Ujiié, H. (1990) Geological history of the Ryukyu Island Arc. In *Nature of Okinawa: Geomorphology and Geology*, ed. H. Ujiié, pp. 251–255. Hirugisha, Naha. (in Japanese)

TROPICAL ISLAND HERPETOFAUNA: Origin, Current Diversity, and Conservation
Edited by Hidetoshi Ota

Geographic variation and biogeography of the geoemydine turtles (Testudines: Bataguridae) of the Ryukyu Archipelago, Japan

Yuichirou Yasukawa and Hidetoshi Ota

Tropical Biosphere Research Center, University of the Ryukyus, Nishihara, Okinawa 903-0213, Japan

Abstract

Three geoemydine species, *Geoemyda japonica*, *Mauremys mutica* and *Cistoclemmys flavomarginata*, occur in the Ryukyu Archipelago, Japan. Of these, *G. japonica* is restricted to the central Ryukyus, with its closest relative, *G. spengleri*, being distantly distributed in southeastern continental China and northern Indochina. A recent comparative study demonstrated remarkable differences between these species in a number of qualitative characters. The other two species, while confined within the archipelago to its southern part, also occur in Taiwan and southern continental China. In both species, the Ryukyu populations are most divergent among conspecific populations. Nevertheless, there were only quantitative (i.e., statistical) differences in most single characters between the southern Ryukyu and other populations, and the degrees of their differences are thus substantially lower than that between *G. japonica* and *G. spengleri*. Such a distinct morphological divergence and highly disparate distribution of the *G. japonica–spengleri* clade suggest that the ancestor of *G. japonica* entered into the Ryukyu Archipelago much earlier than those of *M. mutica* and *C. flavomarginata*. Taking the recently revised paleogeographical hypothesis of the Ryukyus into considerations, it is likely that the ancestral *G. japonica* has been isolated in the central Ryukyus since the Pliocene. On the other hand, populations of *M. mutica* and *C. flavomarginata* in the southern Ryukyus seem to have been isolated from their conspecific populations in Taiwan and southeastern continental China since the middle Pleistocene subsidence of land-bridges in these regions. Recent phylogenetic analyses strongly suggest the monophyly of *Geoemyda*, *Cistoclemmys* and *Pyxidea*. Of the species included in this clade, the three *Geoemyda* species exhibit much restricted and highly isolated distributions. By contrast, ranges of the *Cistoclemmys* and *Pyxidea* species are much broader, and include intervening areas of ranges of the three *Geoemyda* species. Such distributional patterns possibly reflect a much older origin and relict state of *Geoemyda*.

Key words: Ryukyu Archipelago; Biogeography; *Geoemyda japonica*; *Mauremys mutica*; *Cistoclemmys flavomarginata*; Geoemydinae; Population systematics.

1. Introduction

Five species belonging to four genera of the family Bataguridae are distributed in Japan (Iverson, 1992; Yasukawa *et al.*, 1992). In the Main-islands, one batagurine turtle, *Chinemys reevesii*, and two geoemydine turtles, *Mauremys japonica* and *M. mutica*, currently occur (Iverson, 1992). Of these, however, *M. mutica* in western Honshu is considered to have originated through artificial introduction from Taiwan before World War II (Section 3; also see Yasukawa *et al.*, 1996). In the Ryukyu Archipelago, three geoemydine turtles, *Geoemyda japonica*, *M. mutica*, and *Cistoclemmys flavomarginata* occur. *Geoemyda japonica* is a relatively recently recognized species endemic to the Okinawa Group of the central Ryukyus (Yasukawa *et al.*, 1992), whereas the Ryukyu populations of the latter two, both confined to the southern part of the archipelago, constitute endemic subspecies (McCord and Iverson, 1991; Iverson, 1992; Yasukawa *et al.*, 1996).

During the last decade, a few authors studied morphological variation of these species and discussed the systematic and biogeographical significance of resultant geographical patterns (e.g., Ernst and Lovich 1990; Iverson and McCord, 1994; Yasukawa *et al.*, 1992, 1996). However, none of these authors discussed the phylogeographical relationship among these and related species.

In this paper, we review the previous systematic analyses for each of the three Ryukyu geoemydines. We also make additional analyses on the variation of *Cistoclemmys flavomarginata*, because two recent studies on this subject yielded controversial results (Ernst and Lovich 1990; Iverson and McCord, 1994). We then discuss the origin and history of divergences of the Geoemydinae in the East Asian region by synthesizing resultant geographic patterns.

2. Variation between *Geoemyda japonica* and *G. spengleri*

Distribution of the Ryukyu black-breasted leaf turtle, *Geoemyda japonica*, is restricted to Okinawajima, Kumejima, and Tokashikijima Islands of the Okinawa Group, the central Ryukyus, whereas that of *G. spengleri* is confined to southeastern continental China and northeastern Indochina (Iverson, 1992; Yasukawa *et al.*, 1992; Yasukawa and Ota, in press *a*, *b*). Stejneger (1907) reported *G. japonica* as a Japanese population of *G. spengleri*, though he noticed that the Ryukyu specimens can be discriminated from those from the continental China (i.e., *G. spengleri* sensu stricto) in several characters, such as the presence of distinct axillary scutes and a differential plastral formula. Based on

Stejneger's accounts, Fan (1931) recognized two subspecies, *G. spengleri japonica* and *G. s. sinensis*, but without designation of the nominotypical subspecies. Pope (1935), after surveying specimens from continental China, Hainan Island and the Ryukyus, modified Fan's classification and defined the Ryukyu and the continental populations as two subspecies, *G. s. japonica* and *G. s. spengleri*, on the basis of the presence and absence of axillary scutes, respectively. In addition, he suspected that each form actually deserves the status of full species. However, in the absence of further studies, Pope's (1935) taxonomic arrangements were followed by most subsequent authors (e.g., Wermuth and Mertens, 1977; Pritchard, 1979; Ernst and Barbour, 1989; Iverson, 1992). Recently Yasukawa *et al.* (1992) examined a fairly large number of specimens of both *G. spengleri* and *G. japonica*, and made detailed morphological comparisons between these two taxa. Because there were actually considerable morphological differences between these forms, those authors concluded that *G. japonica* and *G. spengleri* are separate full species as below.

2.1. *Differences in quantitative characters between* Geoemyda japonica *and* G. spengleri

Yasukawa et al. (1992) made straight line measurements to the nearest 0.1 mm for the following 31 characters, using calipers: greatest carapace (CL) and plastron lengths (PL), midline carapace (MCL) and plastron lengths (MPL), greatest width of carapace (CW), shell depths between vertebrals 1–2 (SD1–2), 2–3 (SD2–3) and 4–5 (SD4–5), dorsal (DBL) and ventral (VBL) bridge lengths, plastral forelobe width (PWA), anterior width of the plastral hindlobe (PWC), greatest head width (HW), distance between centers of nostrils (INL), length (CEL) and width of cervical (CEW), greatest widths of vertebrals 3 (V3W), 4 (V4W) and 5 (V5W), greatest length of vertebral 5 (V5L), length of vertebral 5 from its anterior margin to the widest position (V5Lm), lengths of pleurals 2 (P2L) and 3 along lateral keel (P3L), greatest lengths of gulars (GL) and anals (AnL), length of seam between marginals 12 (M12L), length of seam between pleurals 4 and vertebral 5 (P4W), and midseam lengths between gulars (G), humerals (H), pectorals (P), abdominals (Ab), femorals (F) and anals (An).

Significant levels for all analyses were set at 0.05. Since no significant sexual differences were detected in each species, MCL, INL in relation to HW, and SD4–5, CEL, CEW, V3W, V5W, GL, P4W, G, Ab, and F in relation to MCL for all adult specimens were pooled for statistical comparisons of *japonica* and *spengleri*. Results of Mann-Whitney's *U*-test revealed that adult MCL is significantly greater in *japonica* than in *spengleri* ($P < 0.0001$). Results of ANCOVA revealed that slopes of regression lines were

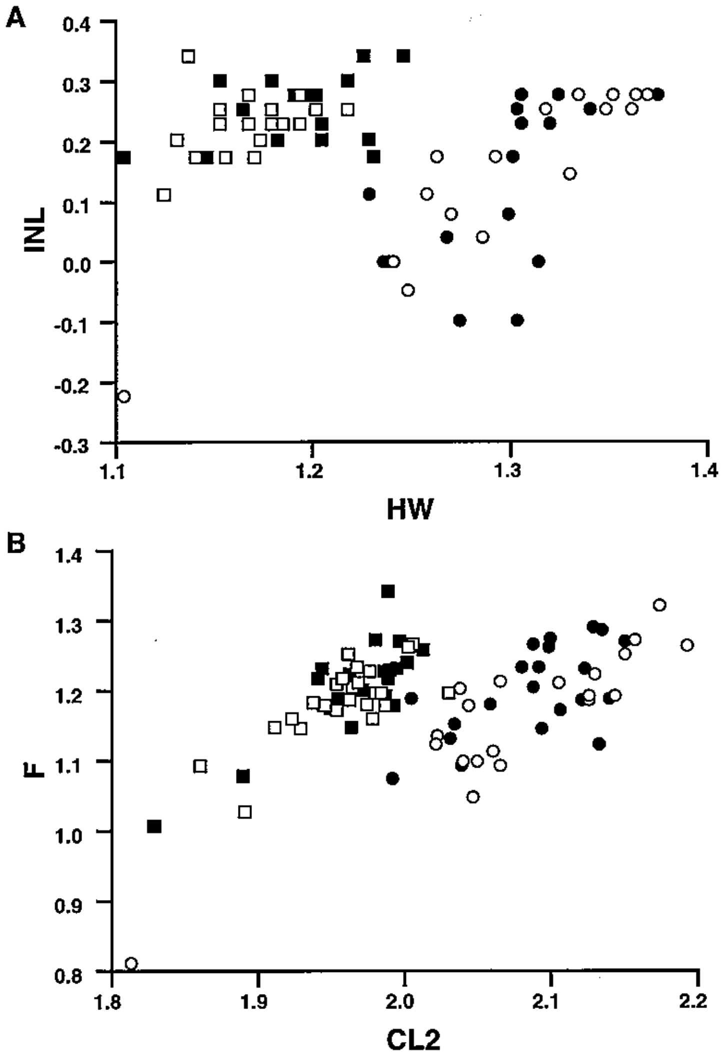

Figure 1. Two dimensional plots of scores of quantitative characters in base 10 logarithm for *Geoemyda japonica* and *G. spengleri*. A, Internarial length (INL) against greatest head width (HW); B, midseam length of femorals (F) against midline length of carapace (MCL). Open circles, male *G. japonica*; Closed circles, female *G. japonica*; Closed squares, male *G. spengleri*; Open squares, female *G. spengleri*. Modified from Fig. 7 in Yasukawa *et al.*(1992).

significantly different for only INL ($P < 0.05$: Figure 1A). Of the other characters, however, all but V3W, V5W, and AB showed significant differences between the two forms in the position of the regression line (Table 1, Figure 1B).

Table 1

Allometric comparisons between *Geoemyda japonica* (J) and *G. spengleri* (S) for characters showing no sexual differences within each species. "–", $P > 0.05$; "+", $P < 0.05$; "++", $P < 0.01$; and "+++", $P < 0.001$. See text for methods of analyses and character abbreviations. Modified from Table 3 in Yasukawa *et al.* (1992).

Character	Interspecific difference	Significance level
MCL	S < J	+++
SD4-5	S < J	+++
CEL	S > J	+++
CEW	S > J	+++
GL	S < J	+++
V3W	S = J	–
V5W	S = J	–
P4W	S < J	+++
G	S < J	+++
AB	S = J	–
F	S > J	+++

The remaining 19 characters showed significant intersexual differences in one or both of the two forms. So, male and female values for these characters were compared separately between *japonica* and *spengleri*. Comparisons were made for all the characters by ANCOVA using MCL as the covariate. Results of the analyses revealed that slopes of regression lines did not differ in any measurement in males or females. However, positions of the lines showed significant interspecific differences in one or both sexes for all measurements but MPL, CW, PWA, PWC, and V5L (Table 2).

2.2. *Differences in qualitative characters between* Geoemyda japonica *and* G. spengleri

Yasukawa *et al.* (1992) reported remarkable qualitative differences in morphological characters between *japonica* and *spengleri*, that are summarized in Table 3. The presence or absence of axillary scutes had already been considered as a valid character to separate the Japanese and the continental *Geoemyda* by previous authors (e.g., Stejneger, 1907; Fan, 1931; Pope, 1935; Ernst and Barbour, 1989: see above), and their results supported this account.

A number of other shell and scute characters also showed distinct differences between *japonica* and *spengleri*. For example, *japonica* had large pleurals 4 with a prominent keel involved by traces of bony plates. On the other hand, *spengleri* had very small

Table 2

Allometric comparisons between *Geoemyda japonica* (J) and *G. spengleri* (S) for characters showing sexual differences in one or both of the species. "–", $P > 0.05$; "+", $P < 0.05$; "++", $P < 0.01$; and "+++", $P < 0.001$. See text for methods of analyses and character abbreviations. Modified from Table 4 in Yasukawa *et al.* (1992).

	Female		Male	
Character	Interspecific difference	Significance level	Interspecific difference	Significance level
CL	S = J	–	S > J	++
PL	S > J	++	S = J	–
MPL	S = J	–	S = J	–
CW	S = J	–	S = J	–
SD1-2	S < J	+++	S < J	+++
SD2-3	S < J	+++	S < J	+++
DBL	S = J	–	S < J	+++
VBL	S > J	+++	S = J	–
PWA	S = J	–	S = J	–
PWC	S = J	–	S = J	–
HW	S = J	–	S < J	+++
V4W	S > J	+++	S > J	+
V5L	S = J	–	S = J	–
V5Lm	S < J	+++	S < J	+++
P2L	S = J	–	S < J	+
P3L	S > J	+++	S = J	–
AnL	S = J	–	S < J	+
M12L	S < J	+++	S < J	+++
H	S = J	–	S > J	+++
P	S = J	–	S < J	+
An	S < J	+++	S < J	+++

pleurals 4 with no or a very weak keel, and even in the latter case, there were no traces of the keel on the bony plates underneath. The pygal reached vertebral 5 in *spengleri*, whereas not in *japonica*. Specimens of *spengleri* had areolae (embryonic scute areas) near posterior margins of vertebrals and pleurals, but in *japonica*, areolae were located much more central in vertebrals 4 and 5 and pleural 4. Moreover, *spengleri* had the interfemoral seam longer than the interanal seam, but relative values of these measurements were opposite in most *japonica*.

The size and location of external nares were strikingly different between *spengleri* and *japonica*. In *spengleri*, nares were very small, and were distantly located from each other near lateral rims of anterior surface of the snout. Specimens of *japonica*, on the other hand, had moderate-sized nares, closely located to each other near the center of the snout. Both of these forms, however, had internal choanae with marked lateral ridges without papillae or flaps.

Differences were also evident in a number of skeletal characters between *japonica* and *spengleri*. In the former, the *processus coronoideus*, *p. trochlearis oticum*, and *p. pterygoideus externus* were more developed, whereas elements composing the temporal

Table 3

Comparisons of qualitative characters between *Geoemyda japonica* and *G. spengleri*. Modified from Table 5 in Yasukawa *et al.* (1992).

Character	*Geoemyda japonica*	*Geoemyda spengleri*
Cervical scute	small or moderate	large
Vertebral 5 (V5)	widest posteriorly	widest medially
Areola on V5	located medially	located posteriorly
Widest vertebral	V3, V4, or V5	V4
Pleural 4 (P4)	as wide as adjacent vertebrals	smaller than other pleurals
Areola on P4	located medially	located posteriorly
Keel on P 4	prominent	weak or absent
Keels on costals under P4	with trace on bony plates	without trace on bony plates
Pygal	not covered by vertebral 5	covered by vertebral 5
Paired axillary scutes	present	absent
Paired inguinal scutes	present	absent
Plastral midseam	anal > femoral	femoral > anal
Size of external naris (EN)	moderate	very small
Relative location of ENs	closely located	separated for a distance
Large scales on forelimbs	with roundish tip	with acute tip
Semispinose scales on thighs and base of tail	long, spiny, and often densely present	short, conical, and sparsely present
Processus coronoideus	prominent	indistinct
P. pterygoideus externus	prominent	indistinct
P. trochlearis oticum	well developed	poorly developed
Vomer under vomer sulcus	not forked at either side	forked at either side
Ventrolateral part of maxilla	projecting posteriorly	not projecting posteriorly
Triturating surface of mandible	with horizontal surface	without horizontal surface
Sexual color differences	absent	present
Connective tissue under carapace scutes	whitish and patternless	grayish or reddish and with complicated fleck pattern

arch, especially the quadratojugal, were less developed when compared with the latter. The anteroventral portion of the quadrate was slightly concave under the *p. trochlearis oticum* in *japonica*, whereas the corresponding portion in *spengleri* was slightly convex. In cryptdiran turtles, the *musculus adductor mandibularis externus* is attached to the *p. coronoideus* and turns around on the *p. trochlearis oticum*, and *m. pterygoideus pars dorsalis* is attached to the pterygoid along the *p. pterygoideus externus* (Gaffney and Meylan, 1988). Therefore, the greater development of these three processes in *japonica* was considered to be probably associated with the greater development of masticatory muscles in this form. Reduction of the temporal arch and the anteroventral concavity of the quadrate also enabled the greater development of masticatory muscles.

Sexual color dimorphism was present in *spengleri*: juveniles and females of this form had reddish or yellowish iris and light stripes and spots on the brownish or grayish head and neck, whereas in adult males, the iris became white or light gray, and the head and neck markings disappeared. In *japonica*, the iris was reddish or yellowish brown, or reddish gold, and head and neck had irregular reddish or yellowish lines or spots on the brown or orange brown ground color in both sexes.

2.3. Phylogenetic relationships of Geoemyda japonica, G. spengleri, *and the other congeneric species*

Based on the above-mentioned differences in both quantitative and qualitative characters, Yasukawa *et al.* (1992) concluded that the two forms, having been considered merely as conspecific subspecies to that date (see above), should be treated as independent species. Nevertheless, results of their comparisons with other apparently closely related geoemydines strongly supported the monophyly of *G. japonica* and *G. spengleri*. They thus defined the genus *Geoemyda* as consisting only of *japonica* and *spengleri*.

Moll *et al.* (1986) reassigned *Heosemys silvatica*, an enigmatic Indian geoemydine known from a few specimens, to *Geoemyda*, since this species shares several features, lacking in other species of *Heosemys*, with *G. japonica* and *G. spengleri*. Recent phylogenetic analyses based on morphological characters revealed the monophyly of *H. silvatica* and the *G. japonica–spengleri* clade (Yasukawa, 1997) and their closer affinity to *Cistoclemmys* and *Pyxidea* than to the typical *Heosemys*, such as *H. grandis* and *H. spinosa* (Hirayama, 1984; Yasukawa, 1997; Yasukawa *et al.*, 1992). These results confirm Moll *et al.*'s (1986) account, and we now regard *silvatica* as the third species of *Geoemyda*.

Recently, McCord *et al.* (1995) assigned other three geoemydines, *Geoemyda yuwonoi*, *Heosemys depressa*, and *H. leytensis*, to *Geoemyda*. In their definition, however, the genus *Geoemyda* suffers paraphyly, with the *G. japonica–spengleri* clade being monophyletic with *P. mouhotii* (Fritz and Obst, 1996). In addition, our preliminary investigations revealed that the taxon-character matrix used for the phylogenetic analysis by McCord *et al.* (1995) includes serious errors most likely due to their misinterpretations of a few skeletal topologies (Yasukawa, Aoki and Hirayama, in prep.). As such, it is obvious that genetic arrangements of *G. yuwonoi*, *H. depressa*, and *H. leytensis* proposed by McCord *et al.* (1995) seriously needs further careful verification, and we thus tentatively regard at present *G. japonica*, *G. silvatica* and *G. spengleri* as components of *Geoemyda*.

3. Geographic variation in *Mauremys mutica*

The Asian yellow pond turtle, *Mauremys mutica*, ranges widely from temperate to tropical East Asia: Kyoto, Shiga and Osaka Prefectures on Honshu, the Main-island of Japan; Akusekijima Island of the Tokara Group, the northern Ryukyus; Okinawajima, Sesokojima, Akajima, and Zamamijima Islands of the Okinawa Group, the central Ryukyus; Miyakojima Island of the Miyako Group, and Ishigakijima, Iriomotejima, and Yonagunijima Islands of the Yaeyama Group, the southern Ryukyus; Anhui, Fujian, Guangdong, Guangxi, Hainan, Jiangsu, Taiwan, Yunnan, and Zhejiang Provinces of eastern and southern China; northern Vietnam (Iverson, 1992; Zhao and Adler, 1993; Yasukawa *et al.*, 1996, in press c). Several authors pointed out that *M. mutica* is highly variable especially in coloration (Ernst and Barbour, 1989; Iverson, 1992; Iverson and McCord, 1989). In addition, Iverson and McCord (1994) assumed that the populations of the Ryukyus deserve a separate subspecific status because of their differences from Chinese and Vietnamese populations in shell proportion and coloration. However, sizes of samples they examined were so small that they deferred the taxonomic conclusion. On the basis of data from much larger samples, Yasukawa *et al.* (1996) made detailed analyses of morphometric and colorational variation in *M. mutica*. Their results confirmed the most divergent status of the Yaeyama populations among conspecific populations. Thus, Yasukawa *et al.* (1996) described these populations as a separate subspecies, *M. m. kami*.

Results of recent morphological analyses, as well as literature records and information from local people, indicate that populations in Honshu, and the Tokara, Okinawa and Miyako Groups had originated from artificial introductions from Taiwan and the Yaeyama Group, respectively (Yasukawa, unpublished data; Yasukawa *et al.*, 1996; in press c). Besides these, the population of Yonagunijima Island may be also of an artificial origin (Toyama, personal communication).

3.1. *Variation in morphometric characters of* Mauremys mutica

In Yasukawa *et al.* (1996), straight line measurements were taken to the nearest 0.1 mm for the following 16 characters using calipers: greatest carapace length (CL), greatest carapace width (CW), greatest shell depth (SD), greatest plastron length (PL), greatest length of the plastral hindlobe (HL), plastral forelobe width (PWA), anterior width of the plastral hindlobe (PWC), posterior width of plastral hindlobe (PWD), right bridge length (BL), maximum ventral width across gular scutes (GW), maximum length of right gular scute (GL), and lengths of right interhumeral (IH), interpectoral (IP), interabdominal (IAB), interfemoral (IF) and interanal (IAN) seams.

They classified the specimens examined into four major regional samples as follows: 1) the Yaeyama sample, consisting of specimens from Ishigakijima, Iriomotejima and Yonagunijima Islands; 2) the Honshu sample, consisting of specimens from Kyoto and Shiga Prefectures; 3) the Taiwan sample, consisting of specimens from the Taiwan Main Island; 4) the continental sample, consisting of specimens from China, including Hainan Island and northern Vietnam.

All measurements except CL for the univariate test were log-transformed before the analyses. Because preliminary intersexual comparisons by multivariate analysis of variance (MANOVA) detected significant variation within each regional sample ($P < 0.001$), analyses of variation among samples were conducted separately for males and females. They made univariate (CL) and multivariate analyses for adult specimens and ANCOVA and Tukey-like tests for adult and subadult specimens. Variations in CL between sexes within each regional sample and among males or females from the four major regions were examined by *t*-test and Kruskal-Wallis and Dunn's multiple comparison test, respectively. Results of *t*-test indicated that CL is significantly greater in males than in females within the Ryukyu sample ($P < 0.01$), but does not differ significantly between sexes within each of the other samples (Figure 2). On the other hand, results of Kruskal-Wallis and Dunn's multiple comparison test revealed significant geographic differences in CL in both males and females (Figure 2, Table 4). In both sexes, CL in the Taiwanese sample was significantly greater than those in the Yaeyama and the continental samples. The sample from Honshu showed a significantly greater CL when compared with the continental samples in males and with the Yaeyama sample in females. No significant differences were recognized in CL between the other combinations of samples.

Geographic variation in each of the other measurements exclusive of IH was also examined by ANCOVA and Tukey-like tests with CL as the covariate. Results of these tests revealed that in males the slope of regression line for IAB significantly differed among the four samples, whereas only positions of the lines significantly differed for CW, SD, PL, HL, BL, GW, GL, IP, IF and IAN. In females, slopes of regression lines significantly differ for PWA, PWC, PWD, GL, IP, and IAN, whereas only positions of the lines significantly differ for CW, SD, HL, GW, IAB and IF (Table 4).

In addition, data for all measurements were subjected to the canonical discriminant analysis (CDA). Standardized coefficients of the 16 measurements calculated for the first three canonical axes (CANs 1–3) are presented in Table 5, together with eigenvalues, differences, and proportions for these axes. Cumulative proportions indicated that CANs 1–3 account for the total variation. In both sexes, CAN1 variable was distinctly smaller in the Yaeyama sample than in the other samples, whereas ranges of its scores largely overlapped among the latter three samples. CAN2 variable in males was smaller in the continental sample than in the other three samples, whereas ranges of its scores largely overlapped among the latter. In females, CAN2 variable was slightly greater in the Yaeyama and Honshu samples than in the other two samples (Table 5, Figure 3). No distinct differences were recognized in CAN3 variable among either male or female

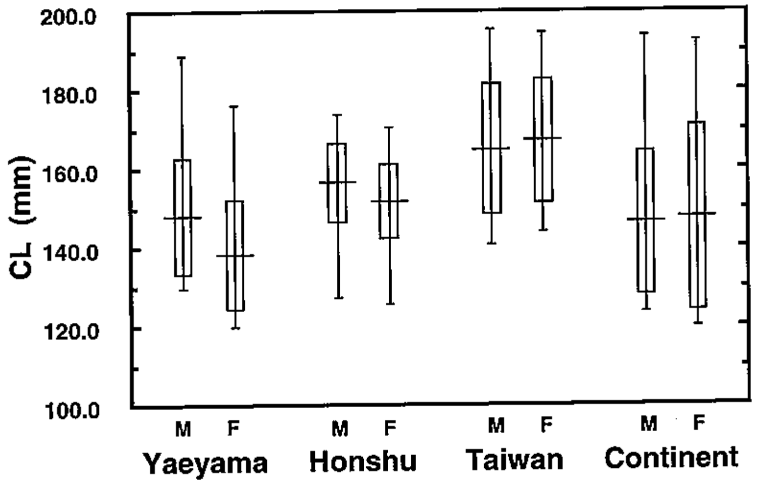

Figure 2. Variation in the greatest carapace lengths (CLs) of adult males (M) and females (F) of *Mauremys mutica* from Yaeyama, Honshu, Taiwan and the Asian continent. Vertical and horizontal bars and rectangles indicate ranges and means of actual values and ranges of single standardized deviations from means, respectively. Modified from Fig. 2 in Yasukawa *et al.* (1996).

Table 4

Allometric comparisons of samples of *Mauremys mutica* from the four major regions; Yaeyama (Y), Honshu (H), Taiwan (T), and the continent (C). See text for methods of analyses and character abbreviations: "–", $P > 0.05$; "+", $P < 0.05$; "++", $P < 0.01$; "+++", $P < 0.001$ in Kruskal-Wallis and ANCOVA. Samples sharing same superscript letters showed no significant differences in Dunn's multiple comparison test and Tukey-like test ($P > 0.05$). Modified from Table 3 in Yasukawa *et al.* (1996).

Variable	Male			Female		
	slope	position	descending order	slope	position	descending order
CL		+++	$T^{a}\ H^{ab}\ Y^{bc}\ C^{c}$		+++	$T^{a}\ H^{ab}\ C^{bc}\ Y^{c}$
CW	–	+++	$T^{a}\ Y^{a}\ H^{b}\ C^{b}$	–	+++	$Y^{ab}\ C^{ab}\ T^{a}\ H^{b}$
SD	–	+++	$H\ T^{a}\ C^{a}\ Y$	–	+++	$H^{a}\ T^{ab}\ C^{b}\ Y$
PL	–	+	$T^{a}\ C^{a}\ Y^{a}\ H$	–	–	
HL	–	+++	$Y^{a}\ T^{a}\ H^{b}\ C^{b}$	–	+++	$Y\ T^{a}\ C^{ab}\ H^{b}$
PWA	–	–		–	–	
PWC	–	–		+++		$C^{a}\ T^{b}\ Y^{c}\ H^{d}$
PWD	–	–		+++		$C^{a}\ T^{b}\ H^{c}\ Y^{d}$
BL	–	++	$T^{a}\ Y^{ab}\ C^{ab}\ H^{b}$	–	–	
GW	–	+++	$Y^{a}\ H^{a}\ T^{ab}\ C^{b}$	–	++	$T^{a}\ H^{a}\ Y^{ab}\ C^{b}$
GL	–	+++	$Y\ C^{a}\ H^{ab}\ T^{ab}$	++		$C^{a}\ Y^{b}\ T^{c}\ H^{d}$
IP	–	+++	$C^{a}\ T^{a}\ H^{a}\ Y$	+		$C^{a}\ Y^{b}\ H^{c}\ T^{d}$
IAB	+		$Y^{a}\ H^{b}\ C^{c}\ T^{d}$	–	+	$H^{a}\ C^{a}\ Y^{b}\ T^{b}$
IF	–	+++	$T^{a}\ Y^{a}\ C^{a}\ H^{b}$	–	+++	$T^{a}\ Y^{a}\ H^{b}\ C^{b}$
IAN	–	+	$H^{a}\ Y^{ab}\ T^{ab}\ C^{b}$	+++		$C^{a}\ T^{b}\ Y^{c}\ H^{d}$

samples. These results strongly suggested that the Yaeyama sample is most divergent among the four regional samples

3.2. *Variation in coloration, scutellation, and osteology of* Mauremys mutica

In the Yaeyama sample, color of carapace usually varied from gray or yellowish tan to light brown, whereas the other samples usually had brown, dark brown, or sometimes almost black carapaces. Likewise, the dorsal and lateral ground color of head was usually paler in the Yaeyama sample than in the others, making the light lateral stripe in the head and neck usually less prominent in the former (Yasukawa *et al.*, 1996, in press *c*).

Comparisons of qualitative characters, such as those in scutellation, and shapes of the skull and shell bony plates, yielded no discernible variations (Yasukawa, unpublished data).

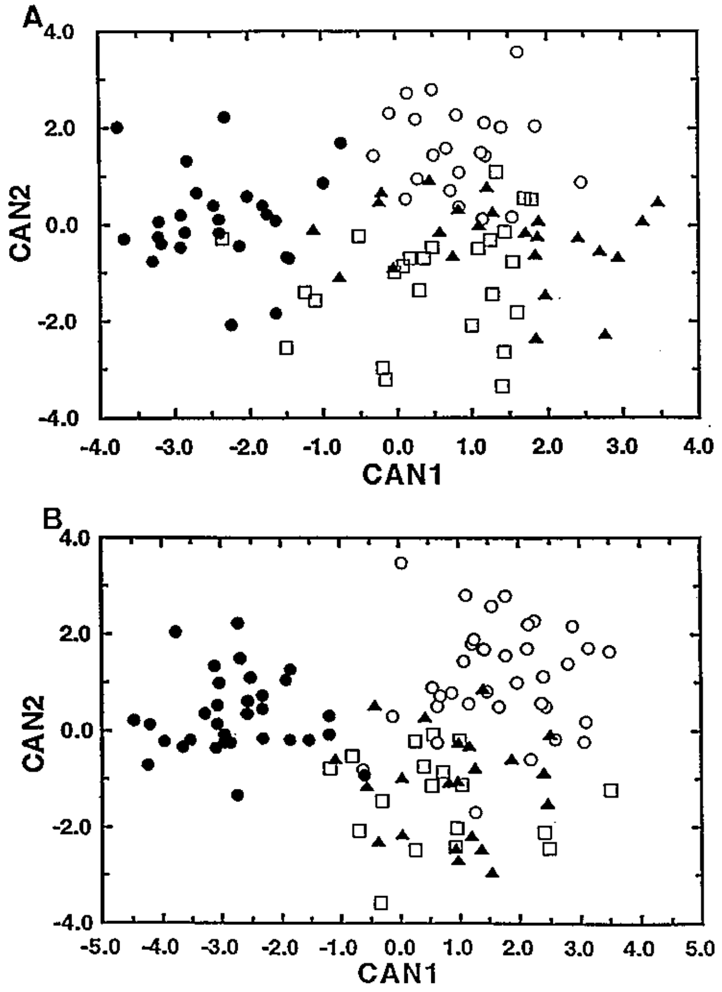

Figure 3. Two-dimensional plots of scores for the first two canonical variables of morphometric characters in four major regional samples of adult male (A) and female (B) *Mauremys mutica*. Closed circles, samples from the Yaeyama Group; Open circles, from Honshu; Closed triangles, from Taiwan; Open squares, from continental China. Modified from Fig. 3 in Yasukawa *et al.* (1996).

4. Geographic variation in *Cistoclemmys flavomarginata*

The yellow-margined box turtle, *Cistoclemmys flavomarginata*, occurs on the Iriomotejima and Ishigakijima Islands of the southern Ryukyus, Taiwan, and Anhui, Fujian, Henan, Guangxi, Hubei, Hunan, Jiangsu, Sichuan and Zejiang Provinces of

Table 5
Standardized coefficients for the first three canonical axes of variation of morphometric characters in adult *Mauremys mutica*. See text for abbreviations. Modified from Table 4 in Yasukawa *et al.* (1996).

Variable	Male			Female		
	CAN1	CAN2	CAN3	CAN1	CAN2	CAN3
CL	0.291	0.570	-1.198	0.680	1.581	1.122
CW	-0.671	-0.649	1.367	-1.597	-1.417	1.435
SD	0.707	1.170	-1.220	2.098	0.977	-0.271
PL	-2.650	-2.208	-1.718	0.115	-6.413	1.785
HL	0.283	1.014	1.072	-1.508	1.354	0.161
PWA	0.730	0.478	0.326	0.959	0.938	-0.848
PWC	0.166	0.106	-0.318	-1.207	0.199	-1.562
PWD	0.487	-0.644	0.395	1.009	-0.976	0.759
BL	-0.491	-0.522	0.564	0.610	0.340	0.826
GW	-0.776	0.829	0.514	-0.252	0.677	1.005
GL	0.164	0.031	-0.087	-0.299	0.679	-0.872
IH	1.752	0.107	0.591	0.114	-0.048	-0.574
IP	2.068	-0.309	0.490	0.701	-0.556	-0.815
IAB	0.286	0.364	0.315	-0.277	1.647	-1.344
IF	0.197	-0.418	0.313	-0.057	0.810	0.239
IAN	-0.025	0.870	0.188	-0.047	1.506	-0.144
Eigenvalue	2.290	0.935	0.823	3.586	1.044	0.699
Difference	1.355	0.066	0.000	2.542	0.345	0.000
Proportion	0.559	0.228	0.212	0.673	0.196	0.131
Cumulative proportion	0.559	0.788	1.000	0.673	0.869	1.000

eastern and southern continental China (Iverson, 1992; Zhao and Adler, 1993; Karsen *et al.*, 1998; Ota and Yasukawa, in press).

Gray (1863) described a new genus, *Cistoclemmys*, to accommodate a new species, *flavomarginata*, from Tamsui, northern Taiwan (Wermuth and Mertens, 1977; Iverson, 1992). At present, *Cistoclemmys* Gray, 1863 is usually regarded as a synonym of *Cuora* Gray, 1855 (e.g., Wermuth and Mertens, 1977; Pritchard, 1979; Ernst and Barbour,1989; Iverson, 1992; David, 1994). We, however, apply that generic name to *flavomarginata*, since recent phylogenetic analyses clearly separated *Cistoclemmys* (as consisting of *flavomarginata* and *galbinifrons*: Hirayama, 1984; Gaffney and Meylan, 1988; Yasukawa, 1997: but also see Wu *et al.*, 1998) from *Cuora* sensu stricto (as consisting of the remainder of *Cuora* sensu lato).

4. 1. Review of previous studies on the geographic variation in Cistoclemmys flavomarginata

Hsu (1930) described the continental populations of *Cistoclemmys flavomarginata* as a new subspecies, *Cuora flavomarginata sinensis*, based on the differences in shell scutellation and relative length of the tail. However, the validity of this subspecies remained dubious, because such variations are common within most emydid and batagurid populations (Pope, 1935; Ernst and Lovich, 1990). Thus, few subsequent authors regarded *C. f. sinensis* as valid until recently.

Based on the results of morphometric comparisons among the samples of *C. flavomarginata* from the Ryukyus, Taiwan, and the continental China, Ernst and Lovich (1990) described the Ryukyu populations as a separate species, *Cuora evelynae*. According to these authors, *C. evelynae* has a large light blotch on each vertebral and pleural, and a large, usually hourglass-shaped, light brown plastral blotch, whereas *C. flavomarginata* has only a small light blotch on each vertebral and pleural, and a large dark plastral blotch, with only a shallow indentation at the bridge. However, some Japanese researchers examining both forms doubted the validity of *C. evelynae* as a full species, because diagnostic characters proposed by Ernst and Lovich (1990) often failed to discriminate the Yaeyama populations from populations of Taiwan and the continental China (Ota and Yasukawa, in press; Hirayama and Sengoku, personal communication). The results of Ernst and Lovich (1990) might be affected by ontogenic and sexual variations, because of the pooled data from juvenile and adult specimens of both sexes before analyses.

McCord and Iverson (1991) analyzed morphometric variation among male and female samples from the southern Ryukyus, Taiwan and the continental China separately. Their results indicated that three populations were more or less differentiated from each other, with the continental samples being most divergent. They thus relegated the status of *C. evelynae* to a subspecies of *C. flavomarginata*, and also tentatively assigned the continental populations to a distinct subspecies, *C. f. sinensis*. This subspecific classification has been followed by most subsequent authors (e.g., Iverson, 1992; David, 1994). McCord and Iverson (1991), however, analyzed a relatively small number of shell measurements only, and sizes of their samples are also much smaller than those of Ernst and Lovich (1990). Furthermore, each of the three subspecies is still rather poorly diagnosed. On this occasion, we attempt to make a more comprehensive analysis of geographic variation among the three currently recognized subspecies of *Cistoclemmys flavomarginata*. Our purpose is to estimate the relative divergence of the Yaeyama populations from the others.

4.2. *Comparisons among the three subspecies of* Cistoclemmys flavomarginata

We examined 32 specimens (18 females, four males, two unsexed adults and eight juveniles) from the Yaeyama Group, 28 specimens (16 females, nine males and three juveniles) from Taiwan, and 31 specimens of *C. f. sinensis* (15 females, four males, three unsexed adults and nine juveniles) from continental China (see "Specimens examined" for further detail). These materials included specimens of whole bodies, and dry shells with and without other skeletal parts. All specimens with midline carapace lengths (MCLs) greater than 110.0 mm were considered as adults, and were sexed based on length of the tail and thickness of the tail base (Ernst and Lovich, 1990; Ota and Yasukawa, in press). Skeletal specimens (MCL > 110.0 mm) were treated as unsexed adults, unless their sexes were confirmed before removal of the soft parts. In each sample, the number of females much exceeded that of males. So, we used data from adult females for statistical analyses of variation among samples, and limited the use of data from adult males, unsexed adults and juveniles for colorational and qualitative comparisons. Osteological characters were compared among two adult specimens from the southern Ryukyus, five adult specimens from Taiwan and five adult specimens from continental China.

Straight line measurements were taken to the nearest 0.1 mm for the following 25 characters using calipers: midline carapace length (MCL), carapace width at the level of the seam between vertebrals 3 and 4 (CW3–4), width between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 3 and 4 (PW3–4), shell depth at the hinge (SDH), medial lengths of the plastral forelobe (PFL) and hindlobe (PHL), greatest ventral width across gular scutes (GW), plastral forelobe width at the level of junction of humero-pectoral seam and plastral margin (PWA), anterior width of the plastral hindlobe at the level of the junction of abdomino-femoral seam (= hinge) and plastral margin (PWC), greatest lengths of vertebrals 1 (V1L), 2 (V2L) and 3 (V3L), greatest widths of vertebrals 1 (V1W), 2 (V2W) and 3 (V3W), greatest lengths of pleurals 2 (P2L), 3 (P3L), greatest width of pleural 3 (P3W), greatest length of a light blotch on pleural 2 (P2ML), and midseam lengths between gulars (G), humerals (H), pectorals (P), abdominals (Ab), femorals (F) and anals (An). Definitions of the last six characters follow Lovich and Ernst (1989).

Significance levels for all analyses were set at 0.05. Variation in MCL among the samples was examined by Kruskal-Wallis and Dunn's multiple comparison test. Each of the other measurements was log-transformed and was tested for correlation with MCL (also log-transformed) within each sample. Correlations were consistently statistically significant in all measurements but H and F in the Taiwanese and continental

samples and P2ML in all samples. We thus analyzed all characters but these three by ANCOVA and Tukey-like test with MCL as the covariate. After log-transformed, data for all measurements but P2ML were also subjected to principal component analyses (PCA) using PRINCOMP procedure of SAS (1990). In addition, P2ML and P2ML/P2L were examined by Kruskal-Wallis and Dunn's multiple comparison test to verify the validity of a diagnostic character of *evelynae* proposed by Ernst and Lovich (1990).

The Kruskal-Wallis and Dunn's multiple comparison tests revealed no significant differences in MCL between any sample pair. On the other hand, ANCOVAs and Tukey-like tests indicated that slopes of regression lines for P2L and G were significantly different among the three samples. Positions of the lines were significantly different among the three samples for CW3–4, PW3–4, SDH, GW, PWA, V2L, V1W, V3W, P3W, and P

Table 6

Results of allometric comparisons among three regional samples of *Cistoclemmys flavomarginata*: Y, Yaeyama; T, Taiwan; M, mainland China. "-", $P \geq 0.05$; "+", $P < 0.05$; "++", $P < 0.01$; "+++", $P < 0.001$. Samples sharing same superscript letters showed no significant differences. See text for methods of analyses and character abbreviations.

Characters	Slope	Position	Descending order		
CW3-4	-	++	M^1	T^1	Y
PW3-4	-	++	M^1	T^{12}	Y^2
SDH	-	+	M^1	T^1	Y
PFL	-	-			
PHL	-	-			
GW	-	++	M^1	T^{12}	Y^2
PWA	-	+	T^1	M^{12}	Y^2
PWC	-	-			
V1L	-	-			
V2L	-	+	T^1	M^{12}	Y^2
V3L	-	-			
V1W	-	+	M^1	T^{12}	Y^2
V2W	-	-			
V3W	-	++	M^1	T^1	Y
P2L	+				
P3L	-	-			
P3W	-	+	M	T^1	Y^1
G	+				
P	-	++	M^1	T^1	Y
Ab	-	-			
An	-	-			

(Table 6). Of these 10 characters, four (CW3–4, SDH, V3W and P) significantly differed between the Yaeyama sample and the remaining samples, whereas only a single character (P3W) and no characters differentiated the continental and Taiwanese samples from the remainder, respectively.

Eigenvectors for the first three principal components (PRINs 1–3), calculated by PCA using data for the 24 measurements, are presented in Table 7, together with eigenvalues, differences, and proportions for these axes. Ranges of PRINs 1 and 2 variables largely overlapped among the samples (ANOVA, $P > 0.05$). In PRIN 3, score of the Yaeyama sample was largely greater than those of the Taiwanese and the continental samples ($P < 0.001$), whereas scores largely overlapped between the latter two samples ($P > 0.05$: Figure 4). Absolute values of factor loadings (Table 7) indicated that differences in An (positive) most greatly contributed to the variation in PRIN 3, followed by GW (negative), V3W (negative) and PWA (positive) in order.

Table 7

Factor loadings on the first three principal components of morphometric variation in adult female samples of *Cistoclemmys flavomarginata*. See text for abbreviations.

Variable	PRIN1	PRIN2	PRIN3
MCL	0.176354	0.127805	-0.021439
CW3-4	0.178783	0.105116	-0.089434
PW3-4	0.180990	0.024439	-0.019692
SDH	0.168347	-0.008115	-0.118222
PFL	0.172188	-0.080018	0.020830
PHL	0.156069	0.042048	-0.053107
GW	0.109656	0.135764	-0.342040
PWA	0.169517	-0.085134	0.182570
PWC	0.162644	0.004749	0.028879
V1L	0.164958	-0.230790	0.121407
V2L	0.167323	0.042881	0.007206
V3L	0.158079	-0.192095	0.113882
V1W	0.158317	0.069387	0.117255
V2W	0.142638	-0.037581	-0.109711
V3W	0.142170	-0.034527	-0.223107
P2L	0.163972	-0.028033	0.037884
P3L	0.160795	-0.136118	-0.072826
P3W	0.169225	-0.182497	0.112420
G	0.147817	-0.224134	0.018746
H	0.167118	-0.183877	0.049051
P	0.174345	-0.143760	0.053201
Ab	0.130931	-0.177216	-0.075973
F	0.141724	0.169950	-0.135231
An	0.127353	-0.217782	0.430996
Eigenvalue	27.8124	2.0409	1.7058
Differences	25.7715	0.3350	0.3000
Proportion	0.67835	0.049777	0.041605
Cumulative proportion	0.67835	0.72813	0.76973

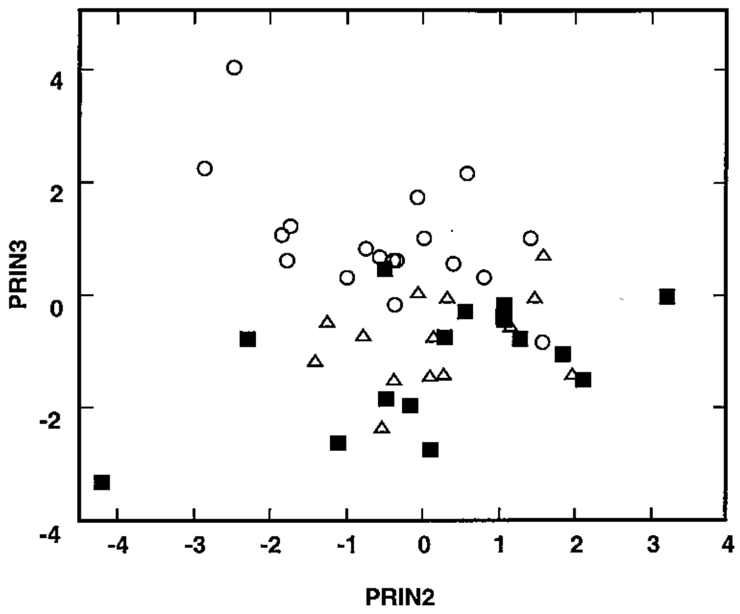

Figure 4. Two-dimensional plots of scores for the second and third principal components of morphometric characters in samples of adult female *Cistoclemmys flavomarginata*: Open circles, samples from the Yaeyama Group; Closed squares, from Taiwan; Open triangles, from the continental China.

Results of the Kruskal-Wallis and Dunn's multiple comparison test revealed no significant differences in P2ML or P2ML/P2L between any combination of the three samples ($P > 0.05$). Values for the latter were highly variable but largely overlapped among the samples (Table 8). In our observations, differences in color or shape of the dark plastral blotch were not evident among the samples, either. We thus conclude that these colorational characters do not serve as discriminant characters for the Yaeyama populations (*contra* Ernst and Lovich, 1990). Furthermore, comparisons in qualitative characters, such as scutellation and skeletal shapes, yielded no distinct differences among the three samples, either.

Table 8
Size variation of the light blotch on the second pleural (P2ML) among adult females of *Cistoclemmys flavomarginata* from the southern Ryukyus, Taiwan and the continent. P2L = the second pleural length.

Subspecies	Mean (*SD*) of P2ML	Range of P2ML	RANGE of P2ML/P2L
Yaeyama	20.956 (3.675)	12.9–27.4	0.499–0.957
Taiwan	20.056 (4.552)	14.6–28.6	0.480–0.850
Continental China	19.638 (6.346)	12.9–27.4	0.451–0.929

4.3. *Infraspecific classification of* Cistoclemmys flavomarginata

Results of the morphometric analyses indicated that the southern Ryukyu populations are most divergent, whereas the Taiwanese and continental populations are hardly discernible from each other. Nevertheless, although Ernst and Lovich (1990) stated that the southern Ryukyu populations differ from the others in having a relatively large light-colored marking on each vertebral or pleural, present results negated the validity of this diagnostic character for *evelynae*. In adult *C. flavomarginata*, the carapacial light blotches tended to be larger in individuals having badly worn carapaces irrespective of their localities. In addition, the light blotches of an individual from each locality could be easily enlarged by filing the surrounding darker portions of the carapace with sandpaper. Very young juvenile specimens (MCL < 50.0 mm) had a relatively large light blotch on an areola of each vertebral and pleural (P2ML/P2L > 0.720), but surrounding portion of the areola was dark-colored. The areola was usually indistinct or lost in larger specimens. Results of our observations on juveniles and relatively small adults, however, indicate that the size of the areola does not change ontogenetically, but that that of the surrounding portion and the relative size of the blotch become greater and smaller with growth, respectively. These observations suggest that in *C. flavomarginata* this character varies with age and individual experience rather than with locality.

Besides colorlational characters, Ernst and Lovich (1990) noted that the Taiwanese populations have more rows of large scales on the anterior surface of the forelimb when compared with the southern Ryukyu and continental China population. However, our examination by Kruskal-Wallis test detected no significant differences in the number of these scales among the adult female or adult samples ($P > 0.05$).

To evaluate geographic variation in shell morphometry of *C. flavomarginata*, McCord and Iverson (1991) conducted canonical discriminant analyses separately for female and male samples from the Yaeyama Group, Taiwan and the continental China. Based on the results, they considered that each of the three populations deserves subspecific status. However, they did not refer to actual characters contributing to the separation along the canonical axes or those being diagnostic of the three subspecies. In addition, sizes of samples they examined were too small to yield convincing results by such an analysis.

Based on the present results, we consider that the most divergent Yaeyama populations deserve taxonomic recognition at the subspecific level as *C. f. evelynae*. This agrees with the tentative account by McCord and Iverson (1991). However, our results negate the subspecific separation of the Taiwanese and continental populations by these authors, since no substantial differences were recognized between samples from these regions. We thus recognize two subspecies within *C. flavomarginata*: *C. f. evelynae*, endemic to the Yaeyama Group, characterized by relatively flat (SDH/MCL in adult female, median [range]:0.444 [0.411–0.479]) and narrow shell (CW3–4/MCL in adult female, 0.694 [0.649–0.749]), and narrower vertebral 1 (C1W/MCL in adult female, 0.181 [0.159–0.214]); and *C. f. flavomarginata* from Taiwan and the continental China, characterized by slightly higher (SDH/MCL in adult female, 0.463 [0.414–0.510]) and wider shell (CW3–4/MCL in adult female, 0.723 [0.666–0.774]), and wider vertebral 1 (C1W/MCL in adult female, 0.203 [0.162–0.231]).

5. Biogeography

In the *G. japonica–spengleri* clade, there are remarkable differences in both morphometric and qualitative characters between the Ryukyu (*G. japonica*) and the non-Ryukyu representatives (*G. spengleri*) (Yasukawa *et al.*, 1992; Section 2). *Geoemyda japonica* is currently confined to the Okinawa Group of the central Ryukyus, but their fossils were discovered from southern part of Okinawajima Island (late Pleistocene) and also from Iejima Island of the Okinawa Group (Holocene) (Hasegawa, 1980; Oshiro, 1987; Toyama, 1997). Considering the fact that this species does not currently occur in the latter localities, recent range reduction of *G. japonica* within the Okinawa Group is obvious. However, no fossil records of this species or of its close relatives have been available from the southern Ryukyus or Taiwan. On the other hand, either *M. m. kami* or *C. f. evelynae*, though being most divergent among the conspecifics, exhibited much poorer differentiation from the other subspecies occurring in the adjacent regions, such as Taiwan and continental China (Yasukawa *et al.*, 1996; Sections 3 and 4). Such differences in the degree of divergence and distributional pattern between the *G. japonica–spengleri* clade and subspecies of *M. mutica* or of *C. flavomarginata* strongly suggest the older origin and relict state of *G. japonica* compared with *M. m. kami* and *C. f. evelynae* in the Ryukyus.

The paleogeography of the Ryukyus and adjacent regions during the Pleistocene is still controversial (See Ota [1998], for review). Kizaki and Oshiro (1977; 1980), mainly based on geological data, postulated that the Ryukyus–Taiwan–southeastern continental region south of the Tokara Gap had a land-bridge connection at the early Pleistocene. They considered that a large portion of this land-bridge submerged in the middle Pleistocene, and that no land-bridges have connected islands of the whole region again since then. On the contrary, a few other geologists argued for the late Pleistocene land-bridge formation from the central Ryukyus to Taiwan (Ujiié, 1990), or even from Kyushu of the Main-islands of Japan to Taiwan through the Ryukyus (Kimura, 1996). Recently, Hikida and Ota (1997) and Ota (1998) analyzed phylogeographical patterns of extant amphibians and reptiles in the subtropical and tropical East Asia, and assessed the previous paleogeographical hypotheses accordingly. Results of their analyses revealed extremely high frequency of relict taxa, such as *G. japonica*, in the central Ryukyus. On the other hand, amphibians and reptiles endemic to the southern Ryukyus, such as *M. m. kami* and *C. f. evelynae*, showed less prominent differentiations from the closest relatives, suggesting their more recent divergences through vicariance. Such phylogeographical patterns favor hypotheses of Kizaki and Oshiro (1977, 1980), but do not support the late Pleistocene land-bridges postulated by Ujiié (1990) and Kimura (1996) (Hikida and Ota, 1997; Ota, 1998). Furthermore, Hikida and Ota (1997) and Ota (1998) suspected that even the early Pleistocene land-bridges did not actually reach the central Ryukyus because of the extreme biogeographical uniqueness of this region.

The biogeographical hypothesis proposed by Kizaki and Oshiro (1977, 1980) and modified by Hikida and Ota (1997) and Ota (1998) is concordant with the distributional-divergence patterns shown by *G. japonica*, the other two geoemydines of the Ryukyus, and their closest relatives. It is likely that the ancestral form of *G. japonica* first entered into the central Ryukyus, earlier than their latest insularization (Pliocene) (Kizaki and Oshiro, 1980; Hikida and Ota, 1997; Ota, 1998). On the other hand, ancestors of *M. m. kami* and *C. f. evelynae* probably entered into the southern Ryukyus through its early Pleistocene land-bridge connection with Taiwan, and then were isolated from their conspecific populations in Taiwan and the continental China through the subsequent (middle Pleistocene) subsidence of the land-bridge.

Recent phylogenetic analyses strongly suggested the monophyly of *Geoemyda*, *Cistoclemmys* and *Pyxidea*, but these three genera are still substantially differentiated and thus deserve separation at generic level (Hirayama, 1984; Gaffney and Meylan, 1988; Yasukawa et al., 1992; Yasukawa, 1997). Distributional ranges of species of *Geoemyda* are much limited and broadly isolated from each other. Interspaces of their ranges are occupied by species of *Cistoclemmys* (i.e., *C. flavomarginata* and *C. galbinifrons*) and *Pyxidea mouhotii* (Figure 5; Das, 1991; Iverson, 1992; Yasukawa *et al*., 1992). Such a distributional pattern seems to reflect the relatively ancient and recent origins of *Geoemyda*, and *Cistoclemmys* and *Pyxidea*, respectively (Das, 1991; Yasukawa et al., 1992; Yasukawa and Ota, in press *a*, *b*).

Recent phylogenetic analyses, while supporting the independency of *Cistoclemmys* from *Cuora* sensu stricto, indicated the closest phylogenetic affinity of *C. flavomarginata* and *C. galbinifrons* from southeastern China and northern Indochina (Figure 5) (Hirayama, 1984; Yasukawa, 1997). Also, two fossil species, *Cuora pitheca* (Late Miocene) from Yunnan, China, and *Cuora miyatai* (Middle Pleistocene) from Kyushu (Oita Prefecture) and Honshu (Tochigi and Yamaguchi Prefectures), have been regarded as close relatives of *C. flavomarginata* (Hasegawa, 1981; Yeh, 1985; Ye, 1994). Preliminary analyses of osteological characters, however, suggested that the former actually belongs to *Cuora* sensu stricto because it has a rather depressed carapace and a distinct posterior notch in the plastron. On the other hand, the latter species seems to be a member of *Cistoclemmys* (Yasukawa and Hirayama, in prep.). It is obvious that our hypothetical

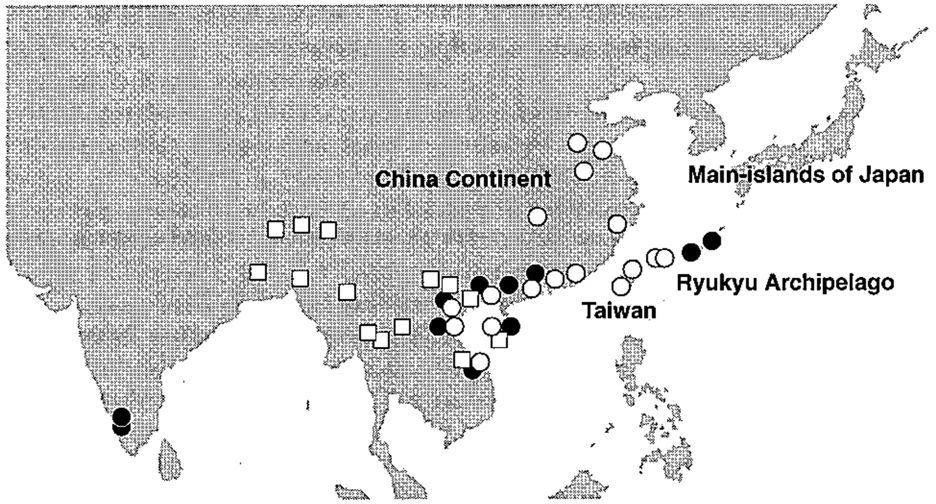

Figure 5. Distribution map of *Geoemyda* (closed circles: *G. japonica*, *G. silvatica* and *G. spengleri*), *Cistoclemmys* (open circles: *C. flavomarginata* and *C. galbinifrons*), and *Pyxidea* (open squares: *P. mouhotii*) based on Das (1991), Iverson (1992), Yasukawa et al., (1992; 1996) and Zhao and Adler (1993). Ranges of introduced populations are not shown.

scenario for the origin of *C. flavomarginata* in the southern Ryukyus can not explain the origin of *C. miyatai* in the Main-islands of Japan. This species may possibly represent another more recent landbridge dispersal through the Ryukyu region, or otherwise a dispersal *via* different landbridge, e.g., that between Kyushu and the Korean Peninsula. More fossil data from broader regions are needed for a convincing scenario to explain the origin of this enigmatic taxon.

Acknowledgments

We wish to express our gratitude to H. Endo, K. Hatooka, R. Hirayama, A. Kamata, T. Takenaka, S. Sengoku and T. Yabe for allowing us to examine specimens in their care, and to S. Ikehara, A. Kamata, S. Kato, N. Kamezaki, T. Otani, M. Tasumi and Y. Tomoda for providing precious specimens. S.-L. Chen, R. Hirayama, H. Otsuka, A. Takahashi and M. Tasumi provided pertinent literature, and R. Hirayama, S. Sengoku, T. Takahashi and M. Toyama provided useful information. We are also much indebted to R. Hirayama and an anonymous reviewer for the critical reading of the manuscript.

This research was partially supported by grants-in-aid from Japan Ministry of Education, Science, Sports and Culture (C-09839024 to H. Ota, and B-08458165 to M. Izawa), and also by grants from Fujiwara Natural History Foundation and National Science Museum, Tokyo, for visiting researchers (both to H. Ota).

References

Das, I. (1991) *Color Guide to the Turtles and Tortoises of the Indian Subcontinent.* R & A Publishing Limited House, Avon.

David, P. (1994) Liste des reptiles actuels du monde. I. Chelonii. *Dumérilia* 1, 7–127.

Ernst C. H. and Barbour, R. W. (1989) *Turtles of the World.* Smithsonian Institution Press, Washington, D. C.

Ernst, C. H. and Lovich, J. E. (1990) A new species of *Cuora* (Reptilia: Testudines: Emydidae) from the Ryukyu Islands. *Proceedings of the Biological Society of Washington* 107, 52–59.

Fan, T. H. (1931) Preliminary report of reptiles from Yaoshan, Kwangsi, China. *Bulletin of Department Biology, College of Science, Sun Yatsen University,* **11**, 1–154.

Fritz, U. and Obst, F. J. (1996) Zur Kenntnis der Celebes-Erdschildkröte, *Heosemys yuwonoi* (McCord, Iverson and Boeadi, 1995). *Herpetofauna,* **18**, 27–34.

Gaffney, E. S. and Meylan, P. A. (1988) A phylogeny of turtles. In *The Phylogeny and Classification of the Tetrapods,* Vol. 1, ed. M. J. Benton, pp. 157–219. Oxford University Press, New York.

Gray, J. E. (1863) Observations on the box tortoises, with the descriptions of three new Asiatic species. *Proceedings of the Zoological Society of London,* **1863**, 173–179.

Hasegawa, Y. (1980) Notes on vertebrate fossils from late Pleistocene to Holocene of Ryukyu Islands, Japan. *Quaternary Research,* **18**, 263–267. (in Japanese with English abstract)

Hasegawa, Y. (1981) Pleistocene hinged terrapin from the Tsukumi limestone quarry, Oita-ken, Japan. *Science Reports of Yokohama National University, Section II,* **28**, 19–23.

Hikida, T. and Ota, H. (1997) Biogeography of reptiles in the subtropical East Asian Islands. In *Proceedings of the Symposium on Phylogeny, Biogeography, and Conservation of Fauna and Flora of East Asian Region,* eds. K.-Y. Lue and T.-H. Chen, pp. 11–28. National Science Council, R.O.C., Taipei.

Hirayama, R. (1984) [1985] Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); A preliminary result. *Studia Geologica Salmanticensia, Volumen Especial 1, Studia Palaeocheloniologica,* **1**, 141–157.

Hsu, H.-F. (1930) Preliminary note on a new variety of *Cyclemys flavomarginata* from China. *Contributions from the Biological Laboratory of the Science Society of China, Zoological Series,* **6**, 1–7.

Iverson J. B. (1992) *A Revised Checklist with Distribution Maps of the Turtles of the World.* Privately printed, Richmond.

Iverson, J. B. and McCord, W. P. (1989) The proper taxonomic allocations of *Emys nigricans* Gray, *Emys muticus* Cantor, and *Geoclemys kwangtungensis* Pope. *Amphibia-Reptilia,* **10**, 23–33.

Iverson, J. B. and McCord, W. P. (1994) Variation in East Asian turtles of the genus *Mauremys* (Bataguridae; Testudines). *Journal of Herpetology,* **28**, 178–187.

Karsen, S. J., Lau, M. W. and Bogadek, A. (1998) *Hong Kong—Amphibians and Reptiles* (2nd edn.). Provincial Urban Council, Hong Kong.

Kimura, M. (1996) Quaternary paleogeography of the Ryukyu Arc. *Journal of Geography,* **105**, 259–285. (in Japanese with English abstract)

Kizaki, K. and Oshiro, I. (1977) Paleogeography of the Ryukyu [sic] Islands. *Marin Science Monthly,* **9**, 542–549. (in Japanese with English abstract)

Kizaki, K. and Oshiro, I. (1980) The origin of the Ryukyu Islands. In *Natural History of Ryukyu,* ed., K. Kizaki, pp. 8–37. Tsukiji-Shokan, Tokyo. (in Japanese)

Leviton, A. E., Gibbs R. H., Jr., Heal E. and Dawson C. E. (1985) Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collection in herpetology and ichthyology. *Copeia,* **1985**, 802–832

Lovich, J. E. and Ernst, C. H. (1989) Variation in the plastral formulae of selected turtles with comments on taxonomic utility. *Copeia,* **1989**, 304–318.

McCord, W. P. and Iverson, J. B. (1991) A new box turtle of the genus *Cuora* (Testudines: Emydidae) with taxonomic notes and a key to species. *Herpetologica,* **47**, 407–420.

McCord, W. P., Iverson, J. B., and Boeadi. (1995) A new batagurid turtle from northern Sulawesi, Indonesia. *Chelonian Conservation and Biology,* **1**, 311–316.

Moll, E. O., Groombridge, B. and Vijaya, J. (1986) Redescription of the cane turtle with notes on its natural history and classification. *Journal of the Bombay Natural History Society, Supplement,* **83**, 112–126.

Oshiro, I. (1987) *Lost Animals and Plants—Fossils of Okinawa.* Shinsei Tosho, Naha. (in Japanese)

Ota, H. (1998) Geographic patterns of endemism and speciation in amphibians and reptile of the Ryukyu Archipelago, Japan, with special reference to their paleogeographical implications. *Researches on Population Ecology,* **40**, 189–204.

Ota, H. and Yasukawa, Y. (in press) *Cistoclemmys flavomarginata*. In *The Conservation Biology of Freshwater Turtles*, eds. P. C. H. Pritchard and A. G. J. Rhodin, IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Gland.

Pope, C. H. (1935) *Natural History of Central Asia. Vol. 10. The Reptiles of China*. American Museum of Natural History, New York.

Pritchard P. C. H. (1979) *Encyclopedia of Turtles*. T. F. H. Publication, Neptune, New Jersey.

SAS (1990). *SAS User's Guide: Statistics*, Version 6. SAS Institute Inc., North Carolina.

Stejneger, L. H. (1907) Herpetology of Japan and Adjacent Territory. *Bulletin of the United States National Museum*, **58**, 1–577.

Toyama, M. (1997) *Geoemyda japonica* from Gushihara Midden, Iejima Island, Japan. *Reports on Cultural Assets of Okinawa Prefecture*, **130**, 189–194. (in Japanese)

Ujiié, H. (1990) Geological history of the Ryukyu Island Arc. In *Nature of Okinawa: Geomorphology and Geology*, ed. H. Ujiié, pp. 251–255. Hirugisha, Naha. (in Japanese)

Wermuth, H. and Mertens, R. (1977) *Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia*, Das Tierreich Lief. 28. Walter de Gruyter, Berlin.

Wu, P., Zhou, K. and Yang, Q. (1998) Evolution of hinged turtles in Bataguridae inferred from sequences of 12S rRNA gene. *Chinese Journal of Applied Environmental Biology*, **4**, 374–378.

Yasukawa, Y. (1997) Phylogeny and Taxonomy of the Subfamily Geoemydinae (Reptilia: Testudines: Bataguridae). *Unpublished Doctoral Dissertations, Kyoto University*, Kyoto. (in Japanese)

Yasukawa, Y., Ota, H. and Hikida, T. (1992) Taxonomic re-evaluation of the two subspecies of *Geoemyda spengleri* (Gmelin, 1789) (Reptilia). *Japanese Journal of Herpetology*, **14**, 143–159.

Yasukawa, Y., Ota, H., and Iverson, J. B. (1996) Geographic variation and sexual size dimorphism in *Mauremys mutica* (Cantor, 1842) (Reptilia: Bataguridae), with description of a new subspecies from the southern Ryukyus, Japan. *Zoological Science*, **13**, 303–317.

Yasukawa, Y. and Ota, H. (in press *a*) *Geoemyda japonica*. In *The Conservation Biology of Freshwater Turtles*, eds. P. C. H. Pritchard and A. G. J. Rhodin, IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Gland.

Yasukawa, Y. and Ota, H. (in press *b*) *Geoemyda spengleri*. In *The Conservation Biology of Freshwater Turtles*, eds. P. C. H. Pritchard and A. G. J. Rhodin, IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Gland.

Yasukawa, Y., Yabe, T., Ota, H., and Iverson, J. B. (in press *c*) *Mauremys mutica*. In *The Conservation Biology of Freshwater Turtles*, eds. P. C. H. Pritchard and A. G. J. Rhodin, IUCN/SSC Tortoise and Freshwater Turtle Specialist Group, Gland.

Ye, X. (1994) *Fossil and Recent Turtles of China*. Science Press, Beijing.

Yeh, X. (1985) Studies on fossils of *Cuora* of China and Japan. *Acta Herpetologica Sinica*, **4**, 81–87.

Zhao, E. and Adler, K. (1993) *Herpetology of China*, Contribution to Herpetology, 10. Society for the Study of Amphibians and Reptiles, Ohio.

Appendix I

Specimens examined.

Catalogue numbers of specimens deposited in herpetological collections of the Department Zoology, Kyoto University, Ogasawara Shellfish Museum, and personal collections of A. Kamata, R. Hirayama, T. Takenaka and T. Yabe are preceded by KUZ, OSM, AK, RH, TT and TY, respectively. The other acronyms are those suggested by Leviton *et al.* (1985).

Cistoclemmys flavomarginata evelynae: Japan, Ryukyu Archipelago, Yaeyama Group, Iriomotejima Island, KUZ 36746–36751, NSMT 02091–02092, 02150, two unnumbered specimens of OSM, four unnumbered specimens of SS, four live specimens released after being examined; Ishigakijima Island, KUZ 36741–36745, NSMT 02090, 03564–03569, RH 982. *Cistoclemmys flavomarginata flavomarginata*: China, Mainland, KUZ 19561, 36644, 36753–36755, 47316, 47318–47320, 47902–47906, RH 698–702, 942, five unnumbered specimens of AK, two captive specimens of TT, four captive specimens of TY; Taiwan, KUZ 36752, NSMT 02087–02089, RH 53, 62–63, 65–66, 105, 208–209, 211–215, 430, 432–440, 442, 444, 445, one captive specimen of TT; locality unknown, OMNH–R 4059, one unnumbered specimen.