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Original Article

Sexual dimorphism and geographic variation of *Calotes versicolor* (Squamata: Agamidae) in northern and southern Thailand

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A B S T R A C T

The garden fence lizard, *Calotes versicolor,* is a common and widely distributed lizard throughout the Middle to Far-East including Indo-Asia and Thailand. Although this species displays variation in its morphology throughout its range, such variation has not been examined in Thailand. Thus, 20 adult lizards were examined from each of three geographically distinct populations in each of northern and southern Thailand to document any sexual and regional variation. Differentiation in characters between sexes and populations were tested using ANCOVA and principle component analysis for the mensural characters, the Mann–Whitney *U*-test for the meristic characters and the χ^2 test for coloration. Sexual dimorphism was found to occur in all populations. Males have a larger relative head size and longer relative limb lengths, whilst females exhibit a longer relative trunk length. The scalation of males was also more prominent than in females. Females in both the southern and northern Thailand populations have brighter patterns on the paired dorsolateral stripe, forearm stripe and paired nuchal spots than the corresponding males. Regional differentiation in mensural characters and coloration was more prominent in males, but no clustering of regional populations was found. Some meristic characters were congruent with regional variation. Males in the southern populations have a larger relative head size and longer relative limb lengths than those from the northern populations, but these differences were not found in females. Males in the southern populations have brighter patterns in dark bands on the trunk and colored throat patch than those in the northern populations.

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Introduction

The Oriental or Eastern garden lizard, *Calotes versicolor* Daudin (Squamata: Agamidae), also known as the garden fence lizard, has adapted to humans and so is commonly found among the undergrowth in human-made habitats; this lizard is distributed widely in Southeastern Iran, Afghanistan, Nepal, Sri Lanka, India, southern China, Myanmar, Thailand, Laos, Vietnam, Peninsular Malaysia and Sumatra in Indonesia (Radder, 2006). Within Thailand, *C. versicolor* probably occurs in all the provinces (Taylor, 1963). Geographic differences among populations have been reported in this species, with specimens from the Himalayan mountain complex in Afghanistan, Pakistan and India being distinctly different from those in other parts of the country (Auffenberg and Rehman, 1993). Thus, *C. versicolor* in this area was divided into two subspecies—*C. v. versicolor* and *C. v. nigrigularis*—which are found at elevations below 300 m and 300–1800 m above mean sea level (amsl), respectively. According to Auffenberg and Rehman (1993), only *C. v. versicolor* is found in Thailand.

Sexual dimorphism has been widely studied in lizards (Ji et al., 2002; Olsson et al., 2002; Kuo et al., 2009), and in *C. versicolor*, as in many other animals, sexual differences occur in morphology, shape, size and color (Auffenberg and Rehman, 1993; Radder et al., 2001; Ji et al., 2002). The occurrence of morphological differences between males and females could arise from natural selection processes, where the different evolutionary trends are explained as the results of three major forces that differentially act on males and females of a population: fecundity, sexual and natural selection (Olsson et al., 2002). Sexual size dimorphism may appear at any stage during the life history of *C. versicolor* (Radder, 2006), whilst differences in color and stripe patterns among adult males, adult females and juveniles are known (Auffenberg and Rehman, 1993).

Although Radder et al. (2001) and Ji et al. (2002) reported sexual differences in this species in some regions, it is still unclear if they

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occur in other parts of its range including within Asia, or in the same patterns. Indeed, sexual dimorphism in this species has not been studied in Thailand. In order to start to address this, in this study the mensural and meristic (scalation) characters plus the stripe patterns of *C. versicolor* from three locations each in the northern and southern region of Thailand were examined. These two regions represent the Indochinese subregion and Sundaic subregion for northern and southern Thailand, respectively. The morphological differences between the regional populations in both sexes were also investigated separately.

Materials and methods

Sampling

A sample of 20 adult *C. versicolor* individuals (10 males and 10 females) was captured from each of the three geographically separated sampling sites in the northern region of Thailand, and the same again for the southern region, between August 2008 and September 2009. These 60 samples (total) per region were collected at three localities each, comprised of Mae Hong Son (47Q 384049 E 2079323 N), Chiang Mai (47Q 509105 E 2084247 N) and Nan (47Q 681552 E 2078573 N) in northern Thailand, and Songkla (47N 656230 E 759923 N), Krabi (47P 513357 E 885169 N) and Ranong (47P 459585 E 1097063 N) in southern Thailand. The northern and southern populations were located between 180–530 m amsl and 4–50 m amsl, respectively. The climatic conditions are different between northern and southern Thailand. In northern Thailand, the average temperature was 26.3 °C (range 12.1–40.8 °C) and the average monthly rainfall was 107.9 mm. In southern Thailand, the average temperature was 27.4 °C (range 17.9–36.1 °C) and the average monthly rainfall was 216.0 mm (climatic data from Thai Meteorological Department for 2000–2009). All samples were cataloged and deposited at the Chulalongkorn University Museum of Natural History, Bangkok, Thailand.

Morphological study

The sex and maturity of each specimen were determined from abdominal dissection (Zug et al., 2006). In this study, 54 morphological characters were recorded for each specimen as follows.

Mensural character

Thirty-two characters were measured: eye-ear length (EyeEar) head height (HeadH), head length (HeadL), head width (HeadW), interorbital width (Interorb), jaw width (JawW), naris-eye length (NarEye), snout-eye length (SnEye), snout width (SnW), snout to pineal (SP), snout to nostril (SN), labial to ear length (LE), labial length (LL), tympanum diameter (ED), 4th finger (4FingLng), 4th toe (4ToeLng), crus length (CrusL), forefoot length (ForefL), hindfoot length (HindfL), lower arm length (LoArmL), pectoral width (PectW), pelvic width (PelvW), snout-vent length (SVL), snout-forelimb length (SnForel), tail thickness (TailTh), tail length (TailL), tail width (TailW), trunk length (TrunkL), upper arm length (UpArmL), upper leg length (UpLegL), total length (TL) and vent width (VentW).

Meristic characters

The 12 scale regions selected for examination were: the canthus rostralis (CanthR), dorsal eyelid scales (Eyelid), dorsal head scale (HeadSLn), head scales (HeadSTr), infralabials (Inflab), snout scales (SnS), supralabials (Suplab), gular scales (GuS), forefoot lamellae (4FingLm), hindfoot lamellae (4ToeLm), ventral scales (VentS) and midbody scales (Midbody).

Stripe patterns

The 10 stripe patterns selected for examined were: the cheek color (CheekCol), cheek strip (CheekSt), paired dorsolateral stripes (DorsSt), forearm stripe (ForearSt), paired nuchal spots (NucSpot), dark bands on trunk (TrnkBand), midventral dark line (MidvLine), throat stripes (ThroatSt), colored throat patch (ThroatPa) and ventral trunk striping (TrunkSt).

Each character, and its abbreviation, followed those defined and used by Zug et al. (2006), and Auffenberg and Rehman (1993). All characters were measured on the right side of the body (Fig. 1). Mensural characters were taken to the closest 0.01 mm using a dial caliper, whilst meristic characters were counted under a stereomicroscope and stripe patterns were observed by eye.

Data analysis

Variations within each region (between the three locality based populations) were analyzed using principal component analysis (PCA) of the mensural and meristic data. All mensural characters were $\log_e$-transformed for parametric tests. Intersexual differences and geographic differences in the mensural characters of adult lizards from the northern and southern populations were compared using ANCOVA with SVL as the covariate. However, the SVL values of these samples were compared using Student's t test. The differences in meristic characters were compared using Mann–Whitney U-tests. Sexual dimorphism and geographical variation were described using PCA. Additionally, stripe patterns were analyzed using a χ^2 test and presented as occurrence percentages. All statistical analysis was carried out using SPSS for Windows (version 17; SPSS Inc.; Chicago, IL, USA). The significance of any differences was tested at the $p < 0.05$ level.

Results

The PCA of within-region samples showed only one group for the three locality-based populations sampled in northern Thailand (Fig. 2), and the same again for the three populations within southern Thailand (Fig. 3). Thus, the samples from the three localities in the northern region were grouped into one northern population of 60 lizards (30 males and 30 females), and likewise the samples from the three localities in southern region were grouped into one southern population of 60 lizards (30 males and 30 females).

Sexual dimorphism

Mensural characters

The mean ± SE of each morphological trait for males and females in both the northern and the southern populations are presented in Tables 1–3. The mean SVL values of males were significantly larger than those of females in both the northern (84.11 ± 0.96 mm versus 78.67 ± 0.99 mm, respectively, $t = 3.942$, $p < 0.001$) and southern populations (87.08 ± 0.86 mm versus 75.74 ± 0.89 mm, respectively, $t = 9.161$, $p < 0.001$).

Eight of the 14 head measurements (EyeEar, HeadL, HeadW, JawW, NarEye, LE, LL and ED) showed significant differences between the sexes in both populations, and head size was significantly greater in males than in females (Table 1). Differences between the sexes in limb, tail and body sizes were also found to be significant. The eight characters associated with limb length (4FingLng, 4ToeLng, CrusL, ForefL, HindfL, LowArmL, UpArmL and UpLegL) were all statistically longer in males than in females (Table 2). Moreover, TailTh and VentW were significantly larger in males than in females in both populations (Table 2).

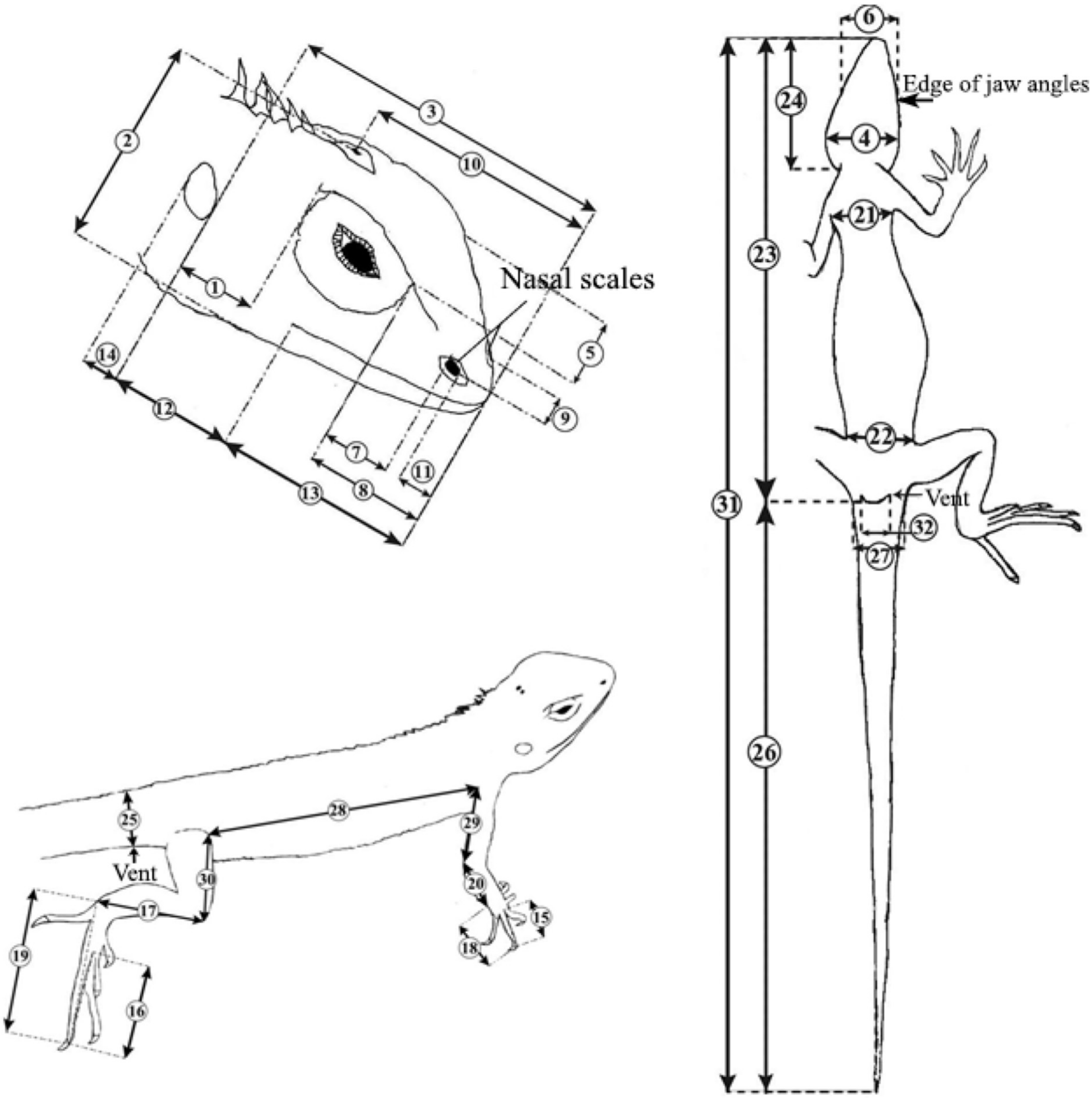

Fig. 1. Measurement of mensural characters in *Calotes versicolor*: (1) EyeEar; (2) HeadH; (3) HeadL; (4) HeadW; (5) Interorb; (6) JawW; (7) NarEye; (8) SnEye; (9) SnW; (10) SP; (11) SN; (12) LE; (13) LL; (14) ED; (15) 4FingLng; (16) 4ToeLng; (17) CrusL; (18) ForefL; (19) HindfL; (20) LoArmL; (21) PectW; (22) PelvW; (23) SVL; (24) SnForel; (25) TailTh; (26) TailL; (27) TailW; (28) TrunkL; (29) UpArmL; (30) UpLegL; (31) TL; (32) VentW.

TailL and TL were significantly larger in males than in females only in the southern population, likewise TailW was significantly larger in males than in females only in the northern population. Note here that *C. versicolor* does not shed its tail, which could otherwise potentially compound any tail length analyses. With respect to the SVL, TrunkL was significantly larger in females than in males in both the northern and southern populations (Table 2).

The results of the multivariate analyses of the mensural characters between sexes also revealed clear differences. The PCA of adult lizards showed a clustering of each sex in both the northern and southern populations (Fig. 4A and B). PCA revealed VentW, TailTh, TailW, HeadW, UpLegL, EyeEar, CrusL, SnForel, HindfL, 4ToeLng, 4FingLng, UpArmL, LoArmL, HeadL, LE, JawW, HeadH, and Interorb being the major loadings on the first component (PC1), whilst the EyeEar, CrusL, SnForel, TL, TailL, ForefL, HindfL, 4ToeLng, 4FingLng, NarEye, UpArmL, LoArmL, HeadL, SnEye, LE and SVL were the major loadings for the second component (PC2) and the SnEye, SnW, PelvW, TrunkL, SN, SVL, JawW, PectW, LL, HeadH, ED, Interorb and SP were the major loadings for the third component (PC3) in the northern populations. PC1, PC2 and PC3 at 26.63%, 26.46% and 24.28% of the total variation, respectively, accounted for 78.40% of the total variance. Additionally, for the southern population the PCA revealed two components—LL, Interorb, SnW, SP, SVL, HeadL, JawW, SnEye, TrunkL, ED, PelvW, SnForel, SN, EyeEar, TailW, PectW, NarEye, UpArmL, TailTh, UpLegL, CrusL, HeadW, LoArmL, LE, HeadH, VentW, TL and TailL were the major loadings for PC1 and SP, SVL, HeadL, SnEye, SnForel, EyeEar, TailW, PectW, NarEye, ForefL, 4FingLng, HindfL, 4ToeLng, UpArmL, TailTh, UpLegL, CrusL, HeadW, LoArmL, LE, HeadH, VentW, TL and TailL were the major loadings in PC2. PC1 and PC2, at 44.36% and 39.31% of the total variation, respectively, accounted for 83.63% of the total variance.

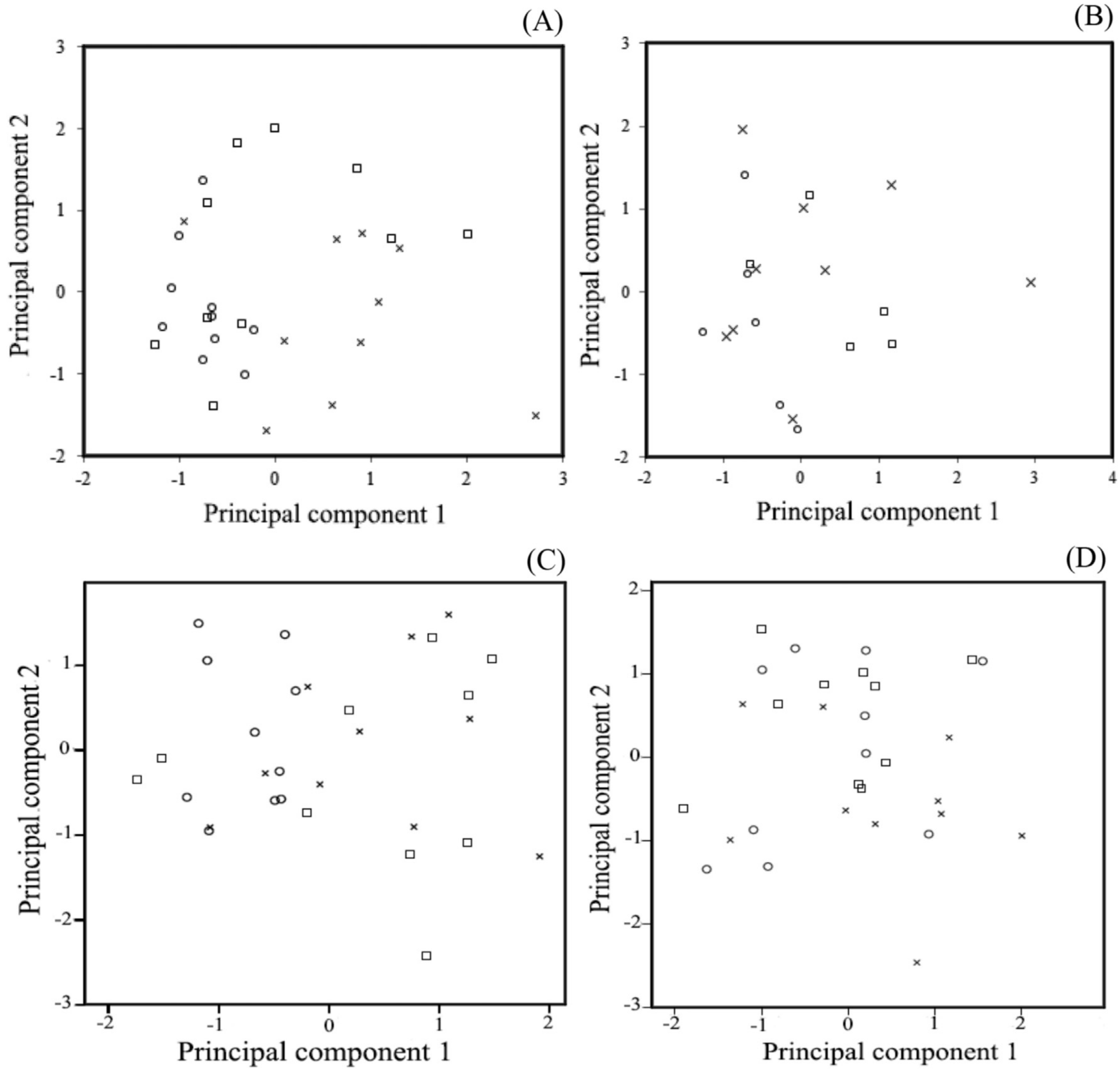

Fig. 2. PCA of *Calotes versicolor* in northern Thailand for: (A) mensural characters in males; (B) mensural characters in females; (C) meristic characters in males; (D) meristic characters in females. (○, Mae Hong Son; □, Chiang Mai; ×, Nan).

Meristic characters

The meristic characters of the mature males and females were found to exhibit a much lower degree of sexual dimorphism than the mensural characters, but significant differences between the genders within populations still existed (Table 3). Across both the northern and southern populations, from the 12 characters evaluated, only one (4FingLm) was significantly different, being more numerous in males than in females in both populations. However, within either regional population, the numbers of HeadSTr, GuS and VentS in males were statistically greater than in females from the northern population, whilst conversely the numbers of CanthR and HeadSLn in males were statistically greater than in females in the southern population (Table 3).

The PCA of the meristic characters in the northern population revealed 15.98%, 15.34%, 12.91%, 12.39% and 11.45% of the total variation was compartmented into PC1, PC2, PC3, PC4 and PC5, respectively, accounting for 68.07% of the total variance. 4FingLm and 4ToeLm were the major loadings on PC1, Suplab and GuS on PC2, Midbody and VentS on PC3, HeadSLn, SnS and Inflab on PC4 and Eyelid, HeadSTr, and CanthR on PC5. However, the PCA of northern populations showed overlapping between sexes (Fig. 4C). In southern populations, the PCA revealed 14.94%, 14.21%, 14.11%, 14.00% and 11.99% of the total variation in PC1, PC2, PC3, PC4 and PC5, respectively, although this accounted for 69.25% of the total variation. Within these groupings, 4FingLm, HeadSTr and 4ToeLm were the major loading traits on PC1, GuS, Inflab and Suplab on PC2, VentS, CanthR and Midbody on PC3, SnS on PC4 and Suplab on PC5. The PCA of the southern population could not be separately discerned (Fig. 4D). However, note that Fig. 4 only shows PC1 and PC2 and not PC3, PC4 and PC5 for the southern and northern populations.

Stripe patterns

Females from the northern populations displayed DorsSt, ForearSt, NucSpot and TrnkBand more frequently than males, whereas CheekCol was more frequently found in males. In the southern populations, DorsSt, ForearSt and NucSpot were more often found in females, whereas ThroatPa was more frequently found in males.

Geographic variation

Mensural characters

The mean SVLs in males from the northern populations were significantly smaller than the SVLs in males from the southern populations (84.11 ± 0.96 mm versus 87.08 ± 0.86 mm, respectively,

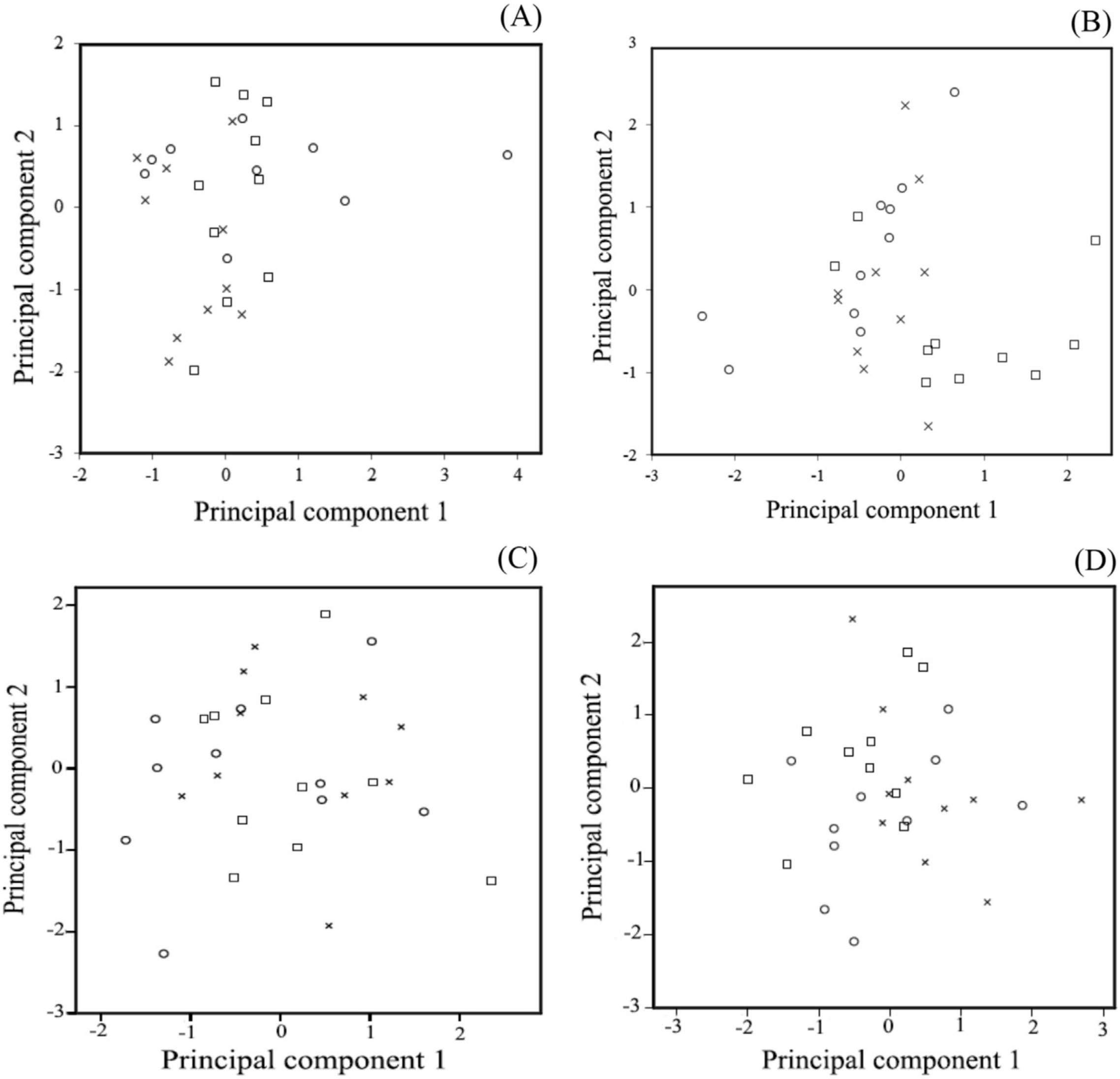

Fig. 3. PCA of *Calotes versicolor* in southern Thailand for: (A) mensural characters in males; (B) mensural characters in females, (C) meristic characters in males; (D) meristic characters in females. (○, Songkla; □, Krabi; ×, Ranong).

Table 1
Summary of head measurements of *C. versicolor* in northern and southern populations in Thailand. Data are shown as mean ± SE with the range shown in brackets and are derived from 30 samples each. All measurements are in millimeters. The *F*- and *p*-values from ANCOVA are also shown.

Character	Northern population				Southern population			
	Males	Females	*F*	*p*	Males	Females	*F*	*p*
EyeEar	5.64 ± 0.10 (4.70–6.62)	4.54 ± 0.06 (4.06–5.25)	77.483	<0.001	6.33 ± 0.10 (5.24–7.28)	4.55 ± 0.06 (3.98–5.53)	73.092	<0.001
HeadH	12.49 ± 0.18 (11.10–14.92)	11.54 ± 0.22 (9.37–14.06)	1.870	0.177	14.05 ± 0.23 (11.70–16.40)	10.87 ± 0.15 (9.67–12.77)	27.272	<0.001
HeadL	19.63 ± 0.21 (17.86–22.10)	17.41 ± 0.25 (14.42–19.62)	26.252	<0.001	21.15 ± 0.23 (18.56–23.52)	17.28 ± 0.21 (15.37–19.87)	33.982	<0.001
HeadW	16.55 ± 0.30 (13.14–19.86)	13.82 ± 0.23 (11.70–16.10)	28.078	<0.001	19.67 ± 0.35 (16.10–23.48)	13.21 ± 0.20 (11.45–15.52)	87.132	<0.001
Interorb	8.19 ± 0.10 (7.14–9.44)	7.42 ± 0.11 (6.38–8.38)	7.296	0.009	8.78 ± 0.09 (7.81–9.70)	7.44 ± 0.13 (6.30–9.16)	–*	
JawW	13.43 ± 0.20 (11.54–15.64)	12.06 ± 0.16 (10.60–13.45)	10.556	0.002	14.26 ± 0.21 (12.40–16.82)	11.78 ± 0.18 (10.20–14.20)	5.085	0.028
NarEye	4.50 ± 0.05 (4.05–5.18)	4.13 ± 0.06 (3.45–4.72)	5.967	0.018	4.77 ± 0.06 (4.21–5.37)	4.02 ± 0.07 (3.52–5.28)	8.550	0.005
SnEye	8.22 ± 0.10 (7.38–9.67)	7.66 ± 0.10 (6.43–8.72)	2.189	0.145	8.77 ± 0.08 (7.98–9.48)	7.55 ± 0.10 (6.73–8.71)	11.342	0.001
SnW	4.91 ± 0.07 (4.12–5.74)	4.69 ± 0.06 (3.91–5.25)	0.295	0.589	5.40 ± 0.06 (4.74–6.15)	4.76 ± 0.08 (4.04–5.70)	1.162	0.286
SP	15.95 ± 0.16 (14.55–18.14)	14.94 ± 0.19 (12.90–17.44)	2.102	0.153	16.70 ± 0.15 (15.16–18.64)	14.49 ± 0.16 (13.12–16.34)	8.937	0.004
SN	3.67 ± 0.07 (3.00–4.40)	3.47 ± 0.05 (3.04–3.97)	–*		3.93 ± 0.04 (3.58–4.54)	3.41 ± 0.05 (2.92–4.09)	9.051	0.004
LE	5.51 ± 0.10 (4.65–6.75)	4.65 ± 0.07 (3.94–5.86)	26.105	<0.001	6.33 ± 0.10 (5.25–7.35)	4.65 ± 0.08 (3.76–5.68)	36.272	<0.001
LL	14.64 ± 0.16 (13.33–16.44)	13.45 ± 0.17 (11.28–14.63)	8.042	0.006	15.39 ± 0.17 (13.03–17.52)	12.99 ± 0.18 (11.37–15.00)	4.409	0.040
ED	3.15 ± 0.08 (2.55–4.30)	2.67 ± 0.05 (2.20–3.24)	9.786	0.003	3.44 ± 0.07 (2.71–4.18)	2.69 ± 0.05 (2.22–3.36)	5.206	0.026

* ANCOVA could not be performed due to heterogeneity of regression slopes.

Table 2
Summary of limb, body and tail measurements of *C. versicolor* in northern and southern populations in Thailand. Data are shown as mean ± SE, with the range in brackets, and are derived from 30 samples each unless indicated otherwise (n). All measurements are in millimeters. The F- and p-values from ANCOVA are shown.

Character	Northern population				Southern population			
	Males	Females	F	p	Males	Females	F	p
4FingLng	9.76 ± 0.15[b] (8.50–11.88)	8.48 ± 0.12 (7.32–9.50)	26.566	<0.001	10.33 ± 0.16 (7.14–11.36)	8.37 ± 0.06 (7.50–8.92)	37.447	<0.001
4ToeLng	14.88 ± 0.17 (13.33–16.81)	13.00 ± 0.14 (11.56–14.35)	46.039	<0.001	16.11 ± 0.15 (14.24–18.00)	13.40 ± 0.10[a] (12.54–14.20)	60.222	<0.001
CrusL	18.15 ± 0.15 (16.72–19.96)	16.27 ± 0.20 (14.33–19.00)	35.952	<0.001	18.91 ± 0.16 (17.33–20.85)	15.89 ± 0.15 (14.16–17.70)	44.394	<0.001
ForefL	13.69 ± 0.19[b] (12.02–15.48)	11.98 ± 0.14 (10.24–13.52)	32.638	<0.001	14.72 ± 0.22 (11.19–16.75)	11.95 ± 0.13 (10.04–13.50)	31.908	<0.001
HindfL	24.24 ± 0.28 (21.02–27.38)	21.44 ± 0.28[a] (18.80–24.36)	26.629	<0.001	25.95 ± 0.25 (22.80–28.80)	21.68 ± 0.19[a] (19.76–23.64)	44.952	<0.001
LoArmL	14.20 ± 0.14 (12.03–15.72)	12.85 ± 0.13 (11.41–14.40)	27.747	<0.001	14.92 ± 0.13 (13.62–16.80)	12.43 ± 0.17 (10.30–15.00)	19.672	<0.001
PectW	14.34 ± 0.24 (12.44–16.88)	12.90 ± 0.20 (10.94–14.66)	5.279	0.025	15.17 ± 0.27 (12.20–19.76)	11.92 ± 0.18 (10.12–13.93)	11.729	0.001
PelvW	12.20 ± 0.22 (10.46–14.70)	11.91 ± 0.14 (10.20–13.37)	–*		13.05 ± 0.18 (10.98–15.07)	11.42 ± 0.19 (9.51–13.44)	0.015	0.902
SnForel	26.12 ± 0.31 (23.10–29.59)	22.32 ± 0.28 (19.40–25.20)	97.060	<0.001	28.94 ± 0.34 (25.54–32.40)	21.99 ± 0.28 (19.46–25.08)	91.564	<0.001
UpArmL	14.10 ± 0.13 (12.49–15.47)	12.88 ± 0.17 (10.90–14.36)	13.140	0.001	15.01 ± 0.18 (13.50–17.42)	12.28 ± 0.13 (11.00–13.88)	35.044	<0.001
UpLegL	19.99 ± 0.21 (16.84–22.50)	18.10 ± 0.20 (16.07–20.80)	21.058	<0.001	21.08 ± 0.22 (18.54–24.44)	17.89 ± 0.18 (15.98–20.00)	21.155	<0.001
TrunkL	39.88 ± 0.62 (34.24–45.42)	38.11 ± 0.68 (31.14–43.88)	4.556	0.037	40.97 ± 0.53 (37.27–49.10)	36.55 ± 0.55 (30.16–43.48)	9.243	0.004
TailTh	10.01 ± 0.14 (8.12–11.22)	6.68 ± 0.11 (5.37–7.84)	346.21	<0.001	10.65 ± 0.15 (8.98–12.64)	6.29 ± 0.13 (5.34–8.32)	210.36	<0.001
TailL	233.63 ± 3.57[e] (210.00–260.00)	208.55 ± 5.94[d] (170.00–280.00)	–*		254.90 ± 2.38[d] (236.00–278.00)	213.14 ± 3.81[c] (174.00–250.00)	6.665	0.014
TailW	10.61 ± 0.15 (9.14–12.11)	9.22 ± 0.14 (7.78–10.92)	21.795	<0.001	10.69 ± 0.15 (9.26–12.92)	8.87 ± 0.19 (7.02–11.28)	2.417	0.126
TL	318.32 ± 4.82[e] (286–357)	282.90 ± 5.77[d] (236.00–324.00)	–*		343.00 ± 3.04[d] (322.00–377.00)	286.52 ± 4.29[c] (239.00–322.00)	11.414	0.002
VentW	9.10 ± 0.15 (7.25–10.58)	7.38 ± 0.12 (6.26–8.87)	51.700	<0.001	9.02 ± 0.14 (7.50–10.00)	6.84 ± 0.18 (5.20–9.12)	16.037	<0.001

* ANCOVA could not be performed due to heterogeneity of regression slopes.
[a] $n = 29$.
[b] $n = 28$.
[c] $n = 21$.
[d] $n = 20$.
[e] $n = 19$.

Table 3
Summary of scalation characters of *C. versicolor* in northern and southern populations in Thailand. Data are shown as mean ± SE, with the ranges shown in brackets and are derived from 30 samples unless indicated otherwise (n). The Z- and p-values from Mann–Whitney U-test are also shown.

Character	Northern population				Southern population			
	Males	Females	Z	p	Males	Females	Z	P
CanthR	7.90 ± 0.14 (7–10)	8.00 ± 0.08 (7–9)	−0.932	0.352	7.87 ± 0.09 (7–9)	7.57 ± 0.09 (7–8)	−2.165	0.030
Eyelid	9.87 ± 0.20 (7–12)	9.37 ± 0.17 (8–11)	−1.949	0.051	10.03 ± 0.20 (8–13)	9.53 ± 0.19 (8–13)	−1.642	0.101
HeadSLn	13.17 ± 0.21 (11–15)	13.43 ± 0.26 (11–16)	−0.709	0.479	13.83 ± 0.19 (11–16)	13.23 ± 0.26 (11–17)	−2.344	0.019
HeadSTr	13.43 ± 0.21 (11–16)	12.47 ± 0.27 (10–19)	−3.633	<0.001	13.40 ± 0.25 (11–16)	13.03 ± 0.22 (11–16)	−1.220	0.223
Inflab	9.50 ± 0.12 (8–11)	9.30 ± 0.16 (8–11)	−0.853	0.394	9.27 ± 0.11 (8–10)	9.33 ± 0.12 (8–11)	−0.104	0.917
SnS	6.13 ± 0.08 (5–7)	6.00 ± 0.08 (5–7)	−1.146	0.252	6.47 ± 0.11 (5–8)	6.40 ± 0.10 (6–7)	−0.457	0.647
Suplab	9.87 ± 0.12[a] (9–11)	9.62 ± 0.12 (8–11)	−1.253	0.210	9.47 ± 0.11 (8–11)	9.17 ± 0.11 (8–10)	−1.797	0.072
GuS	12.20 ± 0.32 (9–15)	11.03 ± 0.23 (9–14)	−2.496	0.013	11.27 ± 0.22 (9–14)	10.83 ± 0.19 (9–13)	−1.427	0.154
4FingLm	19.68 ± 0.25 (16–22)	18.57 ± 0.20[b] (17–21)	−3.366	0.001	20.27 ± 0.24 (18–23)	19.37 ± 0.18 (17–21)	−2.741	0.006
4ToeLm	23.90 ± 0.21[a] (22–26)	23.21 ± 0.23 (21–25)	−1.806	0.071	25.07 ± 0.27[a] (22–28)	24.79 ± 0.23 (23–28)	−0.789	0.430
VentS	58.93 ± 0.74 (52–70)	56.37 ± 0.72 (51–66)	−2.497	0.013	58.70 ± 0.55 (53–64)	58.13 ± 0.62 (52–66)	−0.721	0.417
Midbody	43.53 ± 0.34 (41–48)	44.10 ± 0.44 (38–50)	−1.058	0.290	43.67 ± 0.56 (35–49)	44.50 ± 0.54 (39–51)	−0.813	0.416

$t = 2.296$, $p = 0.025$), but in females this was the other way round with females from the northern populations having a larger SVL than those from the southern populations (78.67 ± 0.99 mm versus 75.74 ± 0.89 mm, respectively, $t = -2.200$, $p = 0.032$).

All of the four head measurements (EyeEar, HeadL, Interorb, and SnW) showed significant differences between populations in both sexes (Table 4). Only two (4ToeLng and HindfL) of the eight limb lengths showed significant differences between populations in both sexes. However, seven of the eight limb lengths evaluated were significantly different between populations of males, whereas only two were significantly different between populations of females (Table 4).

The trunk length was not significantly different between males or between females in all populations, but the two tail measurements, TailL and TL, were significantly different between populations in both sexes (Table 4).

The PCA revealed no clustering in either population of females or males (Fig. 5A and B). The PCA of all females showed 26.44%, 18.89%, 13.08%, 9.30% and 7.89% of the total variation expressed in PC1, PC2, PC3, PC4 and PC5, respectively, which together accounted for 75.60% of the total variation.

Within these five components, SnForel, SnEye, SN, LL, HeadL, EyeEar, Interorb, SnW, NarEye, SP, LE SVL, HeadW, JawW and TailTh were the major loadings on PC1, with SVL, HeadH, VentW, PectW, TailW, HeadW, JawW, PelvW, TailTh and TrunkL on PC2, 4ToeLng, HindfL, ForefL and 4FingLng on PC3, TailL and TL on PC4 and LoArmL, and UpArmL on PC5.

For males, the PCA revealed 26.43%, 17.38%, 16.23%, 9.19% and 8.25% of the total variation expressed in PC1, PC2, PC3, PC4 and PC5, respectively, which together accounted for 77.48% of the total variation. Within these five components, LL, SVL, ED, TrunkL, SnW, HeadL, SP, JawW, SnForel, PectW, HeadH, SN, TailTh, Interorb, PelvW and EyeEar were the major loadings on PC1, HindfL, 4ToeLng, UpLegL, CrusL, ForefL, 4FingLng and UpArmL on PC2, HeadL, SnForel, Interorb, NarEye, SnEye, HeadW, EyeEar and LE on PC3, VentW and TailW on PC4 and TailL and TL on PC5.

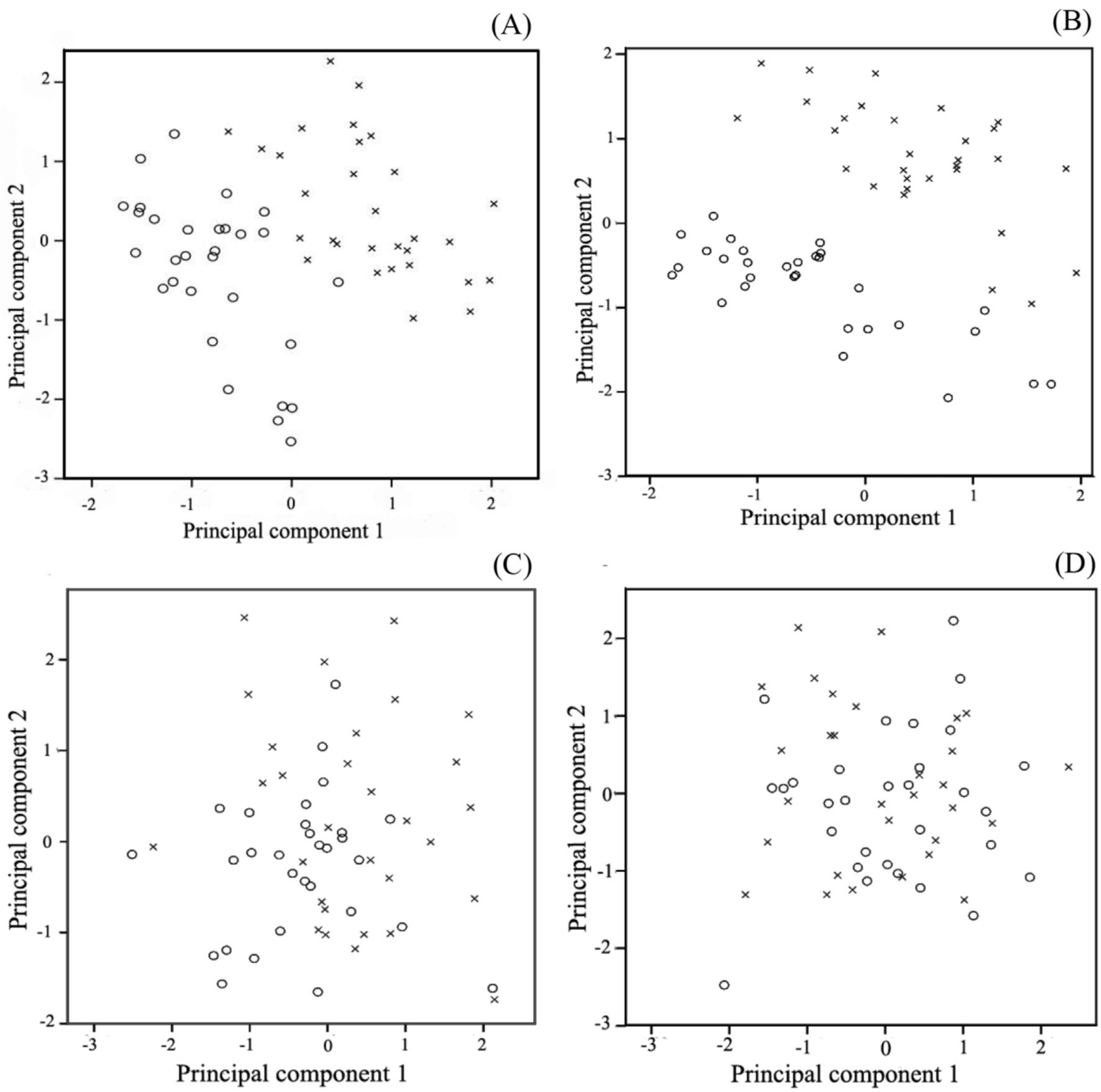

Fig. 4. PCA of *Calotes versicolor* for: (A) mensural characters in northern Thailand; (B) mensural characters in southern populations; (C) meristic characters in northern populations; (D) meristic characters in southern populations. (○, females; ×, males).

Meristic characters

The meristic characters of both populations were found to be slightly different in both sexes, with the numbers significantly different between the northern and southern populations of HeadSLn, SnS, Suplab, GuS and 4ToeLm between populations in males, and the numbers of CanthR, HeadSTr, SnS, Suplab, 4FingLm, 4ToeLm and VentS in females. These were split as having significantly more CanthR, Suplab and GuS in the northern populations compared to the southern ones, but more HeadSLn, HeadSTr, SnS, 4FingLm and 4ToeLm in the southern populations.

PCA revealed no clustering of either population for either females or males (Fig. 5C and D). With respect to females, the PCA revealed 16.56%, 14.59%, 13.61%, 11.68% and 10.93% of the total variation in females being found in PC1, PC2, PC3, PC4 and PC5, respectively, although this only accounted for 67.37% of the total variation. Nevertheless, 4ToeLm and 4FingLm were the major loadings on PC1, Suplab, Inflab and GuS on PC2, Midbody and VentS on PC3, HeadSLn and SnS on PC4 and HeadSTr and Eyelid on PC5.

With respect to males, PCA revealed 16.83%, 15.78%, 15.10%, 11.91% and 9.85% of the total variation in PC1, PC2, PC3, PC4 and PC5, respectively, together accounting for 69.47% of the total variation. Within these components the major loadings were: GuS, Suplab and Inflab on PC1; 4ToeLm and 4FingLm on PC2; VentS, Midbody and Eyelid on PC3; HeadSLn and SnS on PC4; and CanthR on PC5. Fig. 5 shows only PC1 and2 and not PC3, PC4 and PC5 for both sexes.

Stripe patterns

Females showed no significant differences between populations, whilst in males only the TrnkBand ($\chi^2 = 6.405$, $p = 0.011$) and ThroatPa ($\chi^2 = 15.864$, $p < 0.001$) were found more often in southern populations.

Discussion

Sexual dimorphism

Differences in the relative head and body sizes are amongst the most widespread expressions of sexual dimorphism within *C. versicolor* (Radder et al., 2001; Ji et al., 2002; Radder, 2006; Zug et al., 2006). This study confirmed that males have larger heads whilst females have a greater trunk length in both the northern and southern populations in Thailand. Additionally, the tail thickness is

Table 4
F-values and *p*-values from ANCOVA of mensural characters of *C. versicolor* in males and females between populations in northern and southern Thailand.

Character	Males		Females		Character	Males		Females	
	F	*p*	*F*	*p*		*F*	*P*	*F*	*p*
Head					**Body**				
EyeEar	19.803	<0.001	6.433	0.014	PectW	0.725	0.398	8.241	0.006
HeadH	27.322	<0.001	2.298	0.135	PelvW	3.924	0.052	–*	
HeadL	27.895	<0.001	5.807	0.019	VentW	1.252	0.268	3.406	0.07
HeadW	35.663	<0.001	0.246	0.622	**Limb**				
Interorb	12.561	0.001	10.196	0.002	4FingLng	2.604	0.112	–*	
JawW	2.55	0.116	0.996	0.323	4ToeLng	22.617	<0.001	16.779	<0.001
NarEye	6.168	0.016	<0.001	0.996	CrusL	6.324	0.015	0.081	0.777
SnEye	13.272	0.001	1.38	0.245	ForefL	5.998	0.018	–*	
SnW	21.272	<0.001	6.536	0.013	HindfL	13.837	<0.001	5.459	0.023
SP	6.775	0.012	0.004	0.947	LoArmL	7.851	0.007	0.459	0.501
SN	–*		0.032	0.858	UpArmL	9.442	0.003	2.852	0.097
LE	26.008	<0.001	2.466	0.122	UpLegL	6.954	0.011	1.175	0.283
LL	3.929	0.052	0.01	0.919	**Tail**				
ED	2.611	0.112	5.791	0.019	TailTh	3.337	0.073	1.081	0.303
Body					TailL	29.507	<0.001	11.995	0.001
TrunkL	1.828	0.182	0.027	0.871	TailW	0.829	0.366	–*	
SnForel	46.37	<0.001	4.16	0.046	TL	29.888	<0.001	25.884	<0.001

* ANCOVA could not be performed due to heterogeneity of regression slopes.

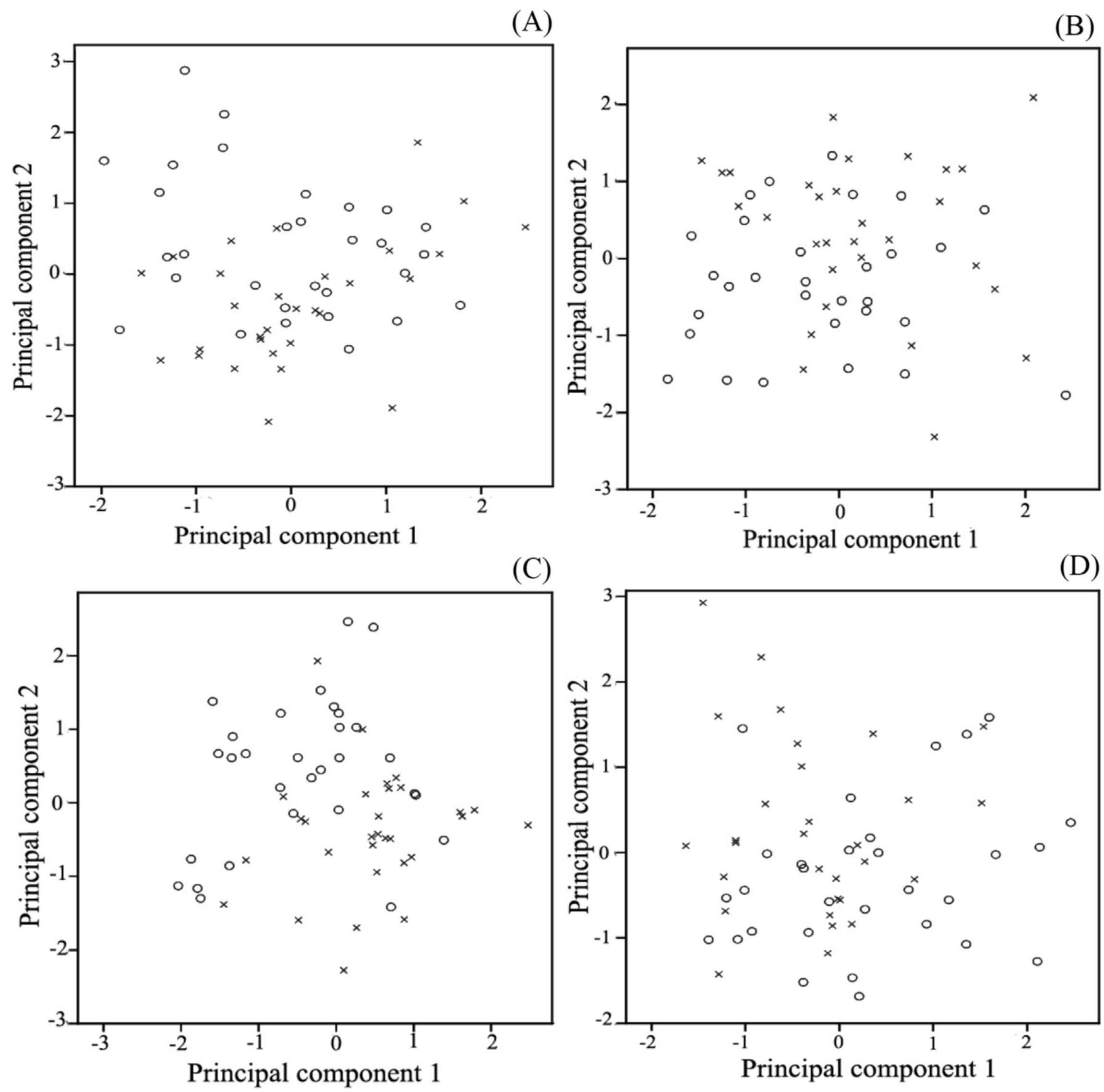

Fig. 5. PCA of *Calotes versicolor* for: (A) mensural characters in females; (B) mensural characters in males; (C) meristic characters in females; (D) meristic characters in males. (○, northern population; ×, southern population).

greater in adult males. Radder et al. (2001) reported that in India, the sexual dimorphism of *C. versicolor* in tail thickness was clearly seen since the juvenile stages, whereas in all the head measurements, the sexual dimorphism was only distinguishable at and after sexual maturity. A larger head size in adult males could perhaps indicate a greater resource holding power, and has been shown to be an advantage in intrasexual competition for territory defense and mate choice, and in intersexual dietary difference in prey size in this and other lizard species (Radder et al., 2001).

The strong sexual dimorphism in the relative trunk length of lizards has been suggested to be the result of fecundity selection (Olsson et al., 2002), where the increase in the relative trunk length in females results from an increased abdominal volume to carry the developing offspring.

Additionally, this research found that limb lengths in males were longer than in females, which may enhance the ability to compete in territorial defense, as suggested by Olsson et al. (2002). Moreover, a robust leg structure and snout-forelimb length could be the result of male–male competition. Differences in the numbers of 4FingLm in this lizard may relate to the perching capacities between males and females. More 4FingLm in males would allow them to perch higher than females. In accordance, this difference had been found in lizards from the Anoles family (Glossip and Losos, 1997).

In some female lizards, their reproductive strategies influence color variation (Vercken et al., 2007). However, the frequency of occurrence in DorsSt, ForearSt and NucSpot between sexes from northern and southern populations of *C. versicolor* may depend on the genetic variation of each individual.

Geographic variation

Geographic differences in the mensural characters between the northern and southern populations of *C. versicolor* in Thailand were obvious in males. All the different characters in males were found in the head size and limb lengths and were larger in the southern populations than in the northern populations. A greater size in southern Thailand had also been found in the common skink, *Sphenomorphus maculatus* (Yamasaki et al., 2001).

Although differences in the prey availability could influence the body size (Karn et al., 2005), this effect should then influence not only males but also females. However, a larger head and longer limbs are potentially more advantageous in male–male competition (Olsson et al., 2002), and so it is possible that males in the southern populations may be involved in stronger male–male competition for resources or mating success than in those northern populations. However, based on the available information, it can only be speculated on what the proximate and ultimate causes of these sex-specific differences are.

With respect to the meristic characters, there was no obvious geographic variation. This low level of congruence in the patterns of geographic variation in meristic characters is consistent with that reported for the lizard, *Gallotia stehlini,* on the Grand Canaria island (Thorpe and Baez, 1993). The greater numbers of GuS in the northern Thailand populations than in southern populations observed here may reflect an altitude effect on scalation, as was previously proposed by Thorpe and Baez (1993), to explain the decreased number of scales with increasing altitude in *G. stehlini*. Likewise, the numbers of 4ToeLm in *G. stehlini* were also significantly correlated with habitat type.

Both habitat type and altitude have been suggested as causes of morphological variations (Thorpe and Baez, 1993). Additionally, climate is thought to influence both the number and the size of scales (Soule and Kerfoot, 1972). In dry environments, many small scales are preferred because the higher surface area of large scales will increase the desiccation potential. The climate may influence the balance between selection for signaling coloration for sexual/territorial purposes and natural selection for crypsis (Thorpe and Brown, 1989).

Furthermore, although morphology and color patterns were slightly different in *Calotes mystaceus* in southern Vietnam, it was separated into a new species (*Calotes bachae*) based on molecular data (Hartmann et al., 2013). Therefore, although, these populations are not strongly differentiated, there are differences between the two (northern and southern) regions within Thailand. Thus, detailed studies on population genetics and molecular information of *C. versicolor* in Thailand should be conducted in the future.

Conflict of interest

The authors declare that there is no conflict of interest regarding the publication of this paper.

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