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**GEOGRAPHIC VARIATION AND SYSTEMATICS IN
THE SOUTH-EAST ASIAN TURTLES OF THE GENUS
MALAYEMYS (TESTUDINES: BATAGURIDAE)**

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(with eight text-figures)

ABSTRACT.— Geographic variation was studied in the south-east Asian turtles of the genus *Malayemys* (Testudines: Bataguridae). Discriminant function analysis of head-stripe and shell characters reveals a clear pattern of geographic variation that is consistent with the topography of south-east Asia and the poor dispersal abilities of these turtles. Two phenotypically and morphologically distinct groups of *Malayemys* occur allopatrically in lowland areas of mainland south-east Asia, and my data concludes that each should be recognized as a distinct species. Turtles from the Mekong River Basin retain the name *Malayemys subtrijuga* (Schlegel and Müller, 1844), whereas those from the Chao Phraya and Mae Klong river basins, coastal areas of south-eastern Thailand, and the Malay Peninsula are assigned the name *Malayemys macrocephala* (Gray, 1859). *Malayemys macrocephala* has four or fewer nasal stripes (99%) and an infraorbital stripe that is relatively wide at the loreal seam (98% of $\text{InfSW}/\text{HW}=0.07\text{--}0.18$) and does not extend or extends only slightly superior to the loreal seam (96%). Conversely, *M. subtrijuga* has six or more nasal stripes (89%) and an infraorbital stripe that is relatively narrow at the loreal seam (92% of $\text{InfSW}/\text{HW}=0.02\text{--}0.06$), extends completely superior to the loreal seam (96%), and usually joins the supraorbital stripe (64%). Female *M. macrocephala* also have relatively longer AnL and relatively shorter Vert5L and PeCL than *M. subtrijuga*. Similarly, male *M. macrocephala* have relatively longer PPLL and AbdL, relatively shorter Pleu1L and PeCL, and greater RLatK values than *M. subtrijuga*. Both species are potentially threatened by overcollection and habitat destruction, and should be protected as separate taxa of concern. In addition, discriminant function analysis of shell and head-stripe characters suggests that *M. subtrijuga* on Java are derived by human intervention primarily from the Mekong River Basin.

KEY WORDS.— Testudines, systematics, Mekong, Chao Phraya, Mae Klong, *Malayemys subtrijuga*, *Malayemys macrocephala*.

INTRODUCTION

Taxonomy is the foundation of traditional conservation practices (Avice, 1989; Daugherty et al., 1990; Lovich and Gibbons, 1997). Such practices emphasize protection of endangered taxa at the single-species level. Modern conservation programs still adhere to this tradition, because species must be discovered and de-

scribed before they can be effectively protected (Avice, 1989; Iverson and McCord, 1997; Lovich and Gibbons, 1997). As such, many as yet undescribed species are in potential danger of extinction because of incomplete taxonomy, unrecognized congeneric variation, and/or the lack of formal species descriptions. An alternative to single-species conservation is biodiversity

conservation at the major landscape and entire ecosystem level. This type of strategy protects communities that encompass sensitive as well as non-endangered species, including undescribed species (Lovich and Gibbons, 1997). Until such a strategy can be implemented on a large scale, good taxonomic research remains an important form of protection for unrecognized species.

“One of the worst mistakes we can make in our efforts to protect biodiversity is to allow the extinction of species because of faulty taxonomy” (Lovich and Gibbons, 1997:427). Two excellent examples of this perspective are the tuataras (*Sphenodon* spp.) and the Alabama map turtles (*Graptemys pulchra* complex). In both cases, perceived monotypy forestalled management intervention on behalf of threatened populations of several unrecognized species. Fortunately for both groups, researchers described these unique forms before they became extinct (Daugherty et al., 1990; Lovich and McCoy, 1992; Lovich and Gibbons, 1997).

Malayemys subtrijuga (sensu lato) is another wide-ranging species that has been generally perceived as monotypic (Ernst and Barbour, 1989; Ernst et al., 2000). It is found in lowland freshwater areas of Thailand, Laos, Cambodia, southern Vietnam, the northern Malay Peninsula, and Java, Indonesia. A detailed study of morphological geographic variation has not previously been done for this species and is therefore required to determine whether unrecognized taxa exist among its populations. Such a study is particularly urgent due to the ongoing turtle crisis in south-east Asia; many south-east Asian turtle populations are in rapid decline because of serious pressure from commercial exploitation and habitat destruction (Behler, 1997; Thirakhupt and van Dijk, 1997; van Dijk et al., 2000). If overexploited populations of *M. subtrijuga* (sensu lato) represent undescribed taxa, it is important that they are discovered before they become extinct.

MATERIALS AND METHODS

I examined museum specimens from throughout much of the known range of *M. subtrijuga* (sensu lato). Specimens were grouped into regional geographic samples representing major drain-

age basins for those on mainland south-east Asia (Kottelat, 1989) and entire islands for those in the Greater Sundas. Sample localities were: Maly = Malay Peninsula including north-eastern and north-western Malaysia and peninsular Thailand; MKl = Mae Klong basin of Thailand; CPhr = Chao Phraya basin of Thailand; SECos = coastal areas of south-eastern Thailand and Cambodia; Mekg = Mekong basin of southern Vietnam, Cambodia, Laos, and north-eastern Thailand; Sumt = Sumatra, Indonesia; Java = Java, Indonesia. The geographic origin of each specimen was based on museum records, and the sample was divided by sex and life stage (juveniles, subadults, adults; see below).

The head-stripe data set consisted of two meristic and one mensural character, whereas the shell data set consisted of one meristic and 28 mensural characters. The number of nasal stripes (NasS) was counted for each specimen. Nasal stripes were defined as the narrow stripes extending downward from the nostrils toward the medial notch of the upper jaw plus those similar stripes running parallel in the nasal region. Partial nasal stripes were counted as entire stripes (Figs. 1 and 2) and partially fused stripes (see Nutaphand, 1979, p. 131) were counted separately. The condition of the infraorbital stripe with respect to the supraorbital stripe and loreal seam (InfLor) was also recorded. The infraorbital stripe was defined as the stripe beginning on each side of the snout just behind the nostrils, curving downward and posteriorly, passing below the orbit to the angle of the mouth. The supraorbital stripe was defined as the stripe extending posteriorly from the tip of the snout along the canthus rostralis and supraorbital rim to the lateral base of the neck. The loreal seam was defined as the seam extending between the nostril and eye on each side of the head, separating the large scale covering the snout and crown and the large scale extending around the upper jaw [i.e., the rhamphotheca] (Figs. 3 and 4). Each specimen was given a numerical score as follows: 1 = infraorbital stripe does not extend superior to loreal seam; 2 = infraorbital stripe extends only slightly superior to loreal seam; 3 = infraorbital stripe extends completely superior to loreal seam but does not join supraorbital stripe; 4 = infraor-

bital stripe extends completely superior to loreal seam and joins supraorbital stripe (Figs. 3 and 4). Finally, the width of the infraorbital stripe was measured at the loreal seam. This character was normalized by dividing it by head width (InfSW/HW) (Figs. 3 and 4).

Dial calipers (accurate to 0.1 mm) were used to take the following straight-line measurements on the shell of each specimen (see Ernst and Lovich, 1986): maximum carapace length (CL); carapace width at the level of the seam separating vertebral scutes 2 and 3 (CW); shell height at the level of the seam separating vertebral scutes 2 and 3 (SH); maximum plastron length (PL); maximum width (APLW and PPLW) and length (APLL and PPLL) of both plastral lobes; minimum bridge length (BrL); maximum width and length of vertebral scutes 1, 2, 3, and 5 (Vert1, 2, 3, 5W and L); maximum width and length of pleural scute 1 (Pleu1W and L); medial seam length of plastral scutes (GulL, HumL, PecL, AbdL, FemL, AnL); and maximum width of gular (GulW), humeral (HumW), femoral (FemW), and anal (AnW) scutes. One meristic character, RLatK, recorded the position (as a proportion) of the right lateral keel as it bisected pleural scute 2. Larger RLatK values corresponded to relatively greater distances from the median keel. The condition of bilateral characters was recorded from the right side of the carapace and the left side of the plastron unless damaged.

Museum acronyms followed Leviton et al. (1985) and Leviton and Gibbs (1988) with the following additions: CRI = Chelonian Research Institute, Oviedo, Florida, USA; KUZ = Kyoto University Zoological Collection, Kyoto, Japan; RH = personal collection of Ren Hirayama, Teikyo Heisei University, Ichihara, Chiba, Japan; ZRC = Raffles Museum of Biodiversity Research, Zoological Reference Collection, The National University of Singapore, Singapore.

Tail morphology was the primary characteristic used for sexual identification in this study. Sexual dimorphism of this character is pronounced in both subadults and adults, with males having much longer and thicker tails (Ernst and Barbour, 1989; Srinarumol, 1995; van Dijk and Thirakhupt, in press). When tail morphology

was not available (shell and skeletal material; some dried specimens), information from museum records formed the basis of sexual identification. Srinarumol (1995) distinguished adults from subadults based on the complete development of testes and ovaries, and subadults from juveniles based on tail morphology. Assignment of specimens to appropriate life stages (juvenile, subadult, adult) in the current study was based primarily on the size classes established by Srinarumol's (1995) dissection work.

Only three geographic samples in the current study had sufficient numbers to warrant intersample comparisons. All methods and analyses that follow pertain to samples from CPhr, Mekg, and Java. Geographic variation of head-stripe characters was examined using multivariate techniques. NasS, InfLor, and InfSW/HW (Figs. 1-4) comprised the entire data set. Preliminary analyses indicated that allometric variation and sexual dimorphism were not present in the head-stripe characters (Brophy, 2002), so all specimens within each geographic sample were combined regardless of sex or life stage. Using the three head-stripe characters, the probability of correctly classifying each turtle relative to its predetermined geographic origin (CPhr, Mekg, and Java) was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Head-stripe differentiation between geographic samples was graphically summarized by plotting canonical discriminant scores (PROC CANDISC; SAS, 1989). Specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data and classified using the head-stripe model described above (PROC DISCRIM; SAS, 1989). Individual medians for the two discrete head-stripe characters (NasS and InfLor) were compared using the Kruskal Wallis test followed by Dunn's post test with $\alpha = 0.05$. Means for InfSW/HW were compared using Analysis of Variance (ANOVA) followed by the Bonferroni multiple comparison test with $\alpha = 0.05$. Assumptions of normality and heterogeneity of variances were tested with Kolmogorov-Smirnov and Bartlett's tests, respectively.

Geographic variation of shell characters was also examined using multivariate techniques.

The twenty-eight mensural shell characters were divided by CL, and the resulting ratios comprised the majority of the data set. RLatK was not divided by CL because it was standardized upon measurement (expressed as a proportion). Preliminary analyses indicated that allometric variation and sexual dimorphism of the shell existed in each of the three geographic samples (Brophy, 2002). To minimize the effects of these factors, only adult and larger subadult turtles (males ≥ 80 mm CL; females ≥ 100 mm CL) were utilized, and males and females were analyzed separately.

Using all 29 shell variables for each sex separately, stepwise selection (PROC STEPDISC; SAS, 1989; significance level for entry and removal = 0.30) was used to obtain a set of potential models that would classify turtles relative to their predetermined geographic origin (CPhr, Mekg, and Java). Final selection of the best model was based on model size and classification accuracy. The best model gave the most accurate cross-validation results (PROC DISCRIM; SAS, 1989) and had no more variables than the number of individuals in the smallest sample. This protocol was designed to select conservative models that had a low number of variables and a high level of classification accuracy.

Using the best model as defined above, the following procedures were performed for each sex. The probability of correctly classifying each turtle relative to its predetermined geographic origin (CPhr, Mekg, and Java) was calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). Shell differentiation between geographic samples was graphically summarized by plotting canonical discriminant scores (PROC CANDISC; SAS, 1989). Specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data and classified using the best models described above (PROC DISCRIM; SAS, 1989). Individual means for shell character ratios were compared using ANOVA followed by the Bonferroni multiple comparison test with $\alpha = 0.05$. Assumptions of normality and heterogeneity of variances were tested with Kolmogorov-Smirnov and Bartlett's tests, respectively.

Since there is some question as to the natural occurrence of *M. subtrijuga* (sensu lato) populations on Java (Dammerman, 1929; Ernst et al., 2000; van Dijk and Thirakhupt, in press), one additional set of multivariate analyses was performed on the shell data. Using the same shell character-sets as the best male and female models above, the probability of correctly classifying each turtle relative to its predetermined geographic origin was again calculated using the cross-validation results of linear discriminant function analysis (PROC DISCRIM; SAS, 1989). This time, however, models were based on the CPhr and Mekg samples only. Specimens from the Java sample were subsequently entered as test data and classified using these new models.

RESULTS

Geographic variation of head-stripe characters was evident in *M. subtrijuga* (sensu lato). Using the three character head-stripe model, cross-validation results of linear discriminant function analysis correctly classified 97.73% of turtles from CPhr, 36.36% of turtles from Java, and 76.00% of turtles from Mekg (Table 1). The majority of misclassifications (83%) were Java individuals classified as Mekg and vice versa. The CPhr sample formed a clearly distinct group with considerable confusion between the Java and Mekg groups. This observation was reinforced by the bivariate plot (CV1 vs. CV2) of canonical discriminant scores (Fig. 5). CPhr formed a distinct cluster that had almost no overlap with Java or Mekg, whereas the Java and Mekg clusters strongly overlapped.

When specimens from geographic samples other than CPhr, Mekg, or Java were entered as test data in the head-stripe model, all specimens from Maly, MKI, and SECos were classified as CPhr. Specimens from Sumt were classified as both CPhr (2 specimens) and Mekg (2 specimens).

An examination of individual medians and means for the head-stripe characters also demonstrated the distinctiveness of CPhr (Table 2). For both NasS and InfLor, median values for CPhr were significantly different ($p < 0.001$) from the median values of both Java and Mekg, whereas median values were not significantly different

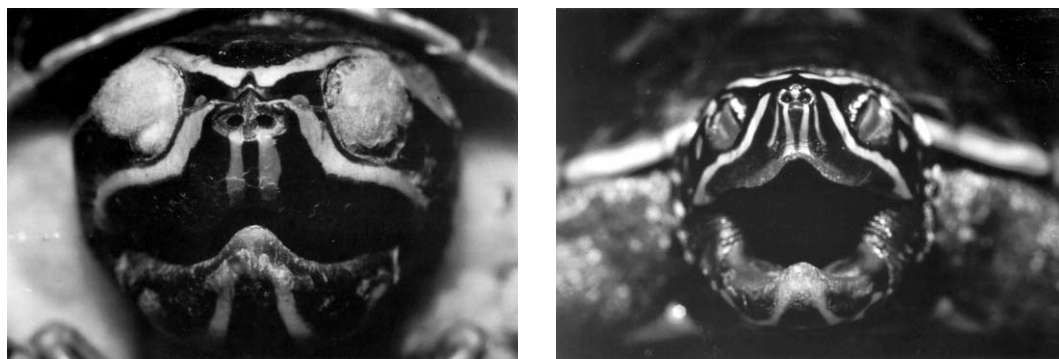


FIGURE 1: Photographs of *Malayemys macrocephala* (Gray, 1859) illustrating NasS values of 2 (left-USNM 71480) and 4 (right-SMF 52865).

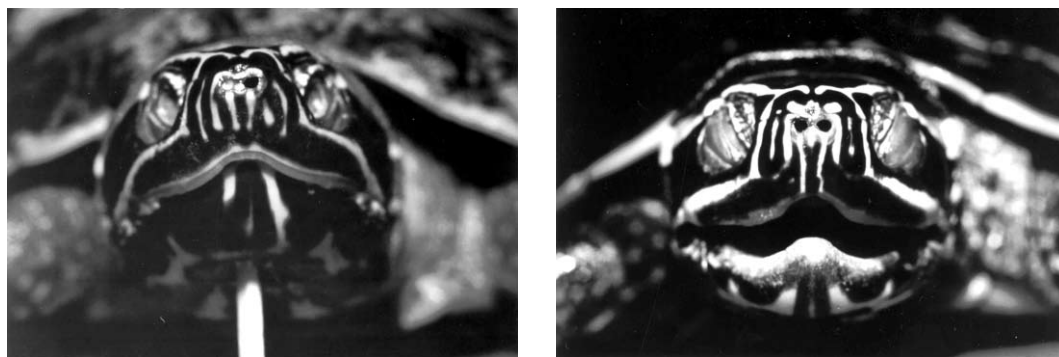


FIGURE 2: Photographs of *Malayemys subtrijuga* (Schlegel and Müller, 1844) illustrating NasS values of 6 (left-MTKD 26087) and 7 (right-ROM 37059). Notice that partial stripes are counted as entire stripes.

between Java and Mekg (Dunn's post test; Table 2). The same pattern emerged for InfSW/HW. Mean values for CPhr were significantly different ($p < 0.001$) from the mean values of both Java and Mekg, whereas mean values were not significantly different between Java and Mekg (Bonferroni multiple comparison test; Table 2). All Kruskal Wallis and ANOVA p values were < 0.0001 . In essence, *Malayemys* from CPhr had fewer nasal stripes, lower InfLor values, and wider infraorbital stripes than their Mekg and Java counterparts.

I also had an opportunity to examine photographs of *M. subtrijuga* from Siem Reap (in the Mekong basin), Cambodia (Kurt Buhlmann, pers. comm.; Peter C. H. Pritchard, pers. comm). All animals for which data could be recovered had six nasal stripes (7 specimens), an InfLor value of ≥ 3 (5 specimens), and an infraorbital stripe that was relatively narrow at the loreal seam (5 specimens). These correspond to

the head-stripe morphology of other specimens from Mekg.

Geographic variation of shell characters was also evident for female and male *M. subtrijuga* (sensu lato). The best model to classify female turtles relative to predetermined geographic origin correctly classified 88% of all individuals and contained seven of the original 29 shell character ratios. These were Vert5W/CL, PPLW/CL, CW/CL, Pleu1W/CL, Vert3L/CL, AnL/CL, and HumL/CL. Using the seven variable model, cross-validation results of linear discriminant function analysis correctly classified 80 to 91% of females (Table 3). The best model to classify male turtles relative to predetermined geographic origin correctly classified 80% of all individuals and contained five of the original 29 shell character ratios. These were PPLL/CL, AnL/CL, AnW/CL, Vert1L/CL, and Vert5L/CL. Using the five variable model, cross-validation results of linear discriminant function analysis

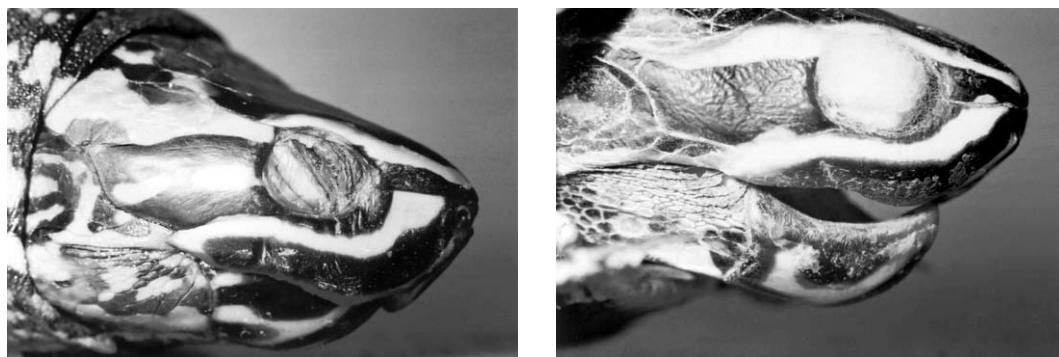


FIGURE 3: Photographs of *Malayemys macrocephala* (Gray, 1859) illustrating InfLor values of 1 (left-GMU 3520) and 2 (right-USNM 71480), and infraorbital stripes that are relatively wide (left-InfSW/HW=0.13; right-InfSW/HW=0.12) at loreal seam.



FIGURE 4: Photographs of *Malayemys subtrijuga* (Schlegel and Müller, 1844) illustrating InfLor values of 3 (left-MTKD 23937) and 4 (right-MTKD 26087), and infraorbital stripes that are relatively narrow (left-InfSW/HW=0.05; right-InfSW/HW=0.03) at loreal seam.

correctly classified 76 to 89% of males (Table 4).

For both females and males, discriminant function analysis demonstrated shell differentiation between the three geographic samples. This differentiation was reinforced by the bivariate plots (CV1 vs. CV2) of canonical discriminant scores (Figs. 6 and 7). Three clusters representing geographic samples were apparent on both the female and male plots, with some overlap between the CPhr and Mekg clusters.

Even though the multivariate analyses of shell character data did not suggest the distinctiveness of CPhr as strongly as the head-stripe data, there were several individual shell characters that reinforced this pattern (Table 5). The mean value of AnL/CL in CPhr females was significantly different ($p < 0.01$) from the mean values of both Java and Mekg, whereas

mean values were not significantly different between Java and Mekg. In addition, the mean values of both Vert5L/CL and PecL/CL in CPhr females were significantly different ($p < 0.01$) from those of Mekg (Bonferroni multiple comparison test). The concordance between head-stripe and shell characters was even stronger in males. Five shell characters in males supported the distinctiveness of CPhr over Java and Mekg. The mean values of Pleu1L/CL, PPLL/CL, PecL/CL, AbdL/CL, and RLatK in CPhr males were significantly different ($p < 0.01$ in all but 2 cases) from the mean values of both Java and Mekg, whereas mean values were not significantly different between Java and Mekg (Bonferroni multiple comparison test for all but RLatK; Dunn's post test for RLatK). For female and male comparisons, all ANOVA and Kruskal Wallis p values were < 0.01 .

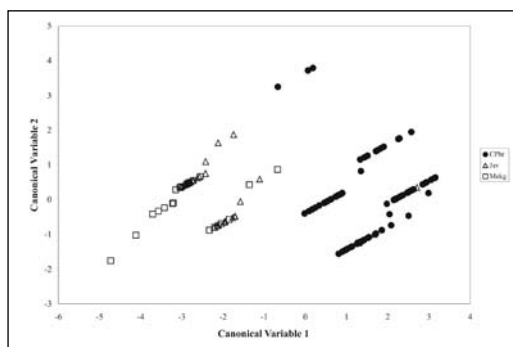


FIGURE 5: Plot of the first two canonical axes for all *Malayemys* based on discriminant function analysis of three head-stripe characters.

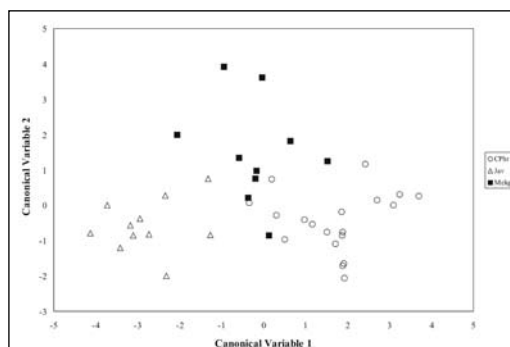


FIGURE 6: Plot of the first two canonical axes for female *Malayemys* based on discriminant function analysis of seven shell character ratios.

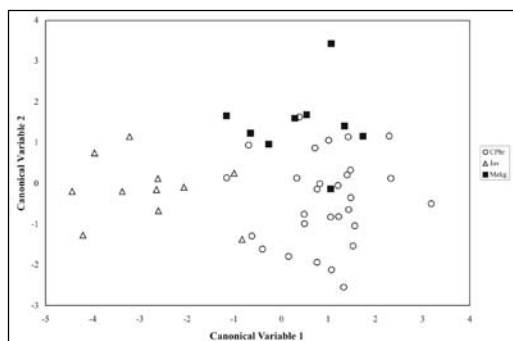


FIGURE 7: Plot of the first two canonical axes for male *Malayemys* based on discriminant function analysis of five shell character ratios.

When specimens from geographic samples other than CPhr, Meko, and Java were entered as test data in the multivariate shell character models (based on CPhr, Meko, and Java), all specimens from Maly and SECos were classified as CPhr. Specimens from Sumt were classified as both CPhr (2 specimens) and Meko (2 specimens). When specimens from the Java sample were entered as test data in the multivariate shell character models based on CPhr and Meko only, all Java females (11/11) and 91% (10/11) of Java males were classified as Meko.

DISCUSSION

Before the major results of this study are discussed, a few issues regarding the natural occurrence of *M. subtrijuga* (*sensu lato*) in Indonesia must be considered. The few records that exist for *M. subtrijuga* from Sumatra are almost certainly based on imported specimens or faulty

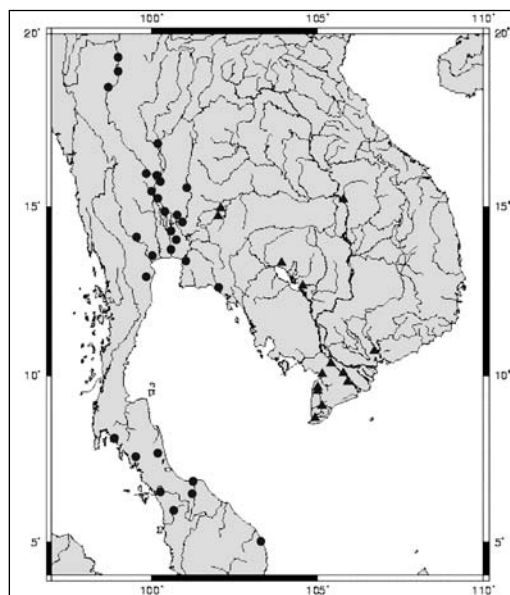


FIGURE 8: Distribution map for *Malayemys subtrijuga* (Schlegel and Müller, 1844) (triangles) and *Malayemys macrocephala* (Gray, 1859) (circles) based on available museum and literature records. See Brophy (2002) for more detailed records.

locality data. Several herpetofaunal surveys have failed to locate *M. subtrijuga* on Sumatra (de Rooij, 1915; van de Bunt, 1990; Fritz and Gaulke, 1997; Gaulke et al., 1998; Shepherd, 2000) and current reptile dealers have little or no knowledge of its presence there (Shepherd, 2000). My own results suggest that Sumatran specimens are of mixed origin (see above) and were, therefore, likely introduced or mislabeled. A single record also exists for *M. subtrijuga* on

Borneo (Wetlands International Indonesia Program, Wetlands Database *in* Samedi and Iskandar, 2000). This record is questionable (Samedi and Iskandar, 2000) and if legitimate, is probably based on imported specimens or a misidentification. I found no such museum specimens, and Lim and Das (1999) make no mention of the presence of *M. subtrijuga* on Borneo.

The question as to the natural occurrence of *M. subtrijuga* (*sensu lato*) on Java, however, is a more complex issue. *Malayemys subtrijuga* has been known from Java for almost 200 years (Temminck and Schlegel, 1834; Schlegel and Müller, 1844; Hoogmoed, 1982). In fact, the syntypes of *M. subtrijuga* (Schlegel and Müller,

1844) were collected in Java's Bantam Province (Temminck and Schlegel, 1834; Schlegel and Müller, 1844; Hubrecht, 1881). There are several lines of evidence, however, that lead me to conclude that *M. subtrijuga* is not native to Java (Dammerman, 1929; Ernst et al., 2000; van Dijk and Thirakhupt, *in press*). First, recent reports indicate that populations of *M. subtrijuga* on Java are dwindling or extinct (Samedi and Iskandar, 2000; van Dijk and Thirakhupt, *in press*; Peter C. H. Pritchard, *pers. comm.*). This may be due in part to the small size of introduced founding populations, but may also be due to extensive long-term habitat alteration on Java (Whitten et al., 1996; Manthey and Grossman,

TABLE 1: Cross-validation results for all *Malayemys* based on linear discriminant function analysis of head-stripe characters. Percentages in parentheses.

Actual group	group classification			Total
	CPhr	Java	Mekg	
CPhr	86 (97.73)	2 (2.27)	0 (0.00)	88
Java	2 (6.06)	12 (36.36)	19 (57.58)	33
Mekg	1 (4.00)	5 (20.00)	19 (76.00)	25

TABLE 2: Head-stripe characters – median and interquartile range (IQR), (range), and [n] – useful in distinguishing CPhr from Java and Mekg. Mean \pm 1 SE substituted for median and IQR in InfSW/HW. For NasS and InfLor, medians with different superscripts are significantly different ($p < 0.001$) according to Dunn's post test (InfSW/HW-Bonferroni multiple comparison test, $p < 0.001$). All Kruskal Wallis and ANOVA p values < 0.0001 .

Character	CPhr	Java	Mekg
NasS	4.0 (IQR=2) ^a (2-6) [98]	6.0 (IQR=0) ^b (2-6) [37]	6.0 (IQR=0.5) ^b (4-9) [35]
InfLor	1.0 (IQR=1) ^a (1-4) [94]	4.0 (IQR=1) ^b (1-4) [35]	4.0 (IQR=1) ^b (1-4) [25]
InfSW/HW	0.11 \pm 0.002 ^a (0.06-0.18) [88]	0.05 \pm 0.004 ^b (0.03-0.13) [33]	0.04 \pm 0.003 ^b (0.02-0.10) [26]

TABLE 3: Cross-validation results for female *Malayemys* based on linear discriminant function analysis of shell characters. Percentages in parentheses.

Actual group	Group classification			Total
	CPhr	Java	Mekg	
CPhr	17 (89.47)	0 (0.00)	2 (10.53)	19
Java	0 (0.00)	10 (90.91)	1 (9.09)	11
Mekg	2 (20.00)	0 (0.00)	8 (80.00)	10

1997; FAO, 2001; Peter Paul van Dijk, pers. comm.). Second, history indicates that humans have been moving between Java and the south-east Asian mainland for over two thousand years (Whitten et al., 1986; Schwartzberg and Bajpai, 1992). Since *M. subtrijuga* is commonly used for food (van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press) and religious practices (van Dijk and Palasuwan, 2000; Hendrie, 2000; van Dijk and Thirakhupt, in press) by non-Islamic peoples (Whitten et al., 1996), it is conceivable that it was brought to Java for one or both of these reasons. Third, the known distribution of *M. subtrijuga* on Java is primar-

ily limited to port cities on the northern coast. This type of distribution is expected for an introduced species (Inger, 1966). Finally, analyses of ancient river systems suggest that *M. subtrijuga* could not have reached Java from the south-east Asian mainland without passing through either Borneo or Sumatra (Burridge, 1992; Lovich, 1994; Inger, 1999; Voris, 2000), and since it is not found on these islands, an introduced origin is probable.

It is likely that *M. subtrijuga* (sensu lato) is one of the many Indochinese endemics whose populations are primarily found north of the Isthmus of Kra (Lovich, 1994; Rainboth, 1996;

TABLE 4: Cross-validation results for male *Malayemys* based on linear discriminant function analysis of shell characters. Percentages in parentheses.

Actual group	Group classification			Total
	CPhr	Java	Mekg	
CPhr	22 (75.86)	1 (3.45)	6 (20.69)	29
Java	1 (9.09)	9 (81.82)	1 (9.09)	11
Mekg	1 (11.11)	0 (0.00)	8 (88.89)	9

TABLE 5: Shell character ratios – mean \pm 1 SE, (range), and [n] – useful in distinguishing CPhr from Java and Mekg. Median and interquartile range (IQR) substituted for mean \pm 1 SE in RLatK. For all except RLatK, means with different superscripts are significantly different ($p < 0.01$ in all but 2 cases) according to Bonferroni multiple comparison test (RLatK-Dunn's post test, $p < 0.001$). All ANOVA and Kruskal Wallis p values < 0.01 .

Character Ratio	CPhr	Java	Mekg
AnL/CL-females	0.14 \pm 0.002 ^a (0.12-0.16) [19]	0.12 \pm 0.004 ^b (0.10-0.15) [15]	0.12 \pm 0.005 ^b (0.09-0.15) [14]
Vert5L/CL-females	0.19 \pm 0.003 ^a (0.15-0.21) [23]	0.20 \pm 0.005 ^{a,c} (0.16-0.22) [12]	0.21 \pm 0.004 ^{b,c} (0.19-0.24) [14]
PecL/CL-females	0.12 \pm 0.003 ^a (0.09-0.15) [19]	0.12 \pm 0.007 ^a (0.06-0.14) [15]	0.14 \pm 0.005 ^b (0.11-0.19) [14]
Pleu1L/CL-males	0.24 \pm 0.002 ^a (0.21-0.28) [32]	0.26 \pm 0.003 ^b (0.24-0.27) [14]	0.25 \pm 0.003 ^b (0.23-0.26) [9]
PPLL/CL-males	0.52 \pm 0.003 ^a (0.50-0.55) [30]	0.49 \pm 0.005 ^b (0.46-0.53) [14]	0.50 \pm 0.003 ^b (0.48-0.51) [9]
PecL/CL-males	0.10 \pm 0.003 ^a (0.07-0.16) [30]	0.12 \pm 0.005 ^b (0.09-0.18) [14]	0.13 \pm 0.004 ^b (0.11-0.14) [9]
AbdL/CL-males	0.21 \pm 0.003 ^a (0.18-0.23) [30]	0.18 \pm 0.004 ^b (0.15-0.22) [14]	0.19 \pm 0.004 ^b (0.17-0.21) [9]
RLatK-males	0.25 (IQR=0) ^a (0.20-0.25) [32]	0.20 (IQR=0.05) ^b (0.20-0.25) [14]	0.20 (IQR=0.05) ^b (0.20-0.25) [9]

Inger, 1966, 1999). Lovich's (1994) analysis of the zoogeography of south-east Asian turtles suggested that less than 50% of Indochinese turtles are found south of the Isthmus of Kra. My own results suggest that *Malayemys* from Java are morphologically similar to those from the Mekong River Basin and were, therefore, probably introduced primarily from that region.

It is also possible, however, that populations of *M. subtrijuga* on Java are Pleistocene relicts. One interesting zoogeographical feature of south-east Asia is the correspondence between the monsoon East Javan and monsoon mainland south-east Asian faunas in contrast to the fauna of the rainforest belt (Thai-Malay Peninsula, Sumatra, and Borneo) (Peter Paul van Dijk, pers. comm.). The Banteng (*Bos javanicus*), Javan rhinoceros (*Rhinoceros sondaicus*), and Russell's viper (*Daboia russelii siamensis*) are all examples of species occurring in Java and the monsoon mainland but not the rainforest belt (Lekagul and McNeely, 1977; Peter Paul van Dijk, pers. comm.). Since none of these would have been transported by humans, they are probably relict populations of a wider Pleistocene distribution, when a drier climate created deciduous forests and seasonally fluctuating rivers and floodplains over a much wider region (Lekagul and McNeely, 1977; Whitten et al., 1996; Peter Paul van Dijk, pers. comm.). Even though *M. subtrijuga* (sensu lato) is more likely than the above species to have been transported by man, it is possible that it too is a Pleistocene relict.

Based on the results of this study, I conclude that two distinct groups of *Malayemys* occur on mainland south-east Asia. Populations from central and peninsular Thailand and northern Malaysia (CPhr, MKI, SECos, Maly) differ significantly and consistently from those in eastern Thailand, Laos, Cambodia, and southern Vietnam (Mekg). These groups were clearly separated by univariate and multivariate analyses of both head-stripe (Tables 1-2; Fig. 5) and shell characters (Tables 3-5; Figs. 6-7). *Malayemys* from CPhr, MKI, SECos, and Maly have four or fewer nasal stripes (99%) and an infraorbital stripe that is relatively wide at the loreal seam (98% of InfSW/HW=0.07-0.18) and does not

extend or extends only slightly superior to the loreal seam (96%) (Table 2). Females from CPhr, MKI, SECos, and Maly also have relatively longer AnL and relatively shorter Vert5L and PecL than their Mekg counterparts (Table 5). Similarly, males from CPhr, MKI, SECos, and Maly have relatively longer PPLL and AbdL, relatively shorter Pleu1L and PecL, and greater RLatK values than their Mekg counterparts (Table 5). Populations from Mekg, on the other hand, have six or more nasal stripes (89%) and an infraorbital stripe that is relatively narrow at the loreal seam (92% of InfSW/HW=0.02-0.06), extends completely superior to the loreal seam (96%), and usually joins the supraorbital stripe (64%) (Table 2).

The observed differences between these two groups are consistent with the topography of the region and the poor dispersal abilities of *Malayemys*. The south-east Asian mainland is a topographically complex region with many lowlands interspersed between mountain chains and hills. The topography of this area was formed in response to the subduction of the Indian subcontinent under the Asian mainland (Molnar and Tapponier, 1975; Lekagul and McNeely, 1977). This created the Himalayas at the main collision front and buckled other areas around its edges. As a result, the mountain and hill ranges in mainland south-east Asia stretch in a general north-south direction (Molnar and Tapponier, 1975; Lekagul and McNeely, 1977). The two distinct groups of *Malayemys* correspond with separate lowland areas that are broadly separated by mountains at the boundary between the Chao Phraya and Mekong river basins.

Turtles of this genus are slow-moving, poor-swimming, bottom-feeders that exclusively inhabit lowland freshwater areas. They are restricted by hilly areas and associated watershed divides, are unable to ascend streams (Thirakhupt and van Dijk, 1995), and despite intensive searches, could not be found in any stream in hilly areas (van Dijk and Thirakhupt, in press). Because of the poor dispersal abilities of *Malayemys*, the boundary between the Chao Phraya and Mekong basins is sufficient to isolate these two groups, thereby restricting gene flow between them.

The specific events that led to this isolation are unclear. One possible explanation, however, may be found in the reconstruction of former river courses. Gregory (1925) hypothesized that the upper Mekong River was once connected to the Chao Phraya River through the present-day Mae Nam Yom. Essentially, the Chao Phraya and Mekong rivers were different channels in a single huge delta, and/or both were major tributaries of the West Sundaland River (Lekagul and McNeely, 1977; Peter Paul van Dijk, pers. comm.). This hypothesis is supported by the high degree of overlap in fish faunas between the modern Chao Phraya and Mekong basins (Kottelat, 1989). This connection may have joined the two *Malayemys* groups, and its severing may have been the final step in their isolation. The severance of the Chao Phraya from the upper Mekong was probably caused by the Chiang Mai uplift during the early Middle Pleistocene (Lekagul and McNeely, 1977; Peter Paul van Dijk, pers. comm.). Once isolated, divergence may have occurred via natural selection, genetic drift, or founder effect.

The question now arises as to the taxonomic status of these two divergent populations. My goal in this study was to discern evolutionarily independent but genetically cohesive units and to recognize them as taxonomic species (Good and Wake, 1993). There is sufficient evidence (topographical, ecological, and geological) to conclude that the two forms of *Malayemys* identified during this study are allopatrically distributed, and that the likelihood of genetic interchange between them is low. Since these morphologically distinct groups are currently allopatric, they are, by definition, independently evolving entities and should be afforded full species status (Simpson, 1961; Wiley, 1978, 1980; Frost and Hillis, 1990). These groups may have been geographically isolated for only a short time, and they might resume interbreeding if they come into contact in the future. Since knowledge of future events is impossible, however, inferences about past events must suffice (Good and Wake, 1993). Furthermore, it is assumed that the longer these two groups are isolated and the more differences that evolve between them, the more likely it is that they will

remain reproductively independent on recontact (Good and Wake, 1993).

A valid species name is available for *Malayemys* from the Mekong River Basin. The three syntypes for *M. subtrijuga* were collected in Java's Bantam Province (former residency in western Java currently known as Banten) by H. Kuhl and J. C. van Hasselt and were sent to the Rijks-Museum (RMNH; currently Nationaal Natuurhistorisch Museum) in Leiden, The Netherlands (Temminck and Schlegel, 1834; Schlegel and Müller, 1844; Hubrecht, 1881). Boie ("1824-1825") incorrectly identified these specimens as *Emys trijuga* Schweigger, 1812 but provided a detailed illustration of one individual (see Hoogmoed, 1982 for discussion of completion date for Boie's manuscript). Temminck and Schlegel (1834) gave a short description of these same three specimens but also identified them as *E. trijuga* Schweigger, 1812. This error was eventually corrected by Schlegel and Müller (1844:30) where they were given the name *Emys subtrijuga*. The three syntypes, one stuffed male and two stuffed females, are currently cataloged as RMNH 6082, 6084, and 6085 (King and Burke, 1997). I have examined these specimens along with Boie's ("1824-1825") unpublished manuscript and all other pertinent literature (Temminck and Schlegel, 1834; Schlegel and Müller, 1844; Hubrecht, 1881), and there is no doubt in my mind that these are the syntypes for *M. subtrijuga* (Schlegel and Müller, 1844).

The identity of the type specimen(s) for *M. subtrijuga* has not always been so clear (Iverson, 1986, 1992; King and Burke, 1997). Iverson (1986:50, 1992:138) listed BMNH 1947.3.4.53 as the holotype for *M. subtrijuga* based on an entry in the BMNH species catalog (King and Burke, 1997). Iverson (1992; in King and Burke, 1997) further stated that the catalog entry identified BMNH 1947.3.4.53 as Boulenger's (1889) specimen "m" which was listed as a composite specimen of *Damonia* (= *Malayemys*) *subtrijuga* and *Nicoria* (= *Melanochelys*) *trijuga*. It is clear to me that Iverson (1986, 1992) mistakenly identified BMNH 1947.3.4.53 as the holotype of *M. subtrijuga* based on incorrect information in the BMNH species catalog. I also obtained a

copy of the BMNH species catalog and it clearly states all that Iverson (1986, 1992) indicates. The problem with the catalog, however, is that it is contradicted by earlier published accounts of BMNH holdings.

The entry for Boulenger's (1889) *Damonia subtrijuga* specimen "m" is identical in all respects to the aforementioned BMNH species catalog, with one exception. Boulenger (1889) does not list specimen "m" as a type of *Emys* [= *Malayemys*] *subtrijuga*. This is significant because it was Boulenger's (1889) custom to indicate type specimens where appropriate. He does note, however, that this is the "Specimen mentioned by Gray as *Emys subtrijuga*" (p. 95). Perhaps this is the original source of the error in the BMNH species catalog

A thorough examination of the literature indicates that the above quote probably refers to Gray (1873). In this publication, Gray refers to an "*Emys subtrijuga*" (*Damonia macrocephala* specimen "e"; catalog no. 48,10,31,16) skeleton and shell which were obtained from the Leyden Museum (currently RMNH). The catalog number given by Gray (1873) is an old number for BMNH 1947.3.4.53 (BMNH species catalog). Gray (1873) failed to identify this as a type specimen, which would have been his custom as well.

This issue is further complicated by the fact that BMNH 1947.3.4.53 was apparently obtained from the Leyden Museum (Gray, 1873). Hubrecht (1881) recognized the potential for confusion, so he stated "the type specimens being all preserved in Leyden it [BMNH 1947.3.4.53] could not have been one of these" (p. 49). Based on the above discussion, there can no longer be any doubt that BMNH 1947.3.4.53 is not the holotype for *M. subtrijuga* and that the true syntypes for this species are RMNH 6082, 6084, and 6085.

As stated previously, my results suggest that *Malayemys* from Java are morphologically similar to those from the Mekong River Basin and are considered here as introduced to Java from that region (Tables 1, 2, 5; Fig. 5). I examined the syntypes for *M. subtrijuga* (RMNH 6082, 6084, 6085) and conclude that they are representative of *Malayemys* from the Mekong basin.

All three specimens have six nasal stripes, an infraorbital stripe that is relatively narrow at the loreal seam (InfSW/HW = 0.0362, 0.0459, 0.0462), and an infraorbital stripe that extends completely superior to the loreal seam and joins the supraorbital stripe (InfLor = 4). In addition, RMNH 6082 and 6085 were classified as Mekg by linear discriminant function analysis of both shell and head-stripe characters (Table 1; Fig. 5). RMNH 6084 was classified as Mekg by linear discriminant function analysis of head-stripe characters (Table 1; Fig. 5), but was not classified by the shell character model because of missing data. For these reasons, *Malayemys* from the Mekong River Basin and Java retain the name *Malayemys subtrijuga* (Schlegel and Müller, 1844) (Fig. 8). Because of its overall condition and morphology, I designate RMNH 6082 as the lectotype for *M. subtrijuga* (Schlegel and Müller, 1844). I am not going to restrict the type locality of *M. subtrijuga* because there is some question as to the natural occurrence of this species on Java (Dammerman, 1929; Ernst et al., 2000; van Dijk and Thirakhupt, in press).

A valid species name is also available for *Malayemys* inhabiting the Chao Phraya and Mae Klong basins of central Thailand, the coastal areas of south-eastern Thailand, and the Malay Peninsula in southern Thailand and northern Malaysia. The two syntypes for *M. macrocephala* were collected in "Siam" by M. Mouhot and were sent to the British Museum in London (Gray, 1859). Gray (1859) described these two specimens as *Geoclemys macrocephala*. He gave a lengthy description that included the following diagnostic character for this group: "...two close streaks under the nostrils to the middle of the upper jaw..." (Gray, 1859:479). This corresponds with two nasal stripes from the current study. Examination of the accompanying Plate XXI reveals that *Geoclemys macrocephala* also has a relatively wide infraorbital stripe that does not extend superior to the loreal seam. The identity of the syntypes for *M. macrocephala* is not nearly as complicated as with *M. subtrijuga*. Boulenger (1889:95) clearly lists *Damonia subtrijuga* specimens "a" and "b" as "Types of *G. macrocephala*". Gray (1873) identifies the types of *Damonia* [= *Malayemys*]

macrocephala as 59,7,8,4 and 59,7,8,5. Gray's (1873) catalog numbers are old numbers for BMNH 1947.3.4.51-52 (BMNH species catalog). These are, without question, the syntypes for *M. macrocephala* (Gray, 1859).

I examined the syntypes for *M. macrocephala* (BMNH 1947.3.4.51-52) and conclude that they are representative of *Malayemys* from CPhr, MKI, SECos, and Maly. Both specimens have two nasal stripes, an infraorbital stripe that is relatively wide at the loreal seam (InfSW/HW = 0.0684, 0.0817), and an infraorbital stripe that does not extend superior to the loreal seam (InfLor = 1). In addition, both specimens were classified as CPhr by linear discriminant function analysis of head-stripe characters (Table 1; Fig. 5). BMNH 1947.3.4.51 was also classified as CPhr by linear discriminant function analysis of shell characters (Table 3). For these reasons, *Malayemys* from CPhr, MKI, SECos, and Maly are assigned the name *Malayemys macrocephala* (Gray, 1859) (Fig. 8). Because of its larger size and overall morphology, I assign BMNH 1947.3.4.52 as the lectotype for *M. macrocephala*. Further, since the type locality for this species was given as "Siam" (Gray, 1859), I restrict the type locality of *M. macrocephala* to Thanyaburi, Pathum Thani Province, Thailand (Chao Phraya River Basin; approx. 50 km NNE of Bangkok; 14.017 N, 100.733 E). Populations of *M. macrocephala* appear to be substantial at this location (Srinarumol, 1995; van Dijk and Thirakhupt, in press) and several specimens from this area are preserved at Chulalongkorn University in Bangkok (CUB 1992.11.10.1-2, 1999.01.05.15-18).

In light of the current taxonomic proposals, *M. macrocephala* (Gray, 1859) and *M. subtrijuga* (Schlegel and Müller, 1844) should be protected as separate taxa of concern. Populations of *M. macrocephala* are relatively stable (van Dijk and Palasuwan, 2000; van Dijk and Thirakhupt, in press) and fairly well protected (Thirakhupt and van Dijk, 1995; Sharma and Tisen, 2000; van Dijk and Palasuwan, 2000) in Thailand and Malaysia. *Malayemys subtrijuga* populations, on the other hand, are vulnerable (IUCN TFTSG & ATWG, 2000) and poorly protected (Hendrie, 2000; Stuart and Timmins,

2000; Stuart et al., 2000; Touch Seang Tana et al., 2000) in Laos, Cambodia, and Vietnam. Population sizes in these areas are severely reduced due to intense harvesting and habitat alteration (Stuart and Timmins, 2000; Touch Seang Tana et al., 2000; van Dijk and Thirakhupt, in press). Fortunately, *M. subtrijuga* in the Mekong basin of north-eastern Thailand enjoy the same protections as their *M. macrocephala* counterparts. The future is worrisome for *Malayemys* populations in south-east Asia. Appropriate conservation measures and additional research are needed to ensure the long-term survival of these species in the region (Thirakhupt and van Dijk, 1995; van Dijk et al., 2000; van Dijk and Thirakhupt, in press).

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CAS 98890, 119939; CUB 1992.11.10.1-2, 1998.04.05.1, 1999.01.05.15-18; FMNH 73815, 171927-28, 190336-42; KU 50509-14; MCZ R-20302-03, R-29506, R-43083; MTKD 17098, 17107, 22274-75, 34593; NMW 1322, 29373.5, 29375; RMNH 10374.1-6, 11367, 14911.1-2; SMF 42960, 52864-67, 70535; UF 69136, 111443; UMMZ 65138-40, 65142-50; USNM 70363, 71480, 72322-23, 79454, 79499, 101580, 102994, 104335; ZMUC R2505-06, R25233; ZRC 2.72; ZSM 17/1956.01-12, 55/1956.01-03; Maly-BMNH 1903.4.13.1; KUZ 36800-01; UF 85286; USNM 22951, 23111; MKI-CUB 1999.01.05.1-14; SECos-USNM 72212; Sumt-NMW 29376.3-4; Thailand-AMNH 80924; BMNH 59.7.8.4-5; FMNH 171915-16, 171926; GMU 3504, 3519-22; MCZ 55149; LACM 8115; NMW 29374.2-3; UF 85203; UMMZ 128404; Other-CRI 3446, 3807; ZMH R00399-400

Malayemys subtrijuga: Java-BMNH 63.12.4.38, 71.4.10.2; MCZ R-7819; MNHN 1905.57; NMBE 44a/14; NMW 29371.1-4, 29373.4; RH 33, 140, 142-44; RMNH 3960, 6082, 6084-85, 22213, 28045; SMF 7532-35, 52792, 58097; USNM 43870-71, 44121-22; ZMH R03088; ZMUC R25229-32; ZSM 2/1949; Mekg-BMNH 60.8.28.6, 1861.4.12.15; CRI 3231, 3276, 3442-45, 3447-48, 3451, 3808, 3853-54, 4077; CUB 1991.9.1.2; MNHN 1963.746; MTKD 18811, 22525, 23937, 26087; NMW 29373.3, 29374.1; ROM 37057-66; ZRC 2.2592; Sumt-NMW 29376.1-2; Other-RMNH 4749.

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