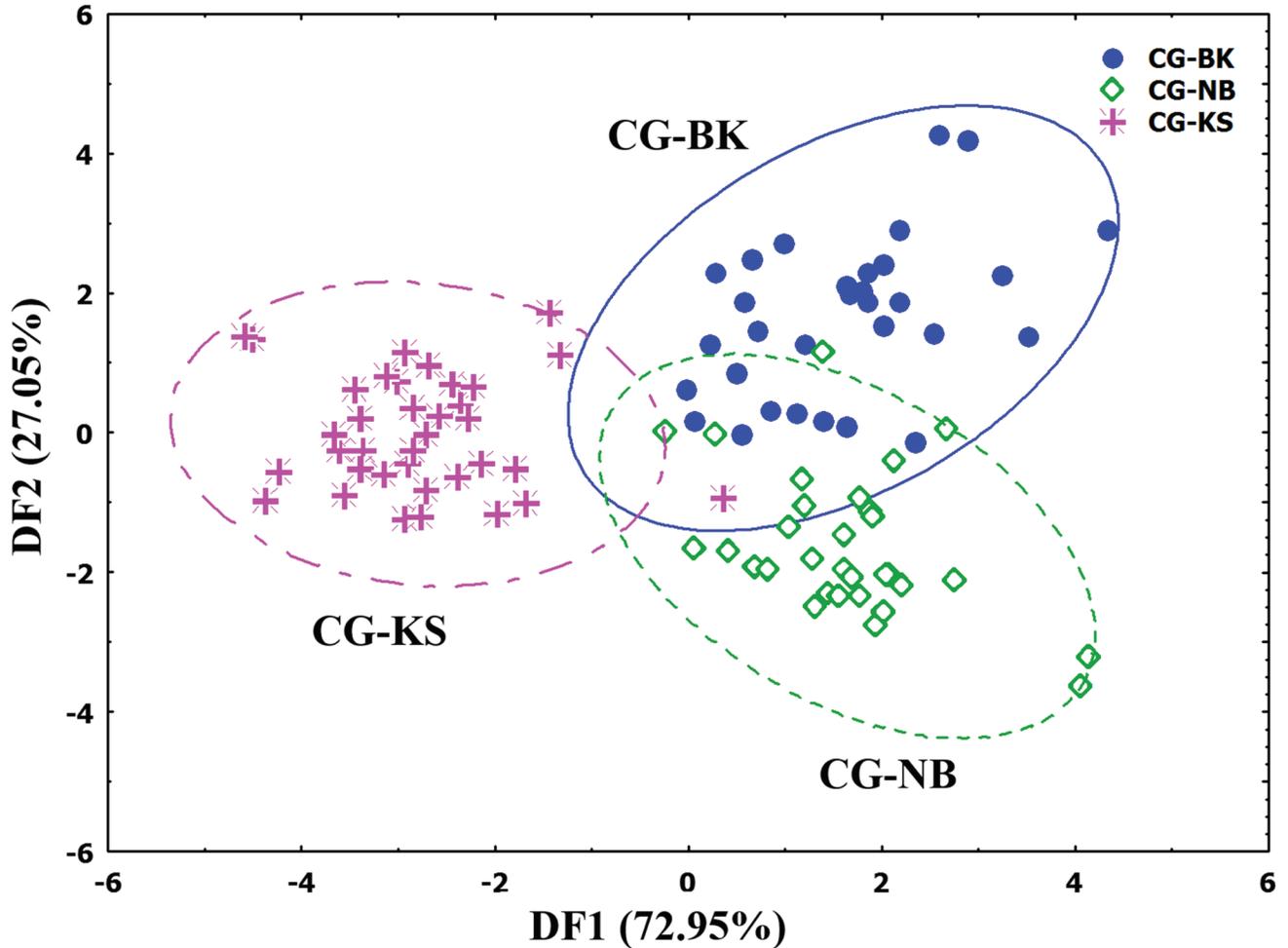


Figure 4. Ordination of all *Channa gachua* specimens along the first two discriminant function axes from discriminant function analysis on truss network data.

## Discussion

The non-significant correlation of transformed TNS variable with SL indicated that effect of body size was successfully removed from shape information by using Burnaby's size adjustment on raw measured data (Sajina et al. 2011). The finding suggested that morphometric analyses in the present study only contribute to variations in body shape among the populations of *C. gachua* (AnvariFar et al. 2011; Nie et al. 2013).

The significant differences obtained from multivariate analysis were evidently considered to discriminate the fish into three existence morphological groups according to their localities (Bagherian and Rahmani 2009; Akbarzadeh et al. 2009; Siddik et al. 2016). Theoretically, a high degree of morphological variations both within and between popula-

tions prone to be happened in fish more than in other vertebrates (Wimberger 1992; Lostrom et al. 2015; Bernatchez 2016). Those of variations are more liable to the induction of environment rather than the influence of genetics alone or the interaction between genetics and environmental factors (Pineiro et al. 2005; Drinan et al. 2012). Even though the phenotypic features are built from a genetically determined-scheme during an early ontogeny which is not fixed but also will be influenced by environmental factors, as known as phenotypic plasticity (Poulet 2008).

The results retrieved from PCA obviously showed morphological variations in head and body features among different sampling locations. Such variations could be reflected from a differential habitat use, especially the exploitation of different ecological niche with diet availability (Gatz 1979; Hegrenes 2001; Gerry et al. 2013; Crichigno et al. 2014). The results from DFA also indicated the differentiation of morpho-

metric characters associating with head characters and body length. The variation in head morphology and body length could possibly be related to differences of feeding regimes and habitat conditions such as water depth, current velocity and physico-chemical parameters of the water (Langerhans et al. 2007; Sajina et al. 2011; Drinan et al. 2012; Khan et al. 2013; Lostrom et al. 2015).

The different environmental conditions that have speedy flowing and small waterways on mountain slopes (Brinsmead and Fox 2002; Langerhans et al. 2003) may result in the large head size, shallow body depth, and short dorsal fin in CG-BK and CG-NB populations. The large head size of fish in the CG-BK and CG-NB populations were also explained the involvement of a big prey feeding behaviour (Wainwright and Richard 1995; Magnhagen and Heibo 2001; Mir et al. 2013), which reasonably correlated to the abundance of large-sized preys in fast-flowing water. Additionally, the shallow body depth was recognised to be suitable forms not only for swimming in rapid flow current (Webb 1984; Boily and Magnan 2002), but also adapted for migration to new shallow water for feeding and living appearance (Peres-Neto and Magnan 2004; Seebacher et al. 2017). In contrarily, the CG-KS fish had deep body which are thought to be an adapted form designing for swimming in low-flowing water (Webb 1984; Seebacher et al. 2017).

The morphological variations among three populations of *C. gachua* in the present study could not resolve whether are the results of genetic difference, phenotypic plasticity or interaction of both mechanisms (Cadrin 2000; Khan et al. 2013). Therefore, more details of the environmental factors from each sampling locations should be included in the further analysis of ecomorphological responses (Turan et al. 2005; Xie 2012). In addition, the geographical isolation of *C. gachua* populations are very little chance for exchanges of genetic materials in between different populations. The morphological divergence of *C. gachua* observed in the present study could possibly be affected by genetic drift and/or differential selection (Samaee and Patzner 2011).

In conclusion, the truss network analysis used in the recent work was successful to exhibit good prospects in the analysis of intraspecific variations of this fish. The analysis also indicated that those three distinctive populations of *C. gachua* analysed here should be considered as the same species with a vast array of morphological variability. The results of the present study suggested that local adaptation responded to environmental conditions can yield morphologically distinct populations. The influence of ecological diversification, especially flow regime, was considerably be involved with the different variations of the whole fish body. To be more accurate, a combination of morphological and molecular approaches will surely bring the light to understand the variations in this fish species, and could reveal relationship between morphological variation and genetic markers.

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