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Geographic Variation and Sexual Size Dimorphism in *Mauremys mutica* (Cantor, 1842) (Reptilia: Bataguridae), with Description of a New Subspecies from the Southern Ryukyus, Japan

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ABSTRACT—The batagurid turtle, *Mauremys mutica,* is widely distributed in tropical to temperate East Asia. Analyses of morphometric characters and coloration revealed that the southern Ryukyu populations of this species are much diverged from the other populations, presumably as a result of their long geographical isolation. We describe those populations as a new subspecies, *M. m. kami.* Analysis of geographic variation also suggested that distinctly isolated populations of the central and northern Ryukyus, and Kyoto and Shiga Prefectures of central Japan have originated from animals artificially introduced from the Yaeyama Group, and Taiwan, respectively. We confirmed the absence of “larger female” sexual size dimorphism (SSD) in *M. mutica* unlike most other aquatic batagurids, and further demonstrated variation in SSD pattern between the subspecies: in *M. m. kami*, the adult male has a significantly greater carapace length than adult females, whereas the adult carapace length does not differ significantly between sexes in the nominotypical subspecies. It is hypothesized that these dimorphic patterns evolved from the widely prevailing “larger female” condition through epigamic selection involving forcible copulatory behavior.

INTRODUCTION

Due to the morphological and ecological constraints on their mobility, terrestrial and freshwater turtles are very susceptible to reproductive isolation in insular environments, and hence are expected to be a suitable material to study the relationship between the insular isolation and differentiation/evolution. Since Temminck and Schlegel (1835) described *Emys vulgaris japonica* (= *Mauremys japonica*) from Japan, quite a few systematic studies have been made on freshwater turtles occurring in the insular region of East Asia, including Taiwan, the Ryukyu Archipelago, and the main islands of Japan. Most studies, however, suffered from the insufficiency in the number and size of samples on which they depended, and thus were unable to examine appropriately the coincidence between geographic variation and geological and other historical events in this region. Only recently, a few authors attempted more comprehensive approaches (e.g., Ernst and Lovich, 1990; Lovich *et al*., 1985), but still they were not completely free from the above mentioned problem (McCord and Iverson, 1991; Ota, 1991; Ota and Yasukawa, 1996).

The batagurid turtle *Mauremys mutica* (Cantor, 1842) is widely distributed in tropical to temperate East Asia, including the insular region (Iverson, 1992; Nakamura and Uéno, 1963; Yasukawa *et al*., 1996a: Fig. 1). Iverson and McCord (1989) pointed out that this species is geographically highly variable, especially in coloration. More recently, Iverson and McCord (1994), after surveying specimens from the continent, Taiwan, and Ishigakijima and Akusekijima Islands of the Ryukyus, demonstrated that the two Ryukyu samples are much diverged from the remainder in morphometric characters, as well as in coloration. They assumed that the Ryukyu populations deserve a distinct taxonomic status, but deferred the conclusion due to the insufficiency in the number and size of samples examined. Iverson and McCord (1994) also considered that *M. mutica* is unique among East Asian *Mauremys* in lacking the “larger female” sexual size dimorphism (SSD). However, reliable quantitative data were not provided for this aspect by these or any other authors [see DISCUSSION for problems in data provided by Mao (1971) and modified by Gibbons and Lovich (1990)].

In the present study, we have made more comprehensive analyses of geographic variation in *Mauremys mutica*

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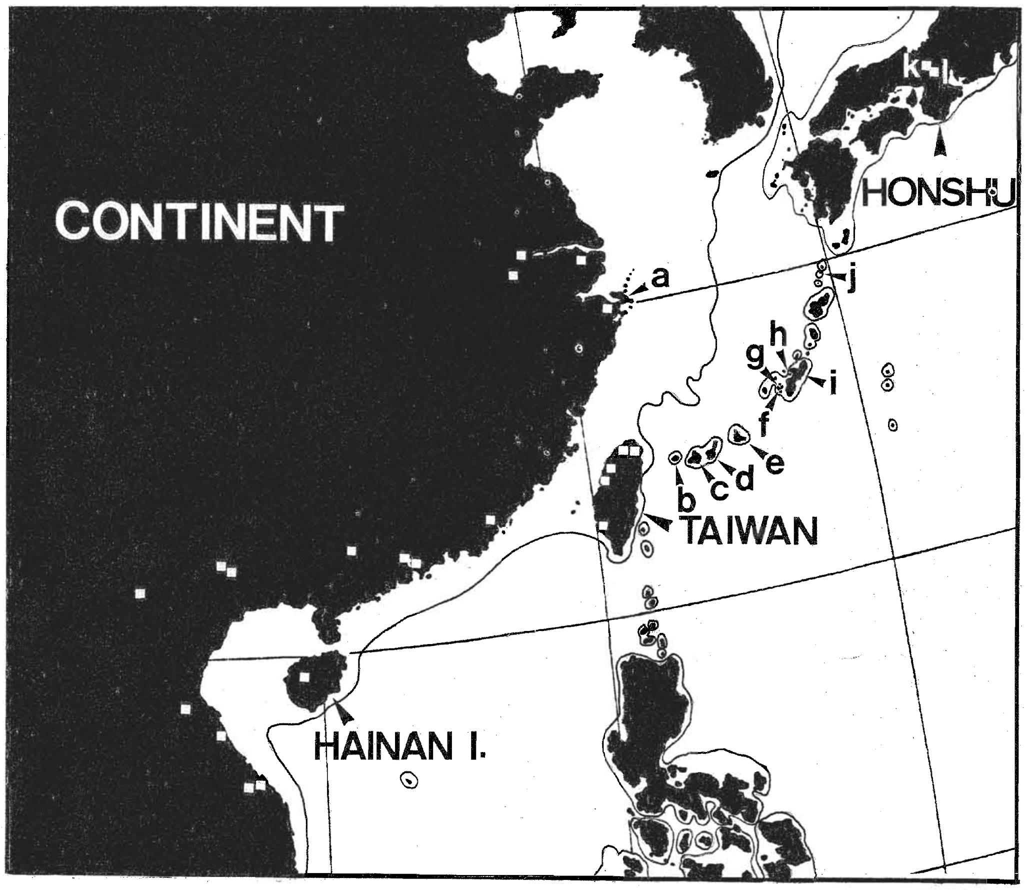

Fig. 1. Map of temperate to tropical East Asia, showing the range of distribution of *Mauremys mutica.* Locality records within the continent, Hainan Island, and Taiwan, represented by white squares, follow Iverson (1992). The other localities are: Chusan Island (a, type locality) of China, Yonagunijima (b), Iriomotejima (c) and Ishigakijima Islands (d) of the Yaeyama Group, Miyakojima Island (e) of the Miyako Group, Akajima (f) Zamamijima (g), Sesokojima (h) and Okinawajima Islands (i) of the Okinawa Group, Akusekijima Island (j) of the Tokara Group, and Kyoto (k) and Shiga Prefectures (l) of Honshu, Japan. Contour lines indicate sea bottoms of 120 m depth (JMSA, 1978), enclosing areas presumably exposed above sea level during the late Pleistocene (Ota *et al.*, 1993).

on the basis of greater samples including representatives of all insular populations except for two recently established ones in the Ryukyus. Results have confirmed the presence of a distinct morphological divergence between the Ryukyu populations and the others. We thus describe the former as a new subspecies, and discuss the process of their differentation in the context of the currently illustrated paleogeographical scenario of the insular region of East Asia. Also, the results have provided valuable insights on the origin of the populations distinctly isolated in Honshu and a few central-northern islands of the Ryukyus.

Besides these, absence of the "larger female" SSD in *M. mutica* has been confirmed. We discuss the evolutionary significance of this phenomenon.

MATERIALS AND METHODS

A total of 226 specimens of *Mauremys mutica* (104 males and 122 females: 52 from the continent, 46 from Taiwan, 70 from the Ryukyus and 58 from Honshu) were examined (see *"Specimens examined"* for further details). Adult individuals were sexed on the basis of the tail shape (longer and thicker in males than in females) and plastral condition (distinctly concave in males, almost flat in females: Yasukawa *et al.*, 1996a).

Preliminary examination of smaller specimens indicated that, in males, gonadal maturity and/or the initiation of copulatory behavior coincided well with the appearance of the above-mentioned secondary sexual features. Because it was impossible to dissect all specimens used in this study (some were live animals, and others were museum materials under strict handling regulations), a given male was considered as an adult when it exhibited distinctly enlarged tail and/or distinctly concave plastron, whereas it was considered as a subadult when it showed only weak developments in these features. In females, the smallest adults were determined for dissected specimens belonging to the Yaeyama and Honshu samples (120.0 mm and 125.8 mm in maximum carapace length (CL), respectively) on the basis of gonadal investigations: a given animal was considered as an adult when it had well-developed ovarian follicles, oviductal eggs, and/or hypertrophied oviducts. We then assumed that all the other females of the Yaeyama and Honshu samples with CL greater than 120.0 mm and 125.8 mm, respectively, were adults. In the Taiwanese sample, the smallest female was 144.0 mm CL, and we thus considered all examined females as adults. We could not strictly define the minimum maturity size in the continental female. Considering the smallest adult CL in the other samples (see above), we tentatively assumed that specimens having CL greater than 120 mm were adults. We included subadult data only in ANCOVAs and Tukey-like tests (see below).

Sexual identities of specimens that were not sexed with certainty by the above procedure (i.e., whole body specimens with body size not reaching that of the smallest male showing more or less distinct secondary sexual features in each sample, and specimens consisting only of articulated shells) were determined by the discriminant function analysis (DFA) using well-defined male and female specimens as representatives of the two alternatives (i.e., classified *a posteriori*).

Fourteen specimens (seven males and seven females) of *M. annamensis*, the closest relative of *M. mutica* (see Iverson and McCord, 1994), were also examined to constitute an outgroup in the cluster analyses of the *M. mutica* samples.

Straight line measurements were taken to the nearest 0.1 mm for the following characters using calipers: maximum (not midline) carapace length (CL), maximum carapace width (CW), maximum shell height (CH), maximum plastron length (PL), maximum length of the plastral hindlobe (HL, measured from interabdomino-interfemoral junction to a line across the posterior ends of the anal scutes), plastral forelobe width (PWA, measured at the level of junction of humero-pectoral seam and plastral margin), anterior width of the plastral hindlobe (PWC, measured at the level of the junction of abdomino-femoral seam and plastral margin), posterior width of plastral hindlobe (PWD, measured at level of the junction of femoro-anal seam and the plastral margin), right bridge length (BL, measured from axilla to inguinal pocket at its shortest dimension), 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. Terminology follows Iverson and McCord (1994).

Because most samples from single localities still suffer from their small sizes for statistical comparisons, for the canonical discriminant analyses (CDA: see below) we classified the whole range of the species into the following four major regions and pooled data for specimens from each region before analysis: 1) the Yaeyama Group, 26 males and 37 females (including four subadults) from Ishigakijima, Iriomotejima and Yonagunijima Islands; 2) Honshu, 22 males and 36 females from Kyoto and Shiga; 3) Taiwan, 24 males and 22 females from the main island; 4) the continent, 30 males (including five subadults) and 22 females (including four subadults) from China, including Hainan Island, and northern Vietnam. This arrangement may be rather arbitrary, but because there was no distinct variation within each regional sample, we believe that it did not much affect the patterns of geographic variation of the total samples revealed by our analyses. *Mauremys mutica* occurs also on Akajima, Sesokojima, Okinawajima, Akusekijima, Zamamijima and Miyakojima Islands of the central to northern Ryukyus, as a result of recent artificial introductions (Hikida *et al.*, 1992; Ota, 1996a; Toyama, 1995; Yasukawa and Kimura, 1995; Yasukawa *et al.*, 1996a). Because the available samples from the former four islands were so small (three adult females from Akajima, one adult male from Sesokojima, one adult female from Okinawajima, and one adult male and one adult female from Akusekijima), we subjected their data to discriminant function analysis (DFA) to infer their affinities with populations of the four major regions defined above. Specimens from Zamamijima and Miyakojima were not available.

Significance levels for all analyses were set at 0.05. All measurements except for CL for univariate comparisons were log-transformed before analysis. Sexual difference in CL was examined by t-test, and expressed by the sexual dimorphism index (SDI) proposed by Gibbons and Lovich (1990) as:

$$+ x/y, \text{ when } x > y; \text{ or } - y/x, \text{ when } x < y$$

where "x" and "y" denote means for adult females and adult males, respectively.

Because preliminary intersexual comparisons by multivariate analysis of variance (MANOVA, Wilks' likelihood-ratio method) detected a significant sexual dimorphism within each regional sample ($p < 0.001$), analyses of geographic variation were conducted separately for males and females. Variation in CL among the four regional samples was examined by Kruskal-Wallis and Dunn's multiple comparison test (Zar, 1984), since homogeneity of variances was violated among female samples. Geographic variation in each of the other measurements was also examined in relation to CL by ANCOVA and Tukey-like test (Zar, 1984).

Prior to the ANCOVAs and Tukey-like tests, we tested correlations between CL and the other variables separately for each regional sexual sample. Correlations were consistently statistically significant in most measurements, except for IH in the Yaeyama and Honshu males and the continental males and females, and GL and IAN in the Honshu females. We thus excluded IH from the ANCOVAs and the ANCOVA and Tukey-like tests, but included GL and IAN in these analyses on the basis of the assumption that they generally correlate with CL and that the apparent absence of their correlations in Honshu females were attributable to sample error.

Besides these, data for all measurements were subjected to the canonical discriminant analysis (CDA) using CANDISC procedure of SAS (1990). To depict relationships among the four regional samples, we clustered Mahalanobis distances (D^2) calculated from the 16 variables by the neighbor-joining method (Saitou and Nei, 1987) using NEIGHBOR procedure of PHYLIP 3.41 (Felsenstein, 1989). Resulting phenograms were rooted at midpoints between the longest intersample branches. We have also conducted the same procedure after adding *M. annamensis* as the outgroup to root the *M. mutica* cluster.

To visualize the variation among the seven insular samples from the Ryukyus, principal component analysis (PCA) was conducted using PRINCOMP procedure of SAS (1990).

In addition, colorations of head, carapace and plastron were compared among the regional samples. Blotch pattern on pectoral and abdominal scutes of the plastron was classified into five grades: A) absent or indistinct; B) distinct, but small; C) large and elongate, but narrowly separated from each other by light interspaces; D) fusing to each other to form a longitudinal broad stripe on each side; E) covering almost all of the pectoral and abdominal scutes.

RESULTS

Variation in raw values and ratios of the 16 measurements are summarized in Tables 1 and 2, respectively.

Sexual size dimorphism

Values of SDI for CL were −1.072, −1.032, +1.013 and +1.008 in the Yaeyama, Honshu, Taiwan and the continental samples, respectively. Sexual difference in this measurement was statistically significant in the Yaeyama sample ($p < 0.01$), but was not significant in either of the other samples ($p > 0.05$: Fig. 2, Table 1).

Geographic variation in morphometric characters

Results of Kruskal-Wallis and Dunn's multiple comparison test revealed that there are significant geographic differences ($p < 0.001$) in CL in both males and females (Fig. 2, Table 3). In both sexes, CL in the Taiwanese sample was significantly greater than those in the samples from Yaeyama and the continent. The sample from Honshu exhibited a significantly greater CL than that from the continent

Table 1. Variation in morphometric characters (in mm; x̄ ± 1 SD, followed by ranges in parentheses) of adult *Mauremys mutica* from Yaeyama, Honshu, Taiwan and the continent. See text for abbreviations.

	Yaeyama		Honshu		Taiwan		Continent	
Variable	Male (n=26)	Female (n=33)	Male (n=22)	Female (n=36)	Male (n=24)	Female (n=22)	Male (n=25)	Female (n=18)
CL	148.3±14.8	138.3±13.8	156.6±10.1	151.7±9.4	165.0±16.6	167.2±15.8	146.4±18.1	147.6±23.6
	(129.9–188.9)	(120.0–176.4)	(127.5–174.0)	(125.8–170.6)	(140.8–195.7)	(144.0–194.6)	(123.8–194.0)	(120.2–192.6)
CW	106.0±9.3	102.0±9.3	108.9±7.0	105.8±6.4	117.6±11.4	118.2±11.6	102.1±12.1	106.6±18.0
	(94.4–135.4)	(91.7–129.5)	(88.2–121.5)	(91.5–120.9)	(99.6–140.3)	(101.8–145.8)	(85.4–134.0)	(86.2–153.7)
CH	53.6±4.3	50.7±4.3	60.9±4.6	61.8±3.9	61.1±5.4	65.0±5.9	54.9±6.4	57.0±9.4
	(47.1–63.5)	(42.5–62.2)	(47.9–67.2)	(54.2–69.4)	(53.2–70.7)	(56.9–76.3)	(45.0–71.5)	(46.4–80.4)
PL	132.6±13.1	128.4±12.4	136.5±7.5	138.5±7.8	147.1±13.6	152.7±13.8	131.6±15.7	136.9±21.7
	(106.5–170.1)	(113.3–163.0)	(115.2–152.4)	(116.7–152.4)	(128.6–175.3)	(128.4–175.1)	(109.7–173.6)	(110.8–183.2)
HL	51.2±3.9	50.3±4.4	50.8±3.2	50.9±2.9	55.8±6.0	56.3±4.8	48.1±5.0	49.1±6.3
	(44.1–62.3)	(44.3–61.4)	(43.9–59.4)	(43.3–55.7)	(45.8–67.5)	(46.0–65.2)	(37.6–61.4)	(39.5–61.3)
PWA	56.9±4.1	56.6±5.3	61.3±3.4	62.7±6.7	64.0±6.2	68.1±7.3	56.5±7.5	61.2±10.2
	(51.4–68.0)	(50.8–75.1)	(53.2–68.9)	(49.4–72.2)	(55.2–80.7)	(58.1–84.5)	(46.0–78.8)	(48.7–84.0)
PWC	62.8±6.5	65.2±5.8	67.4±4.8	68.9±4.0	69.5±6.0	76.0±7.9	62.4±8.6	69.0±13.1
	(46.5–76.9)	(56.8–82.2)	(55.1–80.1)	(57.4–76.7)	(59.8–81.3)	(65.3–95.3)	(53.2–91.5)	(54.9–98.9)
PWD	43.6±3.3	42.5±3.4	46.6±3.5	46.7±3.0	48.9±4.5	50.6±5.0	43.8±6.7	46.4±9.2
	(37.3–50.8)	(36.0–50.3)	(37.0–54.0)	(39.2–52.4)	(41.6–55.7)	(42.7–60.4)	(31.5–62.1)	(33.9–64.9)
BL	48.0±5.5	48.1±5.7	49.0±3.3	52.4±3.6	54.4±4.5	59.6±6.0	46.9±6.5	51.1±9.4
	(40.5–62.8)	(39.7–64.6)	(41.3–57.7)	(43.6–60.2)	(48.4–64.4)	(50.0–71.5)	(37.2–63.9)	(40.0–74.8)
GW	32.9±3.3	29.9±2.6	34.2±2.3	32.3±2.0	34.8±3.7	34.8±2.9	30.3±3.1	30.5±3.8
	(27.7–41.5)	(26.7–38.5)	(27.9–37.8)	(27.6–37.3)	(28.5–43.9)	(29.0–39.9)	(25.6–37.8)	(24.5–37.9)
GL	19.4±2.0	18.5±1.8	18.6±2.3	19.2±1.8	18.7±3.6	19.1±2.5	17.6±3.2	18.8±4.3
	(16.1–24.2)	(16.1–25.1)	(14.6–23.7)	(16.4–22.7)	(13.7–27.4)	(13.9–24.6)	(12.9–25.9)	(13.0–26.2)
IH	16.7±2.9	16.2±3.0	18.0±2.1	16.5±2.5	21.0±3.1	20.5±4.0	17.3±4.2	16.7±4.4
	(11.9–23.4)	(11.8–22.9)	(14.5–21.7)	(10.8–21.0)	(14.1–27.0)	(15.7–30.0)	(10.2–26.3)	(7.0–23.0)
IP	19.2±2.9	19.4±2.3	22.9±1.7	25.1±2.3	24.9±2.7	27.4±3.6	23.1±5.8	26.0±8.2
	(13.7–24.6)	(14.9–24.1)	(20.6–25.6)	(21.2–30.3)	(20.5–31.1)	(17.0–32.0)	(15.4–36.9)	(18.1–46.5)
IAB	27.1±4.1	26.3±3.9	28.0±3.2	29.7±2.8	28.8±3.0	31.3±4.1	26.6±4.7	28.5±6.1
	(20.7–37.7)	(20.6–36.0)	(22.2–37.3)	(21.8–35.5)	(25.1–35.6)	(24.0–39.0)	(17.9–37.0)	(19.9–42.9)
IF	26.2±2.3	24.6±2.8	25.0±2.2	24.3±2.3	28.9±4.0	28.6±2.3	25.1±3.0	23.7±3.6
	(22.5–30.2)	(20.3–31.3)	(20.0–28.8)	(19.0–28.1)	(21.6–37.1)	(23.6–33.5)	(19.0–30.7)	(13.8–29.0)
IAN	15.3±1.6	15.4±2.0	16.7±1.5	17.2±1.8	16.3±1.6	17.3±2.3	14.5±4.0	16.3±5.9
	(13.2–18.9)	(12.6–20.9)	(13.9–19.9)	(13.1–22.1)	(13.8–20.2)	(13.0–23.2)	(9.1–26.6)	(8.7–29.4)

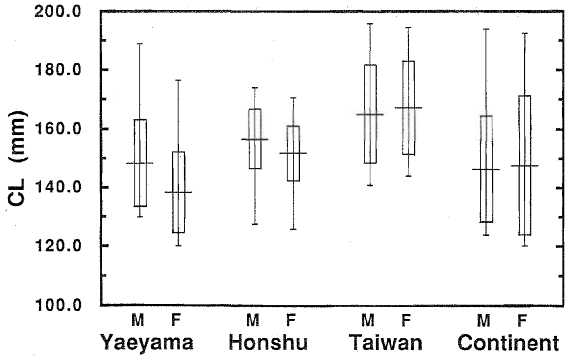

Fig. 2. Variation in the greatest carapace length (CL) of adult males (M) and females (F) of *Mauremys mutica* from Yaeyama, Honshu, Taiwan and the Asian Continent. Vertical and horizontal bars and rectangles indicate range and means of actual values and ranges of standardized deviations from means, respectively.

in males and that from Yaeyama in females, respectively. No significant differences were recognized in CL between the other combinations of samples.

Results of ANCOVAs and Tukey-like tests (using CL as the covariate)(Table 3) revealed that in males the slope of the regression line for IAB was significantly different among the four samples, whereas positions of the lines were significantly different for CW, CH, PL, HL, BL, GW, GL, IP, IF and IAN. In females, slopes of the regression lines for PWC, PWD, GL, IP, and IAN were significantly different, whereas positions of the lines were significantly different for CW, CH, HL, GW, IAB and IF.

Standardized coefficients of the 16 measurements calculated for the first three canonical axes (CANs 1–3) were presented in Table 4, together with eigenvalues, differences, and proportions for these axes. Cumulative proportions indicate that CANs 1–3 account for the total variation, of which 55.9% and 67.3% are expressed by CAN1 in males and females, respectively.

In both sexes, CAN1 variable was distinctly smaller in the Yaeyama sample than in the three non-Ryukyu samples,

Table2. Variation in ratio (median, followed by ranges in parentheses) of adult *Mauremys mutica* from Yaeyama, Honshu, Taiwan and the continent. See text for abbreviations.

Variable	Yaeyama		Honshu		Taiwan		Continent	
	Male (n=26)	Female (n=33)	Male (n=22)	Female (n=36)	Male (n=24)	Female (n=22)	Male (n=30)	Female (n=22)
CW/CL	0.719 (0.64–0.76)	0.745 (0.69–0.82)	0.696 (0.67–0.71)	0.694 (0.66–0.77)	0.713 (0.64–0.76)	0.708 (0.65–0.78)	0.702 (0.64–0.76)	0.726 (0.66–0.80)
CH/CL	0.361 (0.33–0.40)	0.369 (0.33–0.41)	0.386 (0.36–0.41)	0.406 (0.38–0.45)	0.368 (0.34–0.40)	0.387 (0.36–0.43)	0.380 (0.35–0.42)	0.396 (0.34–0.44)
PL/CL	0.898 (0.80–0.94)	0.934 (0.88–0.96)	0.873 (0.83–0.92)	0.911 (0.88–0.95)	0.898 (0.84–0.93)	0.911 (0.87–0.95)	0.898 (0.83–0.95)	0.924 (0.89–0.97)
HL/CL	0.347 (0.30–0.39)	0.366 (0.33–0.39)	0.324 (0.30–0.35)	0.333 (0.30–0.37)	0.335 (0.31–0.37)	0.339 (0.31–0.37)	0.332 (0.29–0.37)	0.335 (0.31–0.37)
PWA/CL	0.357 (0.33–0.45)	0.408 (0.38–0.44)	0.394 (0.37–0.42)	0.416 (0.40–0.45)	0.387 (0.35–0.44)	0.403 (0.36–0.44)	0.390 (0.33–0.42)	0.416 (0.39–0.45)
PWC/CL	0.429 (0.32–0.46)	0.473 (0.43–0.50)	0.431 (0.40–0.46)	0.454 (0.42–0.51)	0.422 (0.39–0.46)	0.457 (0.42–0.49)	0.429 (0.39–0.47)	0.457 (0.43–0.51)
PWD/CL	0.296 (0.26–0.32)	0.310 (0.26–0.37)	0.298 (0.28–0.31)	0.307 (0.28–0.33)	0.292 (0.27–0.35)	0.302 (0.28–0.33)	0.293 (0.25–0.40)	0.302 (0.27–0.38)
BL/CL	0.324 (0.29–0.39)	0.351 (0.31–0.38)	0.309 (0.29–0.35)	0.346 (0.31–0.37)	0.333 (0.30–0.36)	0.357 (0.32–0.41)	0.324 (0.29–0.35)	0.340 (0.32–0.39)
GW/CL	0.223 (0.20–0.23)	0.219 (0.18–0.23)	0.219 (0.20–0.23)	0.213 (0.19–0.24)	0.212 (0.15–0.24)	0.211 (0.18–0.24)	0.211 (0.18–0.24)	0.216 (0.18–0.24)
GL/CL	0.128 (0.11–0.15)	0.136 (0.11–0.15)	0.120 (0.098–0.14)	0.127 (0.099–0.15)	0.112 (0.089–0.14)	0.113 (0.096–0.14)	0.116 (0.082–0.15)	0.123 (0.098–0.16)
IH/CL	0.110 (0.088–0.14)	0.116 (0.091–0.16)	0.114 (0.096–0.14)	0.110 (0.070–0.14)	0.127 (0.086–0.15)	0.118 (0.096–0.17)	0.130 (0.069–0.17)	0.131 (0.054–0.16)
IP/CL	0.130 (0.10–0.15)	0.138 (0.12–0.16)	0.147 (0.13–0.16)	0.162 (0.15–0.19)	0.151 (0.13–0.18)	0.167 (0.11–0.19)	0.152 (0.11–0.23)	0.159 (0.13–0.24)
IAB/CL	0.181 (0.16–0.21)	0.190 (0.16–0.21)	0.179 (0.16–0.22)	0.196 (0.17–0.22)	0.176 (0.14–0.20)	0.185 (0.16–0.21)	0.178 (0.14–0.22)	0.188 (0.16–0.24)
IF/CL	0.178 (0.15–0.20)	0.180 (0.16–0.21)	0.158 (0.14–0.18)	0.162 (0.14–0.19)	0.177 (0.14–0.20)	0.172 (0.16–0.18)	0.173 (0.13–0.21)	0.175 (0.11–0.20)
IAN/CL	0.100 (0.091–0.12)	0.108 (0.089–0.15)	0.106 (0.091–0.12)	0.112 (0.091–0.14)	0.099 (0.088–0.12)	0.104 (0.080–0.13)	0.095 (0.069–0.14)	0.094 (0.072–0.16)

Table 3. Allometric comparisons of samples of *Mauremys mutica* from the four major regions; Yaeyama (Y), Honshu (H), Taiwan (T), and the continent (C). CL was compared by Kruskal-Wallis and Dunn's multiple comparison test, and the other variables were compared by ANCOVA and Tukey-like test using CL as the covariate. "–": $p > 0.05$; "+": $p < 0.05$; "++": $p < 0.01$; "+++": $p < 0.001$ in Kruskal-Wallis and ANCOVA. Samples sharing same superscript letters showed no significant differences in Dunn's multiple comparison test and Tukey-like test ($p > 0.05$). See text for abbreviations.

Variable	Male			Female		
	slope	position	desending order	slope	position	desending 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}
CH	–	+++	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}

Table 4. Standardized coefficients for the first three canonical axes of variation of morphometric characters in adult *Mauremys mutica*. See text for abbreviations.

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
CH	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

whereas ranges of its scores largely overlapped among the latter three samples. The high negative coefficient values of PL, GW and CW in order and positive values of IP, IH, PWA and CH in order were the main discriminating features in males. In females, on the other hand, the high negative coefficient values of CW, HL and PWC in order and positive values of CH, PWD, PWA, IP and CL in order were the main discriminating features.

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. The high negative coefficient values of PL, CW and PWD in order and positive values of CH, HL, GW and IAN in order were the main discriminating features. In females, CAN2 variable was slightly greater in the Yaeyama and Honshu samples than in the other two samples, and the high negative coefficient values of PL, CW and PWD in order and positive values of IAB, CL, IAN, HL, CH and PWA in order were the main discriminating features (Table 4, Fig. 3). No distinct differences were recognized among the samples in CAN3 variable among either the male or female samples.

Medially rooted distance phenograms for the male and female samples (Fig. 4) were identical with each other in branching topology, indicating that the Yaeyama sample is morphologically the most divergent (D^2 between this and other samples ranging 11.43–15.16 in males, 16.65–20.22 in females), whereas the samples from Honshu, Taiwan and the continent closely resemble each other (D^2 between pairs of the three samples ranging 7.16–7.52 in males, 7.46–9.01 in females).

Phenograms for samples including *M. annamensis* indicated that this species is by far the most divergent of the five samples (D^2 between *M. annamensis* and *M. mutica* samples ranging 41.64–57.35 in males, 41.18–54.25 in fe-

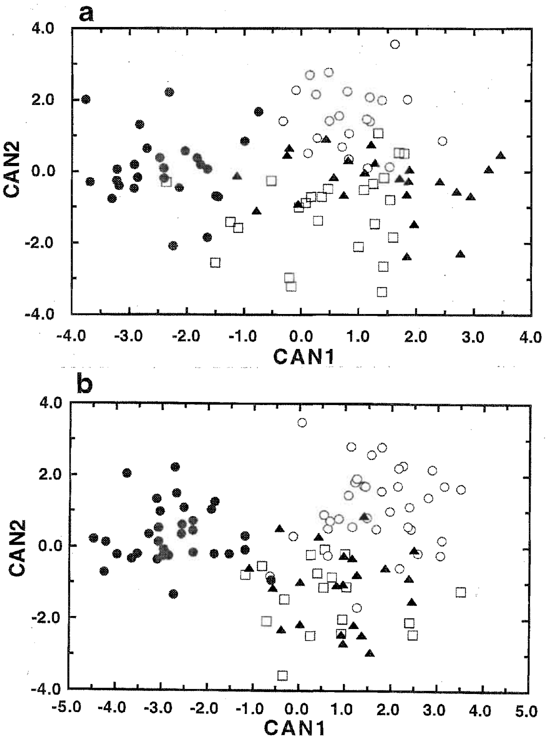

Fig. 3. Two-dimensional plots of the first two canonical variables of morphometric characters for four major regional samples of adult male (a) and female (b) *Mauremys mutica*. Closed circles, open circles, closed triangles, open squares represent scores for specimens from Yaeyama, Honshu, Taiwan and the Asian continent, respectively.

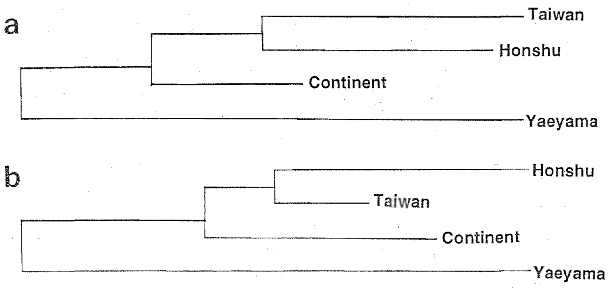

Fig. 4. Medially rooted phenograms for the four major regional samples of *Mauremys mutica* constructed by neighbor-joining method. a: adult males, b: adult females.

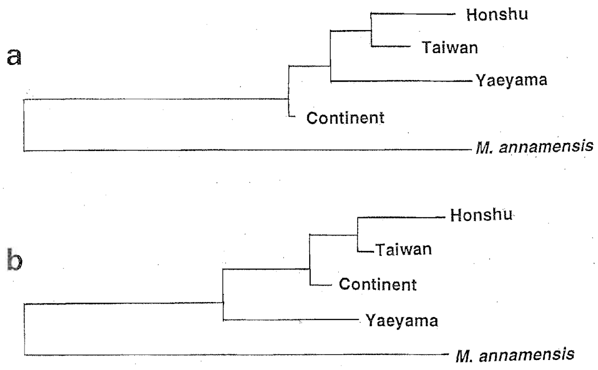

Fig. 5. Phenograms for the four major regional samples of *Mauremys mutica* rooted by the outgroup, *M. annamensis*. a: adult males, b: adult females.

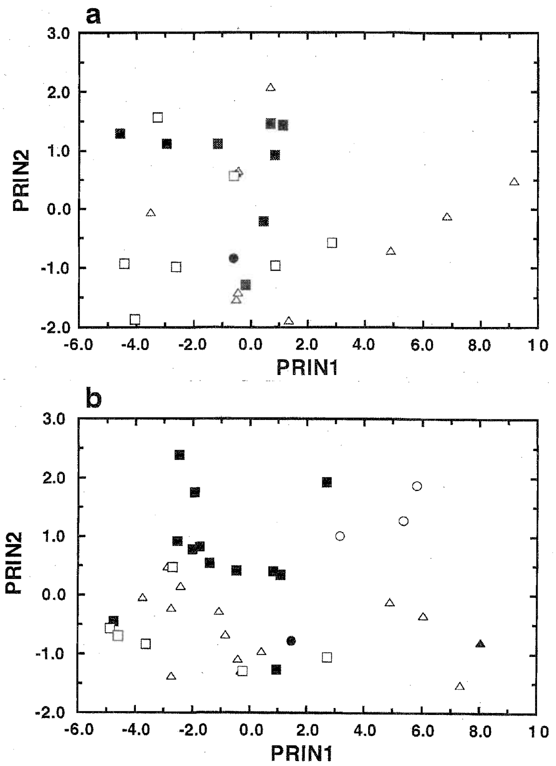

Fig. 6. Two-dimensional plots of the first two principal components of morphometric characters for six insular samples of *Mauremys mutica* from the Ryukyu Archipelago. a: adult males, b: adult females. Closed circle: Akusejima; open circle: Akajima; closed triangle: Sesokojima (a) or Okinawajima (b); open triangle: Ishigakijima; closed square: Iriomotejima; open square: Yonagunijima.

males; between pairs of the four *M. mutica* samples ranging 7.15–15.05 in males, 6.17–18.82 in females), confirming Iverson and McCord's (1994) tentative conclusion regarding the validity of this species that had previously been suspected to be synonymous with *M. mutica* (McDowell, 1964: Fig. 5). Phenograms for male and female *M. mutica* rooted by clusters of *M. annamensis* of corresponding sexes differed from each other in branching topology. The phenogram for female samples was topologically identical with the medially rooted phenograms mentioned above. However, the phenogram for males differed from the others in that the continental sample was most divergent from the others.

The DFAs correctly classified 85.6% of males and 89.9% of females from the four regions (Table 5). DFA assigned the one female from Akusekijima, the one male from

Table 5. Classification accuracy in the discriminant function for adult *Mauremys mutica*. Rows are actual samples, and columns are predicted samples. Figures equal the numbers of specimens assigned to each sample. See text for abbreviations.

Actural Sample	Predicted Sample				
	Yaeyama(%)	Honshu(%)	Taiwan(%)	Continent(%)	Total(%)
Male					
Yaeyama	24(92.3)	2 (7.7)	0 (0.0)	0 (0.0)	26(100.0)
Honshu	0 (0.0)	20(90.9)	2 (9.1)	0 (0.0)	22(100.0)
Taiwan	1 (4.2)	1 (4.2)	21(87.5)	1 (4.2)	24(100.0)
Continent	2 (8.0)	2 (8.0)	3(12.0)	18(72.0)	25(100.0)
Female					
Yaeyama	32(97.0)	0 (0.0)	1 (3.0)	0 (0.0)	33(100.0)
Honshu	0 (0.0)	31(86.1)	5(13.9)	0 (0.0)	36(100.0)
Taiwan	0 (0.0)	2 (9.1)	19(86.4)	1 (4.6)	22(100.0)
Continent	0 (0.0)	0 (0.0)	2(11.1)	16(88.9)	18(100.0)

Table 6. Factor loadings on the first three principal components of morphometric variation in adult samples of *Mauremys mutica* from the Ryukyus. See text for abbreviations.

	Male			Female		
Variable	PRIN1	PRIN2	PRIN3	PRIN1	PRIN2	PRIN3
CL	0.297	–0.080	0.031	0.278	–0.089	0.023
CW	0.297	–0.005	0.091	0.272	–0.059	0.050
CH	0.267	0.240	0.060	0.267	0.129	–0.068
PL	0.295	0.008	0.060	0.283	–0.044	0.011
HL	0.279	0.120	0.000	0.264	0.054	0.022
PWA	0.239	–0.218	–0.030	0.273	–0.133	–0.005
PWC	0.201	–0.086	0.478	0.278	–0.013	–0.006
PWD	0.275	0.150	–0.121	0.251	0.244	–0.087
BL	0.252	0.079	–0.302	0.274	–0.016	–0.053
GW	0.271	0.023	0.137	0.255	–0.017	–0.130
GL	0.236	–0.164	–0.329	0.229	0.015	0.311
IH	0.143	0.656	0.245	0.212	0.218	–0.660
IP	0.203	–0.557	0.015	0.211	–0.262	0.544
IAB	0.235	–0.138	–0.047	0.245	–0.153	–0.012
IF	0.249	–0.096	0.339	0.222	–0.414	–0.138
IAN	0.207	0.202	–0.586	0.144	0.760	0.341
Eigenvalue	10.683	1.391	0.981	12.288	1.088	0.781
Difference	9.291	0.410	0.000	11.199	0.307	0.000
Proportion	0.668	0.087	0.061	0.768	0.068	0.049
Cumulative proportion	0.668	0.755	0.816	0.768	0.836	0.885

Sesokojima, the one female from Okinawajima and the three females from Akajima to the Yaeyama sample, but the one Akusekijima male to the continental sample.

Eigenvectors for the first three principal components (PRINs 1–3) calculated from data for the 16 measurements are presented in Table 6, together with eigenvalues, differences, and proportions for these axes. In both sexes, ranges of PRINs 1–3 variables largely overlapped among the samples (Fig. 6), indicating the absence of distinct differentation among the Ryukyu populations.

Geographic variation in coloration

In the Yaeyama sample, color of carapace was light gray, yellowish tan, or light brown, and the condition of the plastral blotches ranged from grade A to D, with the mode in grade B (Table 7). On the other hand, the non-Ryukyu samples usually had brown, dark brown, or sometimes almost black carapaces, and their plastral blotch condition had a mode in grade C with some extremes in grade E. Only three specimens from Honshu and four from the continent exhibited the grade A condition. The dorsal and lateral ground color of the head in the Yaeyama sample, similar to color of carapace, was also paler than that in the non-Ryukyu samples. Moreover, turtles from Honshu, Taiwan, and the continent had a prominent light yellow or ivory stripe running from the posterior border of the orbit over the tympanum to the anterior part of the neck and occasionally extending anteriorly to the tip of the snout. The stripe was indistinct or completely lacking in the Yaeyama sample (Fig. 7).

Table 7. Variation in plastral dark blotches of *Mauremys mutica* from Yaeyama, Honshu, Taiwan and the continent

Grade	Yaeyama(%)	Honshu(%)	Taiwan(%)	Continent(%)
A	7(10.6)	3 (5.2)	0 (0.0)	4(12.9)
B	40(60.6)	14(24.1)	4(12.1)	3 (9.7)
C	18(27.3)	25(43.1)	12(36.4)	14(45.2)
D	1 (1.5)	12(20.7)	9(27.2)	7(22.6)
E	0 (0.0)	4 (6.9)	8(24.2)	3 (9.7)

CLASSIFICATION

Above results indicate that the Yaeyama populations of *M. mutica* are distinct from conspecific populations of the continent, Taiwan, and Honshu in coloration. Variation of each morphometric character among the four samples revealed by Kruskal-Wallis test or ANCOVA did not necessarily follow this pattern (Table 3). However, morphometric variation revealed by multivariate analyses, methods reasonably considered to be more reliable for elucidation of actual variation than univariate approaches (Willig *et al.*, 1986; Wüster *et al.*, 1992), exhibited a geographic pattern concordant with that of color variation. Furthermore, sexual dimorphic pattern in body size also differs between the Yaeyama and other populations (significant "larger male" SSD present in the former, absent in the latter). On the other hand, variation among samples from the latter three regions is smaller, and those from Taiwan and Honshu exhibited an especially close resemblance with each other.

On the taxonomic treatments of monophyletic but more or less differentiated allopatric populations, very little con-

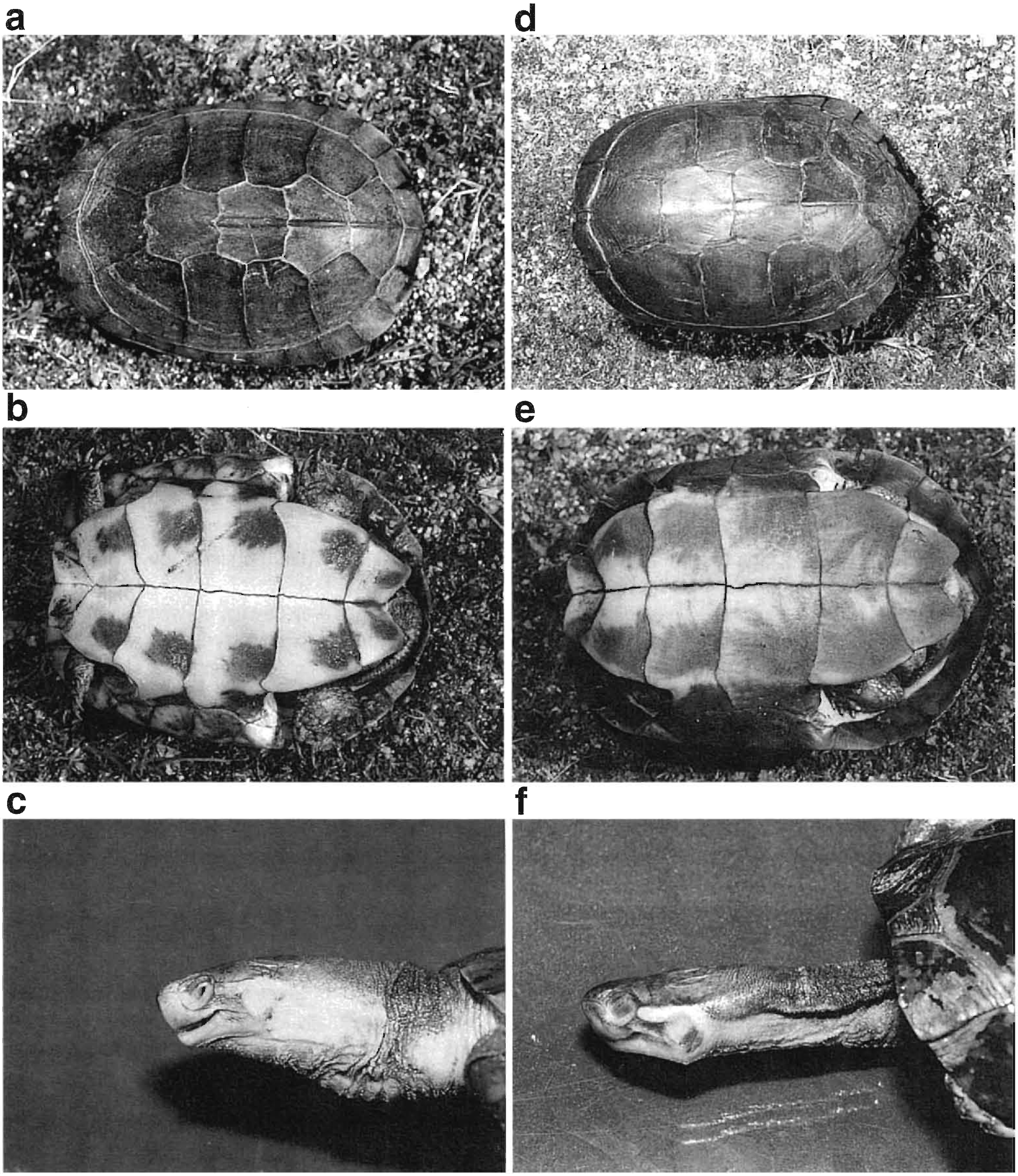

Fig. 7. Holotype of *Mauremys mutica kami* (a, b, c) and a female specimen of *M. m. mutica* from Kyoto (d, e, f).

sensus seems to have yet been attained in herpetology (e.g., Frost and Hillis, 1990; Grismer *et al.*, 1994). We believe that the above-mentioned differences obviously warrant recognition of the Yaeyama populations as a separate taxon. However, the differences seem to be much less distinct when compared with those among the other currently recognized species of the genus *Mauremys* (Ernst and Barbour, 1989; Iverson and McCord, 1994; above results). Furthermore, there is no single character other than those of coloration that completely distinguishes the Yaeyama form from the others because of the large variation within each population. Thus, we propose that it is appropriate to separate these forms at the subspecific level. Because *M. mutica* was first described from Chusan Island of Zhejiang Province, China (Cantor, 1842; Iverson and McCord, 1989; Zhao and Adler, 1993: Fig. 1), we describe the Yaeyama populations as a new subspecies.

Mauremys mutica kami subsp. nov. Fig. 7

Clemmys mutica: Nakamura, 1934: 34 (part); 1934: 425

(part); Nakamura and Uéno, 1963: 81 (part).
Mauremys mutica: McDowell, 1964: 269 (part); Sengoku, 1979: 6 (part); Toyama, 1985: 60 (part); Iverson and McCord, 1989: 27 (part); Ota, 1991: 94 (part); Toyama and Ota, 1991: 60 (part); Iverson, 1992: 144 (part); Zhao and Adler, 1993: 169 (part).
Mauremys nigricans: Ernst and Barbour, 1989: 168 (part).

Holotype. KUZ 19541, an adult female (in ethanol) collected at Okawa, Ishigakijima Is., the Yaeyama Group, Ryukyu Archipelago, Japan, captured by Y. Yasukawa on 31 July 1992.

Paratypes. Eleven males and eighteen females: Okawa, Ishigakijima: BMNH 1994.527, OMNH R4018 on 31 July 1992 by Y. Yasukawa. Yonebara, Ishigakijima: KUZ 19535, 19536, 19542 on 18 August 1991 by H. Ota. Ishigakijima: NSMT 02098, 02099, 02102, 02103 on 3 May 1933. Urauchi, Iriomotejima: CAS 200286, 200287, BMNH 1994.528, KUZ 19508, 19524–19525, 19527–19528, 19537–19539, OMNH R4019, USNM 498367–498368 on 2–4 August 1992 by Y. Yasukawa. Sonai, Iriomotejima: NSMT 02100 in 1963 by K. Tsuchiya. Ohara, Iriomotejima: NSMT 02108 in 1967 by K. Tsuchiya. Kubura, Yonagunijima: KUZ 19533, 19534, 19540 on 15 August 1991 by H. Ota.

Diagnosis. A moderate-sized turtle of the family Bataguridae, CL in adults 129.9–188.9 ($\bar{x} \pm 1$ SD = 148.3 ± 14.7) mm for 26 males, 120.0–176.4 (138.3 ± 13.8) mm for 33 females. This subspecies is discriminated from the nominotypical subspecies in exhibiting lighter carapace and head coloration (light gray, yellowish tan, or light brown: brown, dark brown or almost black in the latter), and in lacking prominent light stripe between posterior border of orbit and anterior portion of neck (present in the latter). In *M. m. kami,* the carapace is usually relatively depressed (CH/CW ranging 0.465–545 in males, 0.385–0.549 in females) and dark blotches on plastral scutes, when present, usually have broad light interspaces, whereas carapace is relatively thick (CH/CW value ranging 0.485–0.611 in males, 0.464–0.623 in females) and such interspaces are usually narrow or almost lacking in *M. m. mutica.*

From the other congeneric species, this subspecies is discriminated by the following combination of characteristics; posterior margin of carapace only scarcely serrated; lateral keel indistinct or absent in adult; male plastron usually deeply concave.

Description of holotype. CL 131.1 mm; CW 98.6 mm; CH 49.2 mm; PL 118.6 mm; HL 45.7 mm; PWA 56.3 mm; PWC 61.8 mm; PWD 39.9 mm; BL 43.3 mm; GW 27.9 mm; GL 18.4 mm; IH 12.6 mm; IP 21.5 mm; IAB 22.4 mm; IF 23.3 mm; IAN 12.9 mm.

Carapace oval, relatively domed, widest at marginals 7; a longitudinal medial keel on carapace, weak on vertebrals 1–2, but well developed on vertebrals 3–4; lateral keels lacking; carapacial margin not serrated anteriorly, scarcely serrated posteriorly; cervical relatively large, nearly trapezoidal, widest posteriorly; dorsal and ventral views of cervical resembling each other; vertebrals 1, 2, 4, 5 wider than long, vertebral 3 longer than wide, vertebral 5 widest; vertebral 1 widest anteriorly, vertebrals 2–4 widest medially, vertebral 5 widest posteriorly; pleurals wide, pleurals 1–3 much wider than neighboring vertebrals, pleural 4 as wide as vertebral 4; surface of carapacial scute almost smooth, with faint latest growth annuli.

Plastron large, flat, elongate, and laterally weakly angulated; hinge lacking; posterior margin of plastron with shallow but wide notch; anterior margin slightly notched; plastral formula: IAB > IP > IF > GL > IH > IAN; bridge short, dorsal border slightly longer than ventral border; entoplastron intersected by gular-humeral and humero-pectoral seams; axillary small; inguinal slightly enlarged, but subdivided into several small elements .

Head moderate in size, dorsal surface smooth, lacking small scales; upper jaw shallowly notched medially, without medial hook; triturating surfaces of upper and lower jaws narrow, without ridge and cusp; internal choanae marked by weak lateral ridges, lacking flaps and papillae; tongue relatively small, thin, heart-shaped, covered with many small projections.

Four limbs well developed with fully-webbed digits; anterior surfaces of forelimbs covered with distinctly enlarged and widened imbricate scales; tips of the scales rounded, oriented distally; similar but slightly smaller scales covering heels of all limbs; very small conical scales sparsely scattered around cloaca; scales on neck and around limb bases minute, making file-like surfaces; tail relatively short and thin.

Color in life. Carapace yellowish or grayish tan or light brown, each scute without distinct markings; posterior part of medial keel darker than adjacent portions; ground color of plastron and bridge varying from pale to grayish yellow, with one small brown blotch on posteromedial part of each plastral scute; seams of both carapacial and plastral scutes usually dark brown or almost black; sutures of bony plates recognizable externally as slightly lighter lines on scutes; bridge and ventral parts of marginals with shadowy brownish markings; ground color of head and dorsal surface of neck olive brown or grayish tan; broad pale yellow or ivory stripe running from posterior border of orbit over tympanum to anterior neck; throat and ventral surface of neck pale to light yellow, lighter than dorsal surface of head and neck; limbs and tail dark olive dorsally and laterally, pale or grayish yellow ventrally; a pair of shadowy yellowish longitudinal stripes on dorsal surface of tail.

Color in ethanol. Coloration of shell not much changed; soft parts faded to slightly paler; lateral stripe on head becoming whitish but still recognizable.

Variation. Variation in measurements and their ratios to CL are presented in Tables 1 and 2, respectively. Some specimens have extra vertebrals, pleurals or marginals. The inguinal is usually an entire element, but sometimes subdivided into several smaller scutes (see description of holotype).

Table 8. Allometric comparisons between sexes of *Mauremys mutica kami.* "–": $p > 0.05$; "+": $p < 0.05$; "++": $p < 0.01$; "+++": $p < 0.001$. All variables were compared by ANCOVA using CL as the covariate. See text for abbreviations.

Variable	slope	position	significant difference
CW	–	+	F>M
CH	–	–	
PL	–	+	F>M
HL	–	+	F>M
PWA	+		F>M
PWC	–	+++	F>M
PWD	–	–	
BL	–	+++	F>M
GW	+		M>F
GL	–	–	
IP	–	++	F>M
IAB	–	++	F>M
IF	–	–	
IAN	–	–	

CL in males is significantly greater than in females (Table 1, Fig. 2). CW, PL, HL, PWC, BL, IP and IAB in relation to CL are greater in females than in males (Table 8). Males usually have a deeply concave plastron, while plastron of females flat. The tail of adult males is longer and thicker at its base than that of adult females, but such sexual difference in the tail morphology is not much distinct, especially in subadults. The vent is located slightly beyond the carapacial rim when the tail is extended backwards in males, whereas located within the rim in females. No morphometric differences are evident among insular populations.

Distribution. Mauremys m. kami is known from Akusekijima Island of the Tokara Group, Akajima, Sesokojima and Okinawajima Islands of the Okinawa Group, and Ishigakijima (type locality), Iriomotejima, and Yonagunijima Islands of the Yaeyama Group (Iverson, 1992; Nakamura and Uéno, 1963; Yasukawa and Kimura, 1995; Yasukawa *et al.*, 1996a). However, the natural distribution is probably confined to the latter three Islands of the southern Ryukyus (see DISCUSSION below).

Ecological notes. Mauremys m. kami is found chiefly in and around shallow and still or slow-running waters with soft bottoms, such as irrigated rice paddies, marshes, swamps, ponds, and shallow streams. Activity of this turtle seems to be much higher during the night or on rainy days, when animals are occasionally observed on land, away from the water body. During the daytime, it remains under water or in the mud in irrigated rice paddies, marshes, etc. (Yasukawa *et al.*, 1996a).

The turtle is omnivorous, feeding on waterweeds, algae, leaves of weeds, fallen fruits, fishes, tadpoles, insects, earthworms, and small crustaceans (Yasukawa *et al.*, 1996a).

Mori (1986) observed in captivity the mating behavior and breeding of individuals from Yonagunijima Island. He reported that in December the male mounted on the female from behind, with copulation in the water while clasping her carapace with his claws and biting onto her nape. Egg-laying was observed twice during August to early September. Each clutch consisted of four eggs, and the major × minor diameters and masses of the eight eggs varied from 36–38 × 22–23 mm and 9.6–10.4 g (35.5 × 21.3 mm and 10.0 g in average), respectively. Only one egg hatched in following September to produce a hatchling, 32 × 25 × 15 mm in length × width × height of the shell and 5.6 g in mass. No information is available regarding the breeding habits in nature.

Etymology. The subspecific epithet *kami* refers to the vernacular name of turtles in the Yaeyama Group, southern Ryukyus.

DISCUSSION

Sexual dimorphism

Based on size data for Taiwanese specimens tabulated by Mao (1971), Gibbons and Lovich (1990) calculated SDI of *M. mutica* as –1.09, indicating that males have a slightly greater body size than females in this species. However, they also noted that the maturity conditions of Mao's (1971) specimens are questionable. In Mao's (1971) table, CLs in male and female specimens ranged from 89–195 and 90–170 mm and their means were 142 and 130 mm, respectively. He did not mention any morphological or behavioral criteria to define maturity in his specimens, and judging from our results, it is almost certain that Mao's (1971) CL values included those of subadult individuals. Our results have suggested that, in the Taiwanese population, mean CL is actually only slightly greater in adult males than in adult females, and that the difference has no statistical significance. In the Yaeyama sample, however, CL in adult males was significantly greater than that in adult females. This tendency seems to be reflected also by their maximum and minimum CL values as well (Table 1), and is consistent with that revealed by separate intersexual comparisons within each of the Ishigakijima (SDI = –1.10), Iriomotejima (SDI = –1.07), or Yonagunijima samples (SDI = –1.07). It is also interesting to note that, in the samples from Honshu and the continent, either mean, maximum, or minimum CL values of adult males and females are very close to each other (Table 1).

In turtles, various patterns of SSD have been reported. Recent reviews elucidated the presence of general trends toward larger females in aquatic or semiaquatic emydid (including batagurid) turtles and larger males in some others such as testudinids [see Berry and Shine (1980) and Gibbons and Lovich (1990), for review]. Berry and Shine (1980) argued that SSD patterns correlate with habitat type and male mating strategy, and that sexual selection is the major cause of body size differentiations between males and females. Gibbons and Lovich (1990), after reviewing the possible phenetic and genetic factors leading to the emergence of SSD in a given set of turtle size data, stressed the substantial role of natural selection on SSD by determining the size and age at maturity in each sex. On the other hand, they raised questions about a few factors postulated for male sexual selection by Berry and Shine (1980).

Our data have indicated that SSD in *M. mutica* is somewhat exceptional of that in the batagurid turtles, because the adult male of this species exhibited a CL as great as or even greater than that in the adult female within each population. Collecting bias might be present (see MATERIALS AND METHODS section), but its effect on the SDIs obtained is probably not so great as to produce substantial errors (Gibbons and Lovich, 1990). There might be some other artificial and/or non-genetic environmental factors that would produce some deviations in the estimated male and female sizes from those intrinsic of natural populations [see Gibbons and Lovich (1990), for review]. However, considering that sympatric populations of other omnivorous freshwater batagurids of similar sizes (thus reasonably expected to have similar habitat preferences and ecological requirements) exhibit a trend toward larger females [*M. japonica:* SDI = +1.47 in Honshu (Yasukawa, unpublished data); *Chinemys reevesii:* SDI = +1.23 in Honshu (Yasukawa, unpublished data), +1.19 in Taiwan (Mao, 1971), + 1.37 in the continent (Pope, 1935); *Ocadia sinensis:* SDI = +1.24 in Taiwan (Mao, 1971)], it is more likely that the characteristic SSD recognized in our samples of *M. mutica* reflects a primarily genetically determined species trait as in SSD of *Trachemys scripta* intensively studied by Gibbons and Lovich (1990).

Berry and Shine (1980) predicted that sexual selection through male-male combat or forcible insemination plays the major role in the increase of the relative male size in a given species. On the other hand, Gibbons and Lovich (1990) stressed the possible importance of predation pressure as a major source of natural selection against the decrease of relative body size in males. The latter authors also assumed that sexual selection through combat and other competitive situations in males supplementarily promotes the trend toward larger males. However, these explanations have been applied chiefly to the explanation of SSD in terrestrial species: no substantial discussions have been attempted on such pattern of SSD in freshwater species.

In *M. annamensis,* the closest relative of *M. mutica* (see Iverson and McCord, 1994), adult females have a significantly greater body size than adult males as in most other batagurids (SDI = +1.09). It is, therefore, highly probable that the greater relative male body size has emerged during or after the divergence of the *M. mutica* clade from the others. Considering that *M. annamensis* has distinctly greater CL, CW/CL and BL/CL values (Yasukawa, unpublished data) and that it is the only *Mauremys* species sympatrically occurring with crocodiles, a possible major predator of freshwater turtles (Iverson and McCord, 1994), it is likely that the predation pressure has been placed more severely on that species than on *M. mutica*. Thus Gibbons and Lovich's (1990) predictive hypothesis does not seem to apply to SDI in *M. mutica*. Field and captive observations of males also suggest that there is no male-male combat in this species (Ota, 1996b, unpublished data), rejecting its role in the emergence of large relative size of the male in this species.

Mori (1986) reported on the apparently forcible copulation observed in captive *M. mutica* from Yonagunijima, involving the male clasping and biting on the female and female's struggling, which occasionally resulted in the falling down of the mounting male before intromission (also see Yasukawa *et al.*, 1996a). Similar behavior was observed in individuals from Taiwan and Honshu as well (Yasukawa, unpublished data). Copulatory behavior of *M. annamensis* remains unknown, but in *M. japonica* (SDI=+1.47: see above), the probable sister group of the *M. mutica-annamensis* clade (Iverson and McCord, 1994), copulatory behavior is known to be strikingly different. In this species, the male attempts to make female receptive to his advances with ritualized courtship behavior in advance of mounting (Yasukawa *et al.*, 1996b). Thus, we suspect that the large relative male size in *M. mutica* has emerged through intersexual behavioral interaction during the copulation, although Gibbons and Lovich (1990) doubted the reality of forcible insemination assumed by Berry and Shine (1980). Whether the apparently forcible copulation by male *M. mutica* is really "forcible" or whether there is an aspect of female mate choice remains an open question for future studies. The ultimate cause of such behavioral difference also remains unknown. In order to test our hypothesis, an examination of the correlation between pattern of SSD and copulatory behavior within *M. mutica*, as well as in other batagurid turtles, seems essential.

Historical relationships of populations and biogeography

In both sexes, Mahalanobis distances calculated for morphometric data indicate that populations of *M. mutica* from the continent, Taiwan and Honshu closely resemble each other, whereas those of the Yaeyama Group, described here as *M. m. kami*, are distinctly divergent. Medially rooted NJ phenograms for both sexes (Fig. 4), as well as the cluster phenogram rooted by *M. annamensis* for females (Fig. 5b), suggest that the primary divergence took place between the Yaeyama populations and the others, followed by the subsequent divergence between the continental populations and those of Taiwan and Honshu. The outgroup-rooted phenogram for male, however, seems to suggest that the first divergence was between the continental populations and the others (Fig. 5a). Even in this phenogram, however, the Yaeyama populations are shown to be the most divergent (D^2 varying 11.59–15.05 between the Yaeyama and other conspecific samples, 7.15–7.75 between pairs of the latter non-Ryukyu samples). Thus, we belive that the actual historical relationships among the populations of the four major regions are reflected by the former three phenograms, and that the location of the root in the latter phenogram is deviated presumably as a result of rapid allometric changes in males between *M. mutica* and *M. annamensis* related to their divergence in the sexual dimorphic pattern (see above).

The highly discontinuous distribution of *M. mutica* in the insular region of East Asia poses a particular biogeographic problem. Nakamura (1934a, b), while recording this species from Kyoto Prefecture for the first time, surmised that it had reached this region by the "step-by-step" mode of dispersal from Taiwan through the Ryukyu Archipelago. However, he did not attempt to explain the presence of the wide distributional gap between the Yaeyama Group and Akusekijima Island, or Akusekijima Island and Kyoto. Most subsequent authors tentatively assumed that populations of Akusekijima and central Honshu are nonnative, originating from human introductions from other regions (e.g., Hikida *et al.*, 1992; Nakamura and Uéno, 1963; Sengoku, 1979). Our results do not support the probability of the "step-by-step" dispersal because they suggest a much closer affinity of the Honshu populations with populations of Taiwan than of the Yaeyama Group. Thus, we suspect that turtles currently prevailing in Kyoto and adjacent regions have originated from artificial introduction from Taiwan. Takashima (1940) documented that *M. mutica* was imported from Taiwan to large cities of Kansai District (i.e., Kyoto and its vicinity) for pets at a time when Japan governed Taiwan. This, as well as the absence of fossil records of *M. mutica* and its relatives in the central and northern Ryukyus and the main islands of Japan (e.g., Hasegawa, 1980), seems to offer circumstantial support for this hypothesis.

Based on the color patterns of available specimens and the DFA for one adult female, we tentatively assign the Akusekijima population to *M. m. kami* with the assumption that it has originated from the artificially introduced animals from the Yaeyama Group. Even so, however, DFA assigned the male specimens to the continental sample. Considering that the Akusekijima population probably has as long a history as that of the Honshu populations (Nagai, 1928; Nakamura, 1934a,b), it might be the case that it has had opportunities to receive individuals from more than one source artificially. On the other hand, results of DFAs suggest that the recently reported central Ryukyu populations (Ota, 1996a; Yasukawa *et al.*, 1996a) are of the Yaeyama origin.

It is generally assumed that the Ryukyu Archipelago experienced land-bridge connections to Taiwan and the continent a few times between the middle Miocene and the early Pleistocene, and that ancestors of most of its fauna entered this region on such occasions (Kizaki and Oshiro, 1980). Also, recent studies have revealed that during the continental glaciation in the late Pleistocene (i.e., 15,000 to 18,000 yrs ago) the sea level was lowered by 120 to 140 m, and that the current sea bottoms of at least as deep as or shallower than 120 m were exposed above the sea as additional land areas (Donn *et al.*, 1962; Hopkins, 1982; Ota *et al.*, 1993). Thus, it is obvious that Taiwan was connected to the continent by broad land bridges, whereas most Ryukyu islands (including those of the Yaeyama Group) remained isolated during that period. Moreover, Ishigakijima and Iriomotejima were almost certainly joined, while Yonagunijima remained isolated (Ota *et al.*, 1993: Fig. 1). This paleogeographical scenario seems to be largely consistent with the pattern of geographic variation in *M. mutica* revealed above, and it is highly likely that *M. m. kami* diverged from the nominotypical subspecies during the long isolation in the Yaeyama islands to which it had probably first migrated from Taiwan through land bridges. It seems to be more difficult to explain the occurrence of *M. m. kami* on Yonagunijima Island on the basis of current paleogeographical knowledge, but considering that several reptilian taxa are shared exclusively between this island and other southern Ryukyu islands (Ota, 1991; Toyama and Ota, 1991), it is likely that additional land connection once existed between Yonagunijima and other islands after their isolation from Taiwan and the continent.

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APPENDIX I

Specimens examined

Catalogue numbers of specimens deposited in herpetological collections of the Department of Zoology, Kyoto University, Columbus Zoo, Teikyo University of Technology, and personal collections of R. Hirayama A. Kamata, M. Matsui, W. P. McCord, T. Yabe and the senior author are preceded by KUZ, CZ, TUT, RH, AK, MM, WPM, TY, YY, respectively. The other acronyms are those suggested by Leviton *et al.* (1985).

Mauremys mutica kami: JAPAN-RYUKYU ARCHIPLAGO: YAEYAMA GROUP: ISHIGAKIJIMA ISLAND, BMNH 1994.527, CAS-SU 21010–21014, 26115–26119, KUZ, 19535, 19536, 19541 (holotype), 19542, NSMT 02098, 02099, 02102, 02103, OMNH R4018, TY 1–5 (live), YY 1 (live); IRIOMOTEJIMA ISLAND, CAS 200286, 200287, BMNH 1994.528, KUZ 19508, 19524–19525, 19527–19528 19537–19539, 19543, 19544, NSMT 02100, 02108, OMNH

R4019, USNM 498367–498368, YY 2–4 (live); YONAGUNIJIMA ISLAND, KUZ 19533, 19534, 19540, one unnumbered specimen of NSMT, RH 460, AK 92.7.1.1–3, AK 1 (live), YY 5–8 (live); ISHIGAKIJIMA, IRIOMOTEJIMA or YONAGUNIJIMA ISLAND (detailed localities unknown), KUZ 19532, one unnumbered specimen of OMNH, YY 9–10 (live); TOKARA GROUP: AKUSEKIJIMA ISLAND, BMNH 1933.5.19.1–2; OKINAWA GROUP: AKAJIMA ISLAND, KUZ 19545, YY11–12 (live); OKINAWAJIMA ISLAND, KUZ 19546; SESOKOJIMA ISLAND, YY 13 (live). *Mauremys mutica mutica:* JAPAN-HONSHU: KYOTO, KUZ 19503, NSMT 02096, 02097, 02118, 02120–02126, RH 289, 491, 492, 537, MM1, TY 6–8 (live), YY 14–16 (live); SHIGA, KUZ 19501, 19502, 19504, 19505, 19507, 19509–19519, YY 17–26 (live), ten live specimens released after being examined and marked; CHINA-TAIWAN, BMNH 1922.6.16.5, FMNH 127187, 127190, 127193, NSMT 02105–02107, RH 193, 194, 199, 200, 408–412, 414–425, YY 27–31; CHINA-MAINLAND, AMNH 31065; BMNH 1922.6.16.6–7, MVZ 23937, WPM 1–8 (live); CHINA-HAINAN ISLAND, AMNH 30154, 30157–30160, 30164–30166, 30168, 30169, BMNH 1929.7.3.5; WPM 9, 10 (live); VIETNAM, ZMH R00274, WPM 11–15 (live), YY 31–34 (live). *Mauremys annamensis:* VIETNAM, CAS-SU 9142, MNHN 1948–39, UF uncatalogued specimens, CZ 1 (live) WPM 16–22 (live); LOCALITY UNKNOWN, KUZ 19684, TUT 9, AK 2, 3 (live), YY 35, 36 (live).

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