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Author(s): Carl H. Ernst, Arndt F. Laemmerzahl, and Jeffrey E. Lovich
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Does the "*kamaroma*"-plastron pattern morph occur in both Philippine subspecies of the turtle *Cuora amboinensis*?

Carl H. Ernst*, Arndt F. Laemmerzahl, and Jeffrey E. Lovich

(CHE) Division of Amphibians and Reptiles, MRC 162, Smithsonian Institution P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A., e-mail: chernst@frontiernet.net;
(AFL) Biology Program, George Mason University, Fairfax, Virginia 22030-4444, U.S.A., e-mail: alaemmer@gmu.edu;
(JEL) U.S. Geological Survey, Southwest Biological Science Center, 2255 North Gemini Drive, MS-9394, Flagstaff, Arizona 86001, U.S.A., e-mail: jeffrey_lovich@usgs.gov

Abstract.—Two subspecies of the turtle *Cuora amboinensis* have been reported from the Philippine Islands, *C. a. amboinensis* and *C. a. kamaroma,* distinguished primarily by their carapace morphology, and secondarily by their plastron patterns. We assessed the utility of using shell and postorbital-stripe morphology instead of plastron patterns to distinguish these putative taxa. Adult *C. amboinensis* from the Philippines were examined to determine the extent of occurrence of *C. a. kamaroma* on the islands. Several morphological carapace characters and one based on the postorbital stripe were found to differ significantly between the subspecies *C. a. amboinensis* and *C. a. kamaroma*, and were used to assign turtles to subspecies. Use of these characters often resulted in conflicting subspecific identifications for those previously assigned by their plastron patterns to *C. a. kamaroma*. This poses important questions. Using the carapace and postorbital-stripe characters, 95.2% of the turtles in the mainland chain of islands were identified as *C. a. amboinensis*, and only 4.8% as *C. a. kamaroma*. Surprisingly, most of those assigned to *C. a. kamaroma* were from the northern islands of Babuyan and Luzon, not from the southern main chain island populations closest to the likely geographic area of invasion by that subspecies. This may be due to the common practice of importation of *C. a. kamaroma* into these northern islands, especially Luzon, for food. Turtles with *kamaroma*-like or *C. a. amboinensis* × *C. a. kamaroma* plastron patterns have been reported from the Sulu Archipelago and Busuanga/Palawan chain, and those specimens we examined from those islands confirmed this. The questions of whether or not *C. a. kamaroma* actually occurs in the Philippines and, if so, what is its island distribution, cannot be answered at this time. All specimens previously identified as *C. a. kamaroma* by their plastron-patterns should be re-evaluated, using the significant carapace and postorbital-stripe characters identified by Rummler & Fritz (1991) and in this paper. Philippine *Cuora amboinensis* cannot be identified to subspecies by their plastron patterns alone.

Keywords: box turtle, Philippine turtle species, plastron patterns, turtle subspecies

The East Indian box turtle, *Cuora amboinensis* was described by Daudin in 1802. That geographic variation occurred within the species was recognized early by

* Corresponding author.

Schweigger (1812) and Gray (1834). In addition to the nominate subspecies, *Cuora amboinensis amboinensis* (Daudin, 1802), from Amboina Island, Indonesia, three additional subspecies have been described; *C. a. couro* (Schweigger, 1812), from northwestern Indonesia (Sumatra, Java, Sumbawa and small satellite islands [Fritz & Havaš 2007]; its zoogeography and distribution to be presented in a paper in preparation); *C. a. kamaroma* Rummler & Fritz, 1991, from southern mainland Asia and Borneo, and *C. a. lineata* McCord & Philippen, 1998, from northern Myanmar. To date, individuals of *Cuora a. couro* and *C. a. lineata* have not been reported from the Philippines.

Cuora amboinensis has long been known to occur in the Philippine Islands (Boettger 1886, De Rooij 1915, Taylor 1920, 1921; Wermuth & Mertens 1961, 1977; Alcala 1986, Ernst & Barbour 1989, Rummler & Fritz 1991, Iverson 1992, David 1994, Filella 1999, Brown et al. 2000, Ernst et al. 2000, Ferner et al. 2000, Bonin et al. 2006, Fritz & Havaš 2007, Diesmos et al. 2008, and others). These turtles were assigned to the nominate subspecies, *Cuora a. amboinensis* (Daudin 1802) by Rummler & Fritz (1991).

Gaulke (1995a, 1995b) first reported, based on both shell morphology and plastron pattern, the presence of *Cuora a. kamaroma* on the islands of Sanga-sanga and Tawi-tawi of the Sulu Archipelago in the southwestern Philippines. Gaulke & Fritz (1998) summarized the distributions of *C. a. amboinensis* and *C. a. kamaroma* in the Philippines and concluded that *C. a. kamaroma* was restricted to the Sulu Archipelago but had not reached the islands of the Palawan chain. They questioned if *C. a. amboinensis* inhabits islands in the Palawan group but stated that if the species occurs there the turtles are probably the subspecies *C. a. kamaroma*.

Since 1995, a number of specimens assigned to the subspecies *kamaroma* have been reported, and its range supposedly extended in the Philippines to include the islands of Balabac (Fidenci 2010) and Dumaran and Palawan (Diesmos et al. 2008). Diesmos et al. (2008) summarized and referenced the more extensive Philippine distribution of *C. a. amboinensis* as the islands of Luzon, Polillo, Verde, Mindoro, Sibuyan, Palawan, Dumaran, Panay, Guimaras, Pan de Azucar, Negros, Cebu, Masbate, Leyte, Samar, Bohol, Dinagat, and Mindanao. Neither Diesmos et al. (2008) nor Fidenci (2010) presented morphological data and apparently based their taxon determination primarily on the turtles' plastron pattern.

According to Diesmos et al. (2008), both subspecies occur in sympatry on the islands of Palawan and Dumaran in the Palawan island group. They also stated that, "The hypothesis that Palawan populations represent a morphological intermediate and currently undescribed taxon warrants additional study (S. Schoppe pers. comm. 2007)." This raises some interesting questions, particularly as the subspecific designations were based solely on plastron pattern differences and no morphometric data were supplied. Why suddenly have so many individuals of *Cuora a. kamaroma* been discovered in the Palawan group, when Gaulke (1995a, 1995b) did not find them during extensive surveys?

What is the distribution of *Cuora a. kamaroma* in the Philippines, and is the *kamaroma*-like plastron pattern the result of intergradation between the two subspecies or does it reflect normal gene introgression within the species? Also, could the distribution of *C. a. kamaroma* be the result of the southeastern Asian food trade?

Our discovery of additional individuals of *Cuora amboinensis* possessing the "*kamaroma*" plastron pattern-morph and intermediate specimens with reduced plastron pigmentation approaching that of *C. a. kamaroma* on the main Philippine islands north of where it has been previously reported prompted us to further examine the presence of *C. a. kamaroma* in the Philippines.

We have been aware that "*kamaroma*" plastron-patterned morphs occur on several Philippine islands since the early 1980s when we began an extensive study of the species throughout its range. We at first hypothesized that turtles resembling "*kamaroma*" represented a new subspecies. However, after morphological comparison with many specimens of *Cuora a. kamaroma* from southern Asia and *C. a. amboinensis* from throughout its range, we are now convinced that this is not the case.

Two possible explanations occur that may explain the distribution of the "*kamaroma*" plastron morphs in the Philippines: first, could the "*kamaroma*" plastron-pattern occur naturally in both subspecies of *Cuora amboinensis* there; or, second, could the presence of such a pattern be the result of unnatural causes? These two hypotheses are examined using our Philippine turtle sample and discussed later in this paper. Could the "*kamaroma*" plastron-pattern morph occur in both subspecies of *C. amboinensis* in the Philippines?

Rummler & Fritz (1991), in their review of geographic variation in *Cuora amboinensis,* emphasized the use of carapace morphology to determine subspecific status, rather than total reliance on plastron patterns. They also found significant variance in the width of the postorbital stripe between *C. a. amboinensis* and *C. a. kamaroma*, and described the two subspecies as follows. *C. a. amboinensis* possesses a flatter, broader carapace with generally flared lateral marginals, while *C. a. kamaroma* has a deeper, narrower carapace with generally reverted (downturned) lateral marginals. The postorbital stripe of *C. a. amboinensis* is much narrower than that of *C. a. kamaroma*. The nominate taxon has a plastron pattern consisting of a relatively large blotch on all plastron scutes; while the latter taxon has a pattern consisting of a smaller blotch only occurring on a few scutes. These differences were used in this study to identify the subspecies occurring on the various Philippine islands, with emphasis on shell morphology over pattern differences. The results are reported below.

Materials and Methods

A total of 367 specimens of *Cuora a. amboinensis* from throughout its range and 100 specimens of *C. a. kamaroma* from southern Asia and Borneo were morphologically compared to 12 previously unreported specimens of the species from the Philippines with the "*kamaroma*" plastron-pattern, and 22 other Philippine turtles with a reduced dark blotch plastron-pattern approaching that of *C. a. kamaroma* (Appendix 1, Tables 1, 2) to determine if these specimens were *C. a. kamaroma* or intergrades between the two subspecies. Data are also supplied on *Cuora amboinensis* from the Palawan island chain that have been suggested as a possible undescribed subspecies.

Notes and drawings were made of head, neck, limb, carapace and plastron patterns of each specimen. Sexes were determined by the characteristics given by Ernst & Barbour (1989) and Ernst et al. (2000). Straight-line measurements of each specimen were taken with dial calipers accurate to 0.1 mm. Variables included: the greatest carapace length (CL, not midline), carapace width (CW) and depth (CH) at the level of the seam separating vertebral scutes 2 and 3, marginal width (MW, the difference between CW and the width across the carapace taken between the points of juncture of the marginal scutes and pleurals at the level of the seam between vertebrals 2 and 3), greatest plastron length (PL), greatest width and length of both plastral lobes (APW, APL,

Table 1.—Carapace and postorbital stripe proportions (presented as percentages) distinguishing adult *Cuora amboinensis amboinensis* from adult *Cuora amboinensis kamaroma*. Abbreviations: CH = carapace depth, CL = carapace length, CW = carapace width, MW = marginal width, PO = postorbital stripe width, * = statistically significant.

	Mean (*SD*) range							
Species and test values	% CH/CL	% CH/CW	% CW/CL	MW (cm)	% MW/CL	% MW/CH	% MW/CW	% PO/CL
C. a. amboinensis	40.5 (3.4) (30.9–57.1)	54.1 (5.1) (44.1–69.9)	75.1 (5.3) (63.0–94.3)	16.85 (4.68) (6.0–32.9)	11.8 (4.5) (3.7–23.5)	29.4 (11.0) (8.8–57.1)	15.5 (5.0) (5.4–28.1)	1.04 (0.398) (1.00–2.60)
C. a. kamaroma	45.8 (4.0) (35.0–54.2)	61.8 (5.5) (51.2–78.3)	74.3 (5.7) (61.6–90.3)	10.3 (5.3) (1.6–26.6)	6.9 (4.1) (0.9–20.7)	15.1 (8.8) (2.2–40.4)	9.0 (5.0) (1.2–23.4)	1.19 (0.289) (0.411–1.724)
Welch's t-test	−9.8927*	−10.0938*	1.0712	9.4547*	8.7341*	10.9864*	9.5606*	−2.6988*
p-value	3.803e-16	2.2e-16	0.2865	1.287e-15	1.744e-14	< 2.2e-16	3.367e-16	0.0089

PPW, PPL), greatest length of the right shell bridge (BL), greatest width and length of the cervical scute (CSW, CSL) and all vertebrals (V_1W, V_1L, etc.), and the medial seam lengths of all plastron scutes (Gul., Hum., Pect., Abd., Fem., An.). The greatest width of the postorbital stripe (PO) was also measured. The number of rows of large scales at the lateral edge of the antebrachium between the knuckle joint of digit 5 and the first horizontal skin fold proximal to the elbow (FLSR) was also counted and recorded.

Statistical tests were executed using R, Version 2.12. Levels of significance were set a priori at $\alpha = 0.05$. Only adult turtles (those that displayed secondary sexual characteristics) were used in the statistical analyses, as only species specific characters were examined (Table 1). All tests were performed using original carapace and postorbital stripe measurements. Juvenile *Cuora amboinensis* have flatter, broader carapaces than those of adults, and skew the results of analyses of the carapace proportions used (see below). However, the plastron pattern of juveniles was used to assign them to subspecies.

Continuous variables and proportions of continuous variables were checked for normality using q-q plots and deemed sufficiently normal. The two subspecies were then compared using a multivariate t-test, followed by individual univariate Welch's t-tests, to tease apart the results for individual variables. Finally, a discriminant analysis (using those carapace and postorbital-stripe variables identified as significant by Welch's test) with cross-validation was done to determine the accuracy of classifying turtles into specific island groups. Shell proportions are expressed as percentages, as is also the width of the postorbital stripe.

Results

The comparative multivariate t-test clearly separated *Cuora a. amboinensis*

Table 2.—Comparison of carapace and postorbital stripe proportions (presented as percentages) of Philippine *Cuora amboinensis* with the "*kamaroma*" plastron pattern, and those with a reduced plastron pattern intermediate between *C. a. amboinensis* and *C. a. kamaroma*. CH = carapace depth, CL = carapace length, CW = carapace width, J = juvenile, MW = marginal width, PO = postorbital stripe width.

Plastron pattern	% CH/CL	% CH/CW	% CW/CL	MW (cm)	% MW/CL	% MW/CH	% MW/CW	% PO/CL
"*kamaroma*" pattern (12)								
Busuanga Island:								
CAS 60549	35.3	50.3	70.2	9.3	5.9	16.6	8.4	1.07
Leyte:								
HMCZ 4427	41.1	49.3	83.4	23.8	23.5	57.0	28.1	0.11
KU 50515	46.2	58.2	79.3	28.4	27.2	15.7	29.1	0.14
Luzon:								
CM 116200 (J)	41.5	45.6	91.0	23.2	24.6	59.3	27.0	1.48
CM 116201 (J)	39.9	45.2	88.3	23.6	25.1	62.9	28.4	1.49
CAS 15380	40.0	46.7	87.3	26.6	19.1	49.1	21.9	0.72
USNM 507807	47.6	60.0	79.3	20.8	15.5	32.6	19.6	0.82
USNM 512453	42.4	54.3	77.9	15.0	12.5	30.6	16.1	0.59
Palawan Group:								
CAS 157467	40.2	53.9	74.6	12.2	8.9	22.2	12.0	0.88
USNM 287378	44.4	51.6	85.9	19.1	17.8	40.2	20.8	1.12
Sulu Archipelago:								
MNHN 6151 (1) (J)	43.9	48.1	91.4	16.7	20.8	47.4	22.8	1.50
MNHN 6151 (2) (J)	43.3	47.6	90.2	16.0	20.2	46.5	22.2	1.26
"Intermediate" pattern (22)								
Alabat Island:								
USNM 507808	38.3	51.3	74.5	11.9	7.9	20.8	10.7	0.93
USNM 507809	41.3	49.8	82.9	18.0	15.0	36.3	18.1	1.25
Leyte:								
MCZ 25572	41.8	59.3	70.4	18.6	11.8	28.3	16.8	0.80
Luzon:								
CAS 15377 (J)	47.3	52.1	90.6	19.5	23.3	49.4	25.8	1.79
CAS 61176 (J)	37.9	46.0	82.4	20.9	18.9	49.8	22.9	1.62
USNM 229635	41.4	56.9	72.8	15.6	9.4	22.6	12.9	0.60
USNM 305350 (J)	42.5	46.3	91.9	21.5	25.9	60.7	28.1	1.40
USNM 305351 (J)	40.3	45.1	89.5	21.3	22.9	56.9	25.7	1.44
USNM 305354 (J)	42.6	47.9	88.9	21.8	24.8	58.3	27.9	1.37
USNM 305356	41.5	56.5	73.5	12.0	7.2	17.4	17.4	0.84
USNM 305358	45.9	59.4	77.3	12.8	8.9	19.4	11.5	0.91
USNM 305359	42.1	52.3	80.3	20.0	25.3	37.6	19.7	1.03
Mindanao:								
CAS 11334	37.9	51.0	74.3	18.4	11.9	31.4	16.0	0.71
FMNH 52771 (J)	42.5	46.2	92.1	22.0	28.0	65.9	13.8	1.78
FMNH 52772 (J)	40.0	42.9	90.8	18.0	28.5	73.2	31.4	1.58
FMNH 52773 (J)	39.8	43.1	92.5	18.1	27.6	69.3	29.9	1.83
FMNH 52785 (J)	36.4	42.3	86.0	12.4	26.3	72.1	30.5	1.69
FMNH 52798 (J)	40.7	43.5	93.7	20.1	30.3	74.4	32.4	0.00
Negros Island:								
USNM 228469	39.4	52.3	75.4	21.3	14.0	35.5	18.6	0.66
USNM 228470 (J)	39.6	45.8	86.4	24.4	28.2	71.1	28.2	1.16
Palawan Group:								
CAS 157295 (J)	39.6	45.9	86.3	19.5	20.8	52.4	24.1	1.28
CAS 157466	40.1	51.0	78.6	15.8	10.7	26.8	13.7	0.95

from *C. a. kamaroma* (DF 1; Pillai's trace 0.41608, approx. F 21.644; Df 8/Df 243; Pr (>F) 2.2e-16; significance level 0.001). This agrees with the findings of Rummler & Fritz (1991). Several of the results from Welch's t-tests were significantly different, and can be used to accurately distinguish between the two subspecies: CH/CL, CH/CW, MW/CL, MW/CH, MW/CW, and PO/CL (Table 1). That of the width of the postorbital stripe is highly significant, as are also the measurements and the carapace proportions regarding MW. Surprisingly, the ratio CW/CL was not significantly different between adults of the two subspecies; indicating the difference in width of these turtles is caused by the greater width of the flared lateral marginal scutes of *C. a. amboinensis* versus the reverted (downturned) more narrow lateral marginals of *C. a. kamaroma*, which is expressed in the significant difference of their marginal width proportions (Table 1).

The carapace and postorbital stripe characteristics of the 12 Philippine specimens that are identified by plastron pattern as *Cuora a. kamaroma* and the 22 other Philippine turtles with intermediate plastron patterns are presented in Table 2. A comparison of those adult turtles in the two groups with the range of proportions of the carapace and postorbital stripe shown in Table 1 to differentiate the two subspecies of *C. amboinensis* is revealing. Most of those reported to be either *C. a. kamaroma* or intermediate with *C. a. amboinensis* have a MW measurement or CL and CH, carapace, and PO characteristics identifiable as those of *C. a. amboinensis*. Juvenile turtles with the above mentioned plastron patterns are listed purely for completeness.

The results of the discriminant analysis presented in Table 3 show just over 88% of adult turtles were classified correctly to subspecies (207, 88.4% correct; 25, 10.8% incorrect). However, dissecting this further shows that of those specimens considered a priori to be *Cuora a. amboinensis* by plastron pattern, only 10 of 204 turtles were misclassified (i.e., 95% correct); and for those specimens identified a priori as *C. a. kamaroma* by plastron pattern, 13 of 28 were misclassified (i.e., 53.6% correct).

Discussion

As noted under Methods, although they were measured and their plastron patterns recorded in Table 2, juvenile Philippine *Cuora amboinensis* were not used in the morphometric analyses because the allometric shell dimensions of juvenile turtles change with growth. In addition, subspecific determination of a population can be questioned if it is based on the plastron patterns of juvenile *C. amboinensis*. Although not proven in *C. amboinensis*, the plastron patterns of juveniles in several turtle families, particularly Emydidae, Geoemydidae and Kinosternidae, become more darkly pigmented with age. If this occurs in *C. amboinensis*, it would cause a shift toward the more extensively pigmented plastron pattern of *C. a. amboinensis*, and thus cloud the question of subspecific integrity.

Until recently, Philippine *Cuora amboinensis* have been considered as representative of the subspecies *C. a. amboinensis* (references above). New collections in the islands, particularly by Diesmos et al. (2008) and Fidenci (2010), revealed that some individuals have a lighter plastron pattern resembling that of *C. a. kamaroma*. This fostered a frenzy of speculation as to the presence and distribution of populations of the latter subspecies in the Philippines (references above). However, are these individuals truly *C. a. kamaroma*?

Table 2 presents morphological data for those individual Philippine *Cuora amboinensis* that we have identified as having either a plastron pattern resem-

Table 3.—Classification by discriminant analysis (cross-validation) of adult turtles from main Philippine Island populations listed from north to south. Note that some specimens listed in Appendix 1 were excluded from the analysis due to missing values.

Island population	*Cuora a. amboinensis* n (%)	*Cuora a. kamaroma* n (%)
Babuyan	30 (88.2)	4 (11.8)
Luzon	46 (95.8)	2 (4.2)
Polillo	32 (100.0)	–
Mindoro	5 (100.0)	–
Leyte/Samar	6 (75.0)	2 (25.0)
Panay	13 (100.0)	–
Cebu/Mactan	4 (100.0)	–
Bohol	2 (100.0)	–
Negros	6 (100.0)	–
Mindanao	12 (100.0)	–
Basilan	1 (100.0)	–
Busuanga	1 (100.0)	–
Total	158 (95.2)	8 (4.8)

bling that of *C. a. kamaroma* (12) or one intermediate between that subspecies and *C. a. amboinensis* (22). The majority of these came from the large northern island of Luzon, 14 of 75 total specimens (18.7%), including 7 juveniles; the large southeastern island of Mindanao, 6 of 36 (16.7%), including 5 juveniles; the more southcentral island of Leyte, 3 of 11 adult specimens (27.3%), or the southcentral Negros Island, 2 of 18 (11.1%), including 1 juvenile. Possibly (see above) with time, the plastrons of at least some of these juveniles from Luzon and Negros with the *kamaroma* or intermediate patterns could darken to match the pattern of *amboinensis*. The adult specimens from Alabat (2) and Busuanga (1) possessed intermediate characters between the two subspecies.

Although Gaulke (1995a, 1995b) found no *Cuora a. kamaroma* from the Palawan Group in the southwestern Philippines, Diesmos et al. (2008) reported that recent herpetological surveys on Palawan found plastron pattern morphs resembling both *C. a. amboinensis* and *C. a. kamaroma*, and that turtles have been found with both pattern morphs occurring in sympatry on the island of Dumaran. That the *C. amboinensis* there appear intermediate between the two subspecies in plastron patterns, suggested to Diesmos et al. (2008) that the Palawan population may represent a currently undescribed taxon. Our findings do not bear this out. The plastron patterns of the population more closely resemble an intergrade one than a separate taxon. The means of shell and postorbital-width proportions for the adult turtles we examined, although our sample is only four, indicate that the adult turtles in the Palawan group more closely resemble *C. a. amboinensis* when compared with the same characters for the two subspecies presented in Table 1: CH/CL 41.5, CH/CW 52.2, CW/CL 76.3, MW 15.6, MW/CL 11.7, MW/CH 29.7, MW/CW 15.1, and PO/CL 0.98.

This also substantiates our hypothesis that the two subspecies of *Cuora amboinensis* can only be accurately identified by using carapace morphological and postorbital-stripe data but not with just plastral patterns. Pleiotrophic genes possibly influencing the plastron pattern of *C. a. kamaroma* may not occur in a relatively high percentage of adults in the Palawan Islands (two of four animals in our sample, Table 2). However, do the plastron patterns of such individuals represent *C. a. kamaroma*, or is this just a case of natural introgression of pleiotrophic plastron pattern genes into the population (see detailed discussion of gene introgression between taxa in Martinsen et al. 2001)? This should be determined by additional studies using both carapace and postorbital width dimensions, as presented in Table 1, and plastron patterns in a large sample of adult turtles. While the concept of subspecies is controversial, there is utility in its application for conservation as reviewed by Haig et al. 2006. The only quantitative metric they found for defining a subspecies was the 75% rule (Amadon 1949, Patten & Unitt 2002); i.e., 75% of the individuals of a population must be distinguishable from all those from the most proximate populations, in this case those of the more northern Philippine islands (*Cuora a. amboinensis*) or Borneo (*C. a. kamaroma*).

The two juvenile *Cuora amboinensis* (MNHN 6151-1,2; CLs: 80.1 mm and 79.4 mm, respectively) from the most southeastern islands, the Sulu Archipelago, have a plastron pattern similar to that of *C. a. kamaroma* but are too small to provide meaningful morphometric or postorbital-stripe data (Table 2). These were the only specimens we examined of *C. amboinensis* from those islands. Gaulke (1995a, 1995b), however, used carapace measurements of adult *C. amboinensis* in his analysis from Sulu. Morphological and postorbital stripe data of additional adult specimens are needed from Sulu to determine if the population there represents *C. a. kamaroma*.

Can the Philippine specimens previously assigned to the two subspecies be accurately identified by using the carapace and postorbital stripe characters listed above? Table 3 presents the result of discriminant analysis (cross-validation) identification of turtles from the main chain of Philippine Islands, using these characters. The analysis shows that all of the sampled populations of *Cuora amboinensis* from those main islands of the Philippine chain were classified as the subspecies *C. a. amboinensis* using the 75% rule. In addition, seven *C. amboinensis* from Dinagat Island and 12 from Marinduque Island that we examined were assigned to *C. a. amboinensis* by their plastron patterns but were excluded from the morphological analysis because of missing data values. Only eight (4.8%) of the 165 turtles used in the analysis of these main *Cuora* populations could be assigned to *C. a. kamaroma* by the significantly morphological characters discussed above.

Unfortunately, no specimens from the Palawan group, from which turtles have been previously assigned to *Cuora a. kamaroma* by their plastron patterns (Diesmos et al. 2008, Fidenci 2010), were used in the analysis because of missing data values. These included specimens we identify in Appendix 1 by their plastron patterns as either *C. a. kamaroma* (Palawan, 2) or intergrade *C. a. amboinensis* × *C. a. kamaroma* (Palawan, 2). The single adult turtle examined from Busuanga Island had a *kamaroma* plastron pattern but was morphologically intermediate (Table 2).

The question of whether *Cuora a. kamaroma* actually occurs in the Philippines cannot be answered at this time. All previously identified adult Philippine specimens assigned to this subspecies should be re-examined using the significant carapace morphological and postorbital-stripe characters listed above. If the race does occur in the Philippines, it probably does so only in the Sulu Archipelago and Palawan Group; but even there, evidence points to intergradation.

We believe that the very low incidence of adult turtles identifiable as *Cuora a. kamaroma* on the main chain of Philippine Islands (Table 3) is the result of occasional natural pleiotrophy of several plastron pattern genes into the various island populations and not due to intergradations; particularly, because 75% of those we identified by plastron pattern as *C. a. kamaroma* occurred in the northern islands, not at the most likely southern area of contact to that subspecies. It is doubtful that genes of the *kamaroma*-like plastron pattern could have been introduced into the Babuyan turtle population via the food or pet trades as *C. amboinensis* is a common turtle there. However, this is not the case in Luzon where an active turtle food trade occurs with specimens coming from throughout southern Asia and Indonesia (Diesmos et al. 2008, Ives et al. 2008), and the presence there of *C. a. kamaroma* may be fairly recent.

A later paper reviewing the patterns, morphology, distribution, and zoogeography is being prepared, and will include distributional maps for all races of *Cuora amboinensis.*

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Appendix 1

Turtles of the *Cuora amboinensis* Complex Examined

Specimens (510) from the following collections were examined: Academy of Natural Sciences, Philadelphia (ANSP); American Museum of Natural History, New York (AMNH); California Academy of Sciences, San Francisco (CAS, CASSU); Carl H. Ernst, personal collection (CHE); Carnegie Museum of Natural History, Pittsburgh (CM); Edward O. Moll, personal collection (EOM); Field Museum of Natural History, Chicago (FMNH); Florida Museum of Natural History, University of Florida, Gainesville (UF); George Mason University, Fairfax, Virginia (GMU); Harvard University Museum of Comparative Zoology, Cambridge (MCZ, HMCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Museum of Zoology, University of Michigan, Ann Arbor; (UMMZ); National Museum of Natural History, Washington, D.C. (USNM, USNM-FS); Naturhistorisches Museum Wien, Vienna (NMW); Natur-Museum und Forschungs-Institut Senckenberg, Frankfort (SMF); Rijksmuseum van Naturrhistorische, Leiden (RMNH); Staatliches Museum für Tierkunde, Dresden (MTKD, MTD); The Natural History Museum, London (BMNH); University of Kansas Museum of Natural History, Lawrence (KU); William H. Randall, personal collection (WR); and Zoologisches Institut und Zoologisches Museum der Universtät Hamburg (ZMH). The specimens are listed below by geographic region. Numbers in parentheses following the collection number indicate multiple specimens catalogued under that number.

Cuora amboinensis amboinensis (367): **Celebes (Macassar [Makassar])**–AMNH 80923; CAS 49241–49244; HMCZ 7624, 125998–125600, 16428, 16429, 16230, 16231, 25405; RMNH 3347; **Celebes (Manado Island)**–BMNH 1871.9.1.52; **Celebes (Sulawesi Island)**–MTKD 39290; MTD 42583; **Celebes (No specific locality)**–BMNH 1872.4.6.117; NMW 1802, 15071, 294651, 294652, 295111, 295112; RMNH 3343, 3345, 6950, osteo a–d(4); SMF 7701, 7702; **Indonesia (Boeroe Island)**–RMNH 113791, 113792; **Indonesia (Ceram [Seram/Serang] Island)**–BMNH 1910.4.26.1, 1910.4.26.2, 1910.4.26.3; **Moluccas (Amboina**, type locality)–BMNH unnumbered specimen (1); FMNH 16887; MNHN 7930, 5075, 5077; NMW 1803, 29641–29643; RMNH 3389, 8493(4), 52151, 52152, 84931–84934, dry specimens a, b; SMF 7681, 7683; USNM 104334, 129253, 204785, 507775; **Moluccas (Batjan)**–RMNH 1861, 1862(3); SMF 7886, 7887; **Moluccas (Halmahera)**–BMNH 1860.8.27.11 **[Gilolo]**; SMF 7693–7696; USNM 216004, 237627–237630, 237633, 237665, 237666; **Moluccas (No specific locality)**–MNHN 52481–52483; **Philippines (Barit Island)**–USNM 507789–507792; **Philippines (Basilan Island)**–USNM 37429, 37430; **Philippines (Bohol Island)**–USNM 229286–229289; **Philippines (Cebu Island)**–CASSU 11436–11438; SMF 7675, 7676; USNM 37428, 37436, 228405, 52974, 529475; **Philippines (Camiquin Island)**–USNM

507774–507788; **Philippines (Dinagat Island)**–BMNH 877.10.9.53, 1877.10.9.54, 1877.10.9.55, 1877.10.9.56, 1877.10.9.57, 1877.10.9.58, 1877.10.9.59(2); **Philippines (Fuga Island)**–CHE 1, CHE 2; USNM 507630, 507793–507795; **Philippines (Leyte)**–CAS 60926–60929; FMNH 44984; MCZ 25571, 25572, 164827; NMW 294711–294715; **Philippines (Luzon)**–AMNH 88199, 88200; BMNH 1872.8.20.79; CAS 15375, 15376, 15378, 15379, 15381, 15382, 61175, 61177, 61178; CHE/GMU 1012; CM 116200, 116201; UF 53666, 54809, Unnumbered (1); MNHN 2065, 58001, 58002; MTKD 940; NMW 1314, 29471, 29471; SMF 7682, 71627; UMMZ 173094; USNM 229632–229634, 229636, 305540, 305349, 305352, 305353, 305355, 305357, 305360, 498949, 499260, 499261, 499261, 507804–507806, 507808, 507810–507813, 507814, 512452, 512454, 512455; USNM-FS 121623, 121624, 180322, 222534; **Philippines (Mactan Island)**–CM 4239, 25643; USNM 129394; USNM-FS 195647, 195697, 195698, 196003, 196222, 196336, 196337, 196050; **Philippines (Marinduque Island)**–CM 62133–62144; **Philippines (Mindanao)**–CAS 11324–11333, 11335–11337; FMNH 14331, 14339, 14340; MNHN 58641, 58642; USNM 37428, 37436, 52756, 52760, 52774, 52785, 52786, 52793, 52796, 52798, 229388, 228405; **Philippines (Mindoro Island)**–SMF 7677–7680; USNM 228287–228289, 507814; **Philippines (Negros Island)**–CAS 133090–133092, 134330; FMNH 62907; NMW 1799, 294701–294703, 290704; USNM 78128, 228759, 228760, 228469–228471; **Philippines (Panay Island)**–MTD 43823; USNM 78746–78748, 78081–78104; **Philippines (Paraqua Island)**–MNHN 1884.59; **Philippines (Polillo Island)**–CAS 62438–62443; USNM 507796–507801, 507896–507898, 507800–507803, 507810, 512447–512451, 512453–512455; **Philippines (None or questionable data)**–BMNH 402–404, 1848.10.31.14, 1847.3.5.21, 1851.11.10.76; CAS 11443, 11444; FMNH 16886, 16888–16891; MNHN 1983.905, 1983.906; SMF 7700, 71096; USNM 61242, 328431, 494385; ZMH 280, 287.

Cuora amboinensis kamaroma (100): **Borneo**–ANSP 29768, 28769; BMNH 1856.9.27.4, 1863.12.4.48, 1863.12.4.121, 1863.12.11.139, 1895.5.1.1, 1911.1.30.1, 1933.6.20.34; FMNH 121244, 121153, 121179, 121180; NMW 1314, 294721, 294722; RMNH 3340, 3886; SMF 7685, 7697, 7698, 70532, 70533; **Bunguran Island, Indonesia**–USNM 28173, 28174, 28177–28179; **Cambodia**–MTKD 40391, 41275, 42510, 42512; **India**–BMNH 401; **Malaysia**–BMNH 1895.10.7.1, 1898.9.22.6; EOM 2208, 2218, 2223, 2229–2233, 2253, 2254, 2275–2278, 2281, 2292–2300, 2311, 2312, 2359, 2361, 2436, 2437; USNM 30963; **Singapore**–AMNH 89360; BMNH 405; CAS 11352–11355; SMF 53637; **Thailand**–AMNH 92772, 92773, 94562; BMNH 1859.7.8.3, 1921.4.1.185; FMNH 171918, 171920, 171921; MCZ 29539; KU 47173; MNHN 7933, 20321, 20322; NMW 1323, 3674; RMNH 149021, 149022; SMF 64641, 68190; UF 564211; WR 330; **None or questionable locality data**–AMNH 118760; BMNH 1869.3.6.4; MNHN 9101 (Soohog?); SMF 7511, 71164; USNM 241427.

Philippine Cuora amboinensis with kamaroma plastron patterns (12): **Philippines (Busuanga Island)**–CAS 60549; **Philippines (Leyte)**–HMCZ 4427; KU 50515; **Philippines (Luzon)**–CM 116200, 116201; CAS 15380; 507807, 512453; **Philippines (Palawan Group)**–CAS 157467; USNM 287378; **Philippines (Sulu Archipelago)**–MNHM 6151 (1), 6151 (2).

Philippine intermediate Cuora a. amboinensis × *C. a. kamaroma plastron patterns* (22): **Philippines (Alabat Island)**–USNM 507808, 507809; **Philippines (Leyte)**–MCZ 25572; **Philippines (Luzon)**–CAS 15377, 61176; USNM 229635, 305350, 305351, 305354, 305356, 305358, 305359; **Philippines (Mindanao)**–CAS 11334; FMNH 52771–52773, 52785, 52798; **Philippines (Negros Island)**–USNM 228469, 228470; **Philippines (Palawan Group)**–CAS 157295, 157466.