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Geographic Variation in Skull Morphology of the Green Turtle, *Chelonia mydas*, with a Taxonomic Discussion

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ABSTRACT.—This study analyzes the geographic variation of skull morphology in the green turtle, *Chelonia mydas*, including the eastern Pacific population sometimes recognized as *C. agassizii*. One hundred and forty-five skulls from six nesting sites (Comoros, Seychelles, Ogasawara [Japan], Galapagos [Ecuador], Tortuguero [Costa Rica], and Guyana) were measured. Samples from Comoros, Seychelles, and Guyana were greater in absolute skull length than those from Ogasawara, Tortuguero, and Galapagos. Discriminant analyses showed that four of the six local samples could be completely or nearly completely classified correctly. Comoros and Seychelles samples were not discriminated. The Galapagos sample was completely separated from other samples by a canonical discriminant analysis, and this result indicates distinctness of the eastern Pacific population. The Galapagos sample, however, was not differentiated from the others by any character dimension relative to skull length. From these results, we support the recognition of the eastern Pacific population as a distinct subspecies, *C. mydas agassizii*, but not as a distinct species.

The green turtle, *Chelonia mydas*, is distributed widely in the Atlantic, Pacific, and Indian oceans, chiefly in tropical and subtropical waters, and has nesting sites on both insular and continental shores of these oceans (Pritchard and Trebbau, 1984).

Geographically, this species is not uniform in external morphology. Of the five regional names that have been proposed (for review, see Groombridge and Luxmoore, 1989), Carr (1952) recognized two as valid and classified *C. mydas* into two subspecies. The typical form, *Chelonia m. mydas* ranges in the Atlantic, Mediterranean, Pacific, and Indian oceans. The other subspecies, *C. m. agassizii*, occurs in the East Pacific and was originally described by Bocourt (1868) as a full species. Carr's taxonomic treatment was supported by some subsequent authors (e.g., Ernst and Barbour, 1989). However, some authors proposed to revive full specific status for *C. m. agassizii* (e.g., Pritchard et al., 1983). On the other hand, Ernst and Barbour (1989), although admitting the distinctiveness of this form, considered that *C. agassizii* is best regarded as a subspecies of *C. mydas* until further studies are done.

Comparative morphometric study is useful for determining taxonomic relationships within animal groups, but few such data are available for *Chelonia*. This stems from the difficulty in obtaining adequate samples, both because of its worldwide distribution, and because few collections have adequate material of these very large animals. In this study, we investigated geographic variation in skull morphometrics for *Chelonia* from localities representative of at least the three tropical oceans. We also discuss the taxonomic status of *C. m. agassizii* on the basis of the results of our morphometric analyses.

MATERIALS AND METHODS

The skulls of *C. mydas* examined were from six areas: the Seychelles, Comoros, Ogasawara (Japan), Galapagos (Ecuador), Tortuguero (Costa Rica), and Guyana (Table 1; Appendix I). These samples encompass the known nesting range of the species (Iverson, 1992; Fig. 1). The specimens from Ogasawara are deposited in Kamezaki's private collection, and the others are in USNM, UF-FSU, and in Dr. P. C. H. Pritchard's private collection (PCHP). Institutional acronyms are those suggested by Leviton et al. (1985).

TABLE 1. Localities of skull samples of *Chelonia mydas* used and the sea surface temperature in each locality. Sea surface temperatures (degree C) were read from the climatic chart in Marine Department, The Japan Meteorological Agency (1991). Mean = mean of monthly temperatures.

Localities	Maximum number of specimens	Sea surface temperature		
		Feb	Aug	Mean
Comoros (43°E, 12°S)	28	28	25	26.9
Seychelles (55°E, 4°S)	22	28	26	27.5
Ogasawara (144°E, 27°N) (Japan)	43	20	28	24.2
Galapagos (90°W, 0°N)	19	26	21	23.5
Tortuguero (83°W, 10°N) (Costa Rica)	15	25	28	27.3
Guyana (58°W, 8°N)	18	27	28	27.4

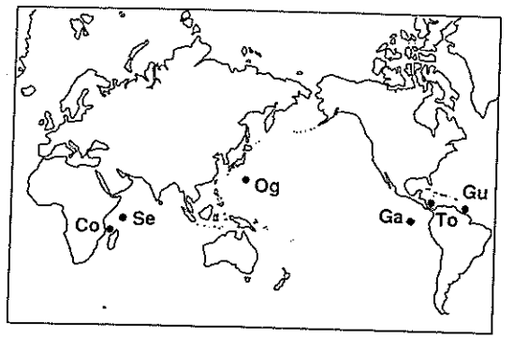

FIG. 1. Map showing sampled localities. Abbreviations: Co = Comoros, Se = Seychelles, Og = Ogasawara, Ga = Galapagos, To = Tortuguero, Gu = Guyana.

Twenty cranial and four mandibular measurements were examined for a total of 145 skulls and 103 mandibles, respectively (Fig. 2). The skull measurements taken were: (1) Cranial length, measured from anterior tip of premaxilla to posterior tip of supraoccipital (LC1); (2) Cranial length, measured from anterior tip of premaxilla to posterior tip of condylus mandibularis of quadrate (LC2); (3) Length of upper jaw (LUJ); (4) Height of cranium (HC); (5) Width of postorbital (WPTO); (6) Width of cranium (WC); (7) Width of exoccipital (WEO); (8) Width of condylus mandibularis (WCM); (9) Minimum width across pterygoid (MWP); (10) Length of secondary palate (LSP); (11) Maximum diameter of orbit (DO); (12) Height of orbit (HO); (13) Height of nasal opening (HN); (14) Width of nasal opening (WN); (15) Height of premaxilla (HPM); (16) Minimum distance between orbit and nasal opening (MDON); (17) Width of supraorbital (WSO); (18) Width of preorbital (WPO); (19) Width of zygomatic (WZ); (20) Width between squamosals (WSM); (21) Height of mandible (HM); (22) Length of mandibular symphysis (LJA); (23) Width of mandible (WM); and (24) Length of mandible from anterior tip to lateral posterior tip (LM). Usually, paired structures were measured on the left side of the skull and mandible unless there was a defect or anomaly on that side.

The specimens examined included 73 females, 19 probable females, 12 males, and 61 specimens of unknown sex. Previous results on the Ogasawara sample (Kamezaki and Suganuma, 1991) indicated the presence of minor sexual differences in only a few characters, and all of our analyses were made without discrimination of sex.

Geographic variation in overall skull size was examined by comparing LC1, LC2, and WC between the six local samples. Multivariate analyses were performed by SAS (SAS, 1985a, b). Multiple-group principal components analysis

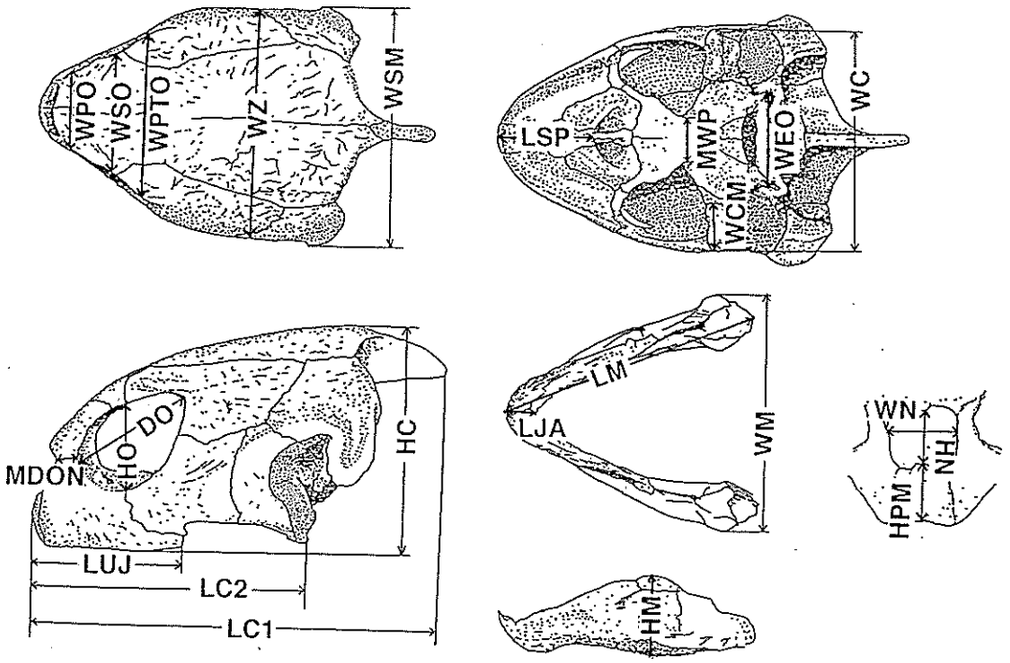

FIG. 2. Skull measurements. See text for abbreviations.

(Thorpe, 1983a, b; Thorpe and Leamy, 1983) was first conducted using GLM and PRINCOMP procedures of SAS (Smith and Patton, 1988) with 24 skull measurements including the mandible, and 20 cranial measurements excluding the four mandibular measurements. In order to visualize geographic differences between local samples, the first principal component scores that represented overall size variation were removed, and the remaining scores were then used for canonical discriminant analysis using the CANDISC procedure. Finally, the percentage of specimens correctly classified into the original sample was calculated by a discriminant analysis based on 1st, 2nd, and 3rd canonical scores.

In order to examine variation in each character dimension among the samples, an analysis of covariance (ANCOVA) was performed using LC2 as the covariate. All measurements were log-transformed in this procedure. Because significant deviations from 1 in the slope of the regression line were observed in only few cases, each character dimension was then converted to a percentage ratio to LC2 for further comparisons. For these ratio variables a two-tailed Mann-Whitney's U test was performed to detect the presence or absence of differences in the frequency distributions, the significance level being set at 5%.

RESULTS

Ranges and means of skull measurements in the six local samples are shown in Table 2. To compare overall skull sizes among the six local samples, presence or absence of differences in LC1, LC2, and WC was examined by Mann-Whitney's U test. The six local samples were divided into two groups by the size of LC1 and LC2. Dimensions of both characters were significantly greater in the Seychelles, Comoros, and Guyana samples than in the remaining three samples ($P < 0.01$). Sample means of LC1 or LC2 showed no significant correlation with either latitude, absolute value of latitude, sea surface temperature in February, sea surface temperature in August, or mean of monthly temperatures of the sample localities.

By the magnitude of WC, the six local samples could be divided into four groups. The greatest WC was found in the Guyana sample, significantly greater than in the group with the next widest skulls (Comoros and Seychelles). These in turn had greater WC than the Ogasawara and Tortuguero samples. The Galapagos sample had significantly smaller WC than all the other samples ($P < 0.01$). The positive correlation of the mean WC of each sample with annual average sea surface temperature (degree C) of each locality was significant ($r = 0.749$; $P < 0.05$).

In the canonical discriminant analyses, the first, second and third canonical axes accounted, respectively, for 44.2%, 27.8%, and 14.2% of the among-localities variability in 24 skull measurements. The Galapagos sample was completely separated from the other samples on the first canonical axis (Fig. 3A). Also, each of the samples from Guyana and Ogasawara was well separated from the others by the first and second canonical axes. The Tortuguero sample largely overlapped with samples from Seychelles and Comoros in the first two axes, but was completely separated from the others by the first and third axes. The absolute magnitudes of the standardized canonical coefficients (Table 3) were proportional to the relative importance of each character in separating samples along each canonical discriminant axis. Examination of the table indicated that WM was the greatest contributor to separation on the first axis (1.961), followed by WC (−1.881), WCM (1.355) and WPTO (−1.272). Variables each with the highest contribution on the second and third axes were LC1 (1.073) and LM (1.376), respectively.

Similar results were obtained in the analysis using 20 cranial measurements excluding the mandible. The first, second and third canonical axes accounted, respectively, for 46.2%, 31.0%, and 12.0% of the among-localities variability. In this analysis, the Galapagos sample was again completely separated from the other samples on the first canonical axis (Fig. 3B). The Guyana sample was better separated on the first canonical axis than in the analysis using 24 measurements including the mandible. Conversely, the separation of the Tortuguero sample was worse on the third axis in this analysis. The greatest contributor in separation on the first axis was WCM (1.584), followed by WSO (0.688), and HC (0.637), whereas on the second and third axes, WCM (1.045), WZ (0.845), and WPTO (−0.842), and WPTO (−0.971) and WZ (0.825), respectively, were high contributors.

Discriminant analysis, based on the first, second, and third canonical scores, showed that all specimens from Galapagos, Tortuguero, and Guyana were classified correctly, and 95% of the Ogasawara sample were also classified correctly when all characters of cranium and mandible were included (Table 4). In contrast, specimens from the Comoros and Seychelles were frequently misclassified. When characters of the lower jaw were excluded, the rate of correct identification decreased in specimens from Galapagos, Tortuguero, and Guyana, although at least 85% of these specimens were classified correctly. By contrast, the rate of specimens correctly classified did not decrease in the Ogasawara sample, and even increased in the Comoros and Seychelles samples. Again, about

TABLE 2. Skull measurements (mm) of *Chelonia mydas* in the six local samples. Means ± SD, followed by ranges.

Variable	Comoros N	Comoros Mean ± SD	Seychelles N	Seychelles Mean ± SD	Ogasawara N	Ogasawara Mean ± SD	Galapagos N	Galapagos Mean ± SD	Tortuguero N	Tortuguero Mean ± SD	Guyana N	Guyana Mean ± SD
LC1	23	210.1 ± 8.8 192.0–230.0	13	212.6 ± 9.3 198.0–226.5	42	194.5 ± 7.8 177.5–211.0	17	193.4 ± 10.8 172.5–210.5	23	193.1 ± 7.9 181.5–208.3	12	208.2 ± 10.4 191.0–225.0
LC2	28	132.5 ± 5.4 121.0–142.0	20	134.9 ± 6.7 121.0–147.0	43	125.0 ± 4.5 113.0–132.0	18	123.4 ± 7.9 110.0–136.0	15	122.4 ± 6.5 109.5–134.0	17	134.4 ± 8.5 120.0–149.0
LUJ	28	71.3 ± 4.3 62.0–81.0	21	73.5 ± 3.9 66.0–79.0	43	68.3 ± 3.8 58.0–74.0	19	66.7 ± 6.4 59.0–79.0	15	64.7 ± 4.4 58.0–72.0	14	70.1 ± 5.0 62.5–78.0
HC	28	106.3 ± 4.5 99.0–115.0	22	106.8 ± 4.5 98.5–113.0	43	103.0 ± 4.3 94.0–116.0	19	95.3 ± 5.4 87.5–105.5	15	100.4 ± 3.6 94.0–106.0	13	109.3 ± 5.5 98.0–118.0
WPTO	28	98.7 ± 3.7 91.5–105.2	22	101.2 ± 5.1 92.1–112.7	43	93.7 ± 4.7 81.9–103.6	19	95.8 ± 6.4 86.2–110.3	15	94.6 ± 4.6 87.7–106.3	18	104.6 ± 5.4 94.7–114.6
WC	28	117.3 ± 4.4 110.3–129.6	19	116.8 ± 5.6 105.4–126.3	43	112.5 ± 5.3 101.5–124.1	18	106.0 ± 7.3 94.1–123.1	15	111.8 ± 4.7 103.7–120.7	12	124.7 ± 6.6 115.5–136.3
WEO	28	53.6 ± 2.9 47.3–60.0	14	52.2 ± 3.3 46.4–58.0	43	49.1 ± 3.5 42.2–56.2	18	48.9 ± 4.3 43.2–58.4	12	48.9 ± 3.0 44.2–54.0	15	54.5 ± 2.4 51.0–58.8
WCM	28	25.1 ± 1.0 23.6–27.1	21	24.8 ± 1.2 21.6–26.3	43	24.5 ± 1.5 21.9–29.4	19	21.0 ± 1.9 18.0–25.5	14	24.5 ± 1.3 22.1–27.3	13	28.5 ± 2.2 25.0–31.9
MWP	28	24.9 ± 2.2 21.2–29.8	21	25.9 ± 1.8 21.2–27.9	43	25.3 ± 2.1 21.7–29.9	18	23.9 ± 2.3 19.8–27.8	15	23.6 ± 1.9 20.8–27.2	18	26.5 ± 1.8 23.8–29.9
LSP	28	53.9 ± 2.7 50.2–61.3	20	53.5 ± 3.1 46.6–57.1	43	50.4 ± 2.8 43.7–56.4	19	48.5 ± 3.4 44.5–56.2	15	49.4 ± 2.6 43.9–54.0	18	53.0 ± 3.2 45.0–59.3
DO	28	68.6 ± 2.7 62.7–73.0	22	68.4 ± 2.3 64.2–74.2	43	62.0 ± 2.8 56.8–68.6	19	61.3 ± 3.9 54.5–69.6	15	63.7 ± 2.8 58.6–69.0	18	69.9 ± 3.3 64.9–76.5
HO	28	50.2 ± 2.0 45.9–53.1	22	51.2 ± 2.3 46.4–56.6	43	46.4 ± 2.2 42.0–52.0	19	45.1 ± 2.7 40.4–50.5	15	46.8 ± 2.1 43.7–49.6	18	50.3 ± 3.3 45.7–55.7
HN	28	22.4 ± 1.8 18.9–26.5	17	22.6 ± 1.7 19.7–25.1	43	20.1 ± 2.0 15.0–23.8	19	22.2 ± 2.4 17.2–27.3	15	18.7 ± 1.5 16.3–21.4	18	21.3 ± 2.2 18.6–26.2
WN	28	27.0 ± 1.7 23.8–30.0	21	27.2 ± 1.8 23.0–30.2	34	26.6 ± 1.8 23.3–30.3	19	26.8 ± 1.9 23.9–31.9	15	24.4 ± 1.5 22.7–27.4	18	26.8 ± 2.1 22.6–30.0
HPM	28	25.9 ± 2.4 20.4–31.6	18	25.7 ± 2.8 21.2–31.3	43	26.7 ± 2.6 21.4–33.2	19	23.2 ± 2.6 18.6–29.6	15	23.2 ± 2.0 20.3–25.7	14	25.6 ± 3.5 19.6–29.5
MDON	28	12.8 ± 1.1 10.4–15.0	22	14.1 ± 1.3 12.1–16.4	43	13.1 ± 1.4 9.8–16.4	19	13.1 ± 1.2 9.5–14.8	15	12.3 ± 1.0 10.2–14.0	18	13.1 ± 0.9 11.5–14.7
WSO	26	60.3 ± 3.8 54.0–66.8	22	63.4 ± 5.4 53.8–75.8	43	59.2 ± 4.8 49.7–71.5	19	57.5 ± 5.1 50.6–69.4	15	55.8 ± 4.4 46.5–63.1	18	65.0 ± 6.2 56.3–76.9
WPO	28	43.8 ± 2.1 37.7–46.4	21	45.1 ± 2.4 41.5–51.1	43	43.9 ± 2.6 39.4–49.7	19	43.3 ± 3.1 37.6–49.5	15	40.8 ± 2.0 37.2–43.3	18	44.5 ± 2.3 41.3–48.4
WZ	27	127.6 ± 5.4 113.2–139.5	22	129.4 ± 6.0 117.3–143.6	43	123.8 ± 6.7 109.6–139.5	19	118.7 ± 7.2 108.3–133.5	15	118.7 ± 5.9 106.0–127.8	18	134.9 ± 7.8 123.7–150.0

TABLE 2. Continued.

Variable	Comoros N	Comoros Mean ± SD	Seychelles N	Seychelles Mean ± SD	Ogasawara N	Ogasawara Mean ± SD	Galapagos N	Galapagos Mean ± SD	Tortuguero N	Tortuguero Mean ± SD	Guyana N	Guyana Mean ± SD
WSM	27	133.8 ± 5.3 124.6–144.6	17	137.3 ± 6.8 124.4–148.4	43	130.3 ± 6.2 119.3–146.5	19	126.7 ± 6.3 117.7–145.3	14	127.3 ± 5.5 118.2–135.0	15	143.4 ± 7.1 134.1–154.1
HM	20	36.4 ± 1.9 31.3–39.4	9	37.1 ± 2.2 33.5–40.7	42	34.9 ± 2.1 30.5–40.5	15	34.1 ± 2.1 31.1–38.6	13	34.4 ± 2.1 31.9–37.8	4	37.7 ± 2.8 34.3–41.2
LJA	20	28.1 ± 1.7 25.0–31.0	9	27.6 ± 2.6 24.0–32.7	42	26.9 ± 1.8 22.6–30.2	15	25.6 ± 2.0 22.1–29.9	13	27.2 ± 1.1 25.1–28.8	4	27.0 ± 1.6 25.4–28.9
WM	19	113.5 ± 3.5 106.2–120.1	9	113.9 ± 5.8 107.8–122.6	41	111.0 ± 5.5 99.7–122.6	14	101.6 ± 7.1 91.5–117.6	13	110.3 ± 4.4 103.0–118.1	4	117.7 ± 6.0 109.8–124.3
LM	20	137.4 ± 5.1 126.8–146.0	8	139.9 ± 6.6 128.8–147.3	42	130.0 ± 4.9 118.2–139.7	11	126.6 ± 8.8 112.9–138.3	13	127.5 ± 4.6 117.5–134.1	3	141.7 ± 2.7 138.6–143.8

two-thirds of the specimens of the Comoros and the Seychelles could not be separated. Thus, each of the six local samples, except for Comoros-Seychelles, could be differentiated fairly well by the cranial dimensions.

Results of ANCOVA showed that only LSP had significant correlation with LC2 in all the six samples, and all the remaining characters correlated insignificantly to LC2 in at least one local sample (e.g., Guyana or Tortuguero). Thus for only seven out of 23 characters, did five out of the six samples show significant correlations. This is probably due to the low sample sizes or to the wide variation in each character. Only six characters (LUJ, WPTO, WC, WCM, LSP, and WPO) out of 23 differed significantly in the slope of regression lines among local samples, but the slope for each sample did not differ from 1 in most cases. Deviation from 1 in the slope of regression lines occurred only in few cases, and even for characters like DO, WZ, and LM, which correlated with LC2 rather well, no more than 60% of the samples showed significant deviation.

On the other hand, the six samples frequently differed in the elevation of the regression lines. Out of 17 characters that showed no difference in slopes, 15 (LC1, HC, WEO, MWP, DO, HO, HN, WN, HPM, MDON, WSO, WZ, WSM, WM, and LM) differed in the position of regression lines among local samples. Some populations showed unique allometric patterns in several characters. The Galapagos sample had the steepest slope in LUJ and the lowest position in HC; the Ogasawara sample was unique in that it had the steepest slope in each of WPTO, WC, WCM, LSP, and WPO and the highest position in HPM among the six samples, whereas the Guyana sample had the highest position in WSM.

Since results of ANCOVA were rather complicated, and significant deviation from 1 (=isometric relationship: Gould, 1977) was not observed in slopes of regression lines in most cases, the relative size of each character dimension was simply expressed by percentage ratio to LC2 (Table 5). In relative values, LC1, WPTO, WEO, MWP, LSP, HO, and HM did not differ among the six samples, but the remaining characters differed more or less significantly in many combinations among the samples. Characters that showed marked variability were WCM and WM.

Thus, the Galapagos sample, which was found to be distinct from all the other samples in canonical discriminant analyses, was characterized by having a relatively low and narrow cranium, a high and wide nasal opening, a narrow condylus mandibularis, a wide preorbital and a narrow mandible. On the other hand, the Guyana sample had a relatively wide cranium, a wide condylus mandibularis, a high premax-

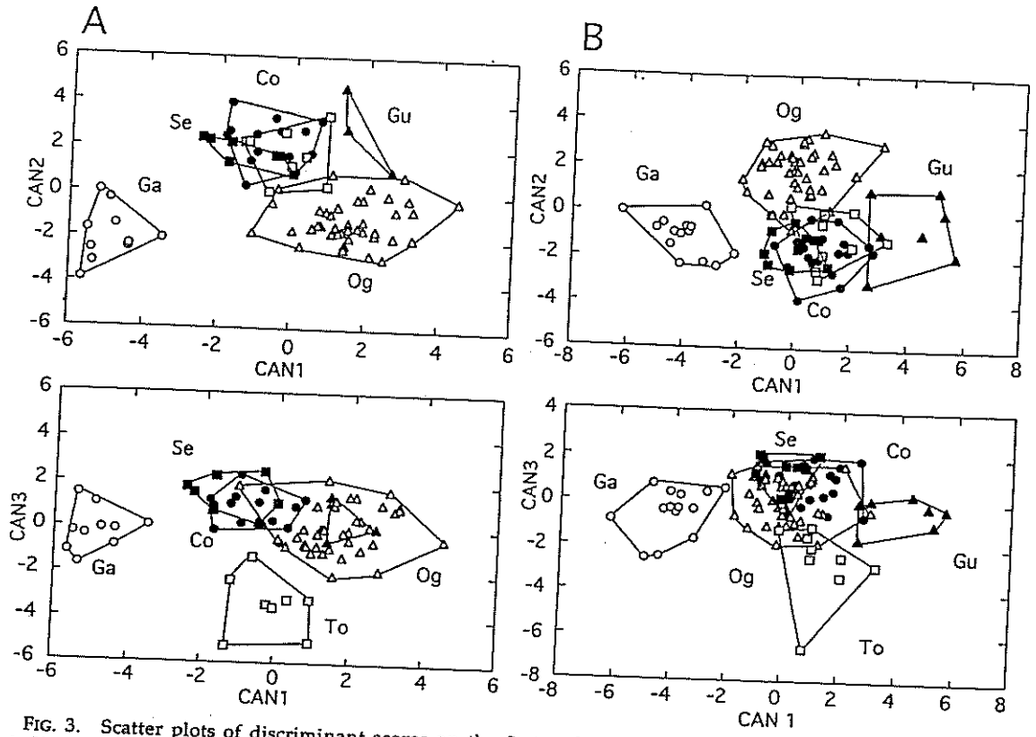

FIG. 3. Scatter plots of discriminant scores on the first and second canonical axes. A: analysis using 24 skull measurements, B: analysis using 20 cranium measurements excluding the mandible. Abbreviations: Co = Comoros, Se = Seychelles, Og = Ogasawara, Ga = Galapagos, To = Tortuguero, Gu = Guyana.

TABLE 3. Standardized canonical coefficients for the first three canonical axes of variation in *C. mydas*.

	Cranium and mandible			Cranium		
	CAN1	CAN2	CAN3	CAN1	CAN2	CAN3
LC1	−0.6139	1.0730	0.1803	−0.0145	−0.7919	0.0921
LC2	−0.7484	0.3289	−0.7236	−0.4116	−0.5236	−0.2034
LUJ	0.0440	−0.6785	0.6447	−0.2543	0.5672	0.6065
HC	0.9627	0.0198	0.0620	0.6379	0.4601	0.4172
WPTO	−1.2728	0.1991	−1.2337	−0.0240	−0.8426	−0.9710
WC	−1.8814	0.5178	−0.9536	−0.1633	−0.6780	−0.6625
WEO	−0.1743	0.1176	0.0765	−0.0713	−0.2445	0.2378
WCM	1.3550	0.5175	0.1666	1.5843	1.0452	−0.0655
MWP	0.0088	0.0999	0.3871	0.0137	0.2039	0.1700
LSP	−0.1482	−0.0006	−0.5285	0.0333	−0.3078	−0.6130
DO	−0.1791	0.5061	0.1643	0.4593	−0.5735	0.1561
HO	0.7524	0.4935	0.5474	0.4694	−0.0257	0.7036
HN	−0.1188	−0.2086	0.4055	−0.2793	−0.2180	0.4087
WN	0.3492	−0.4989	0.6672	−0.3382	0.7131	0.3386
HPM	0.8004	−0.2193	0.3673	0.2498	0.5656	0.3168
MDON	−0.2370	−0.3463	0.1098	−0.3524	−0.0252	0.1680
WSO	0.8424	0.2189	0.1470	0.6889	0.0305	0.2167
WPO	−0.1889	−0.5543	−0.0675	−0.5158	0.1968	0.0871
WZ	0.6886	−0.5242	1.2698	−0.1672	0.8452	0.8252
WSM	−0.4191	0.1283	−0.3331	−0.2372	−0.5182	−0.3395
HM	−0.4019	0.0079	0.1939			
LJA	0.1017	0.1486	−0.7953			
WM	1.9614	−0.6941	−0.3601			
LM	−0.2834	0.2404	1.3767			

TABLE 4. Results of discriminant analysis among six local samples based on the first, second and third canonical scores of 20 cranium and four mandible measurements and 20 cranium measurements.

Locality (N)	Percent classified into					
	Comoros	Seychelles	Ogasawara	Galapagos	Tortuguero	Guyana
Cranium and mandible						
Comoros (14)	57.1	35.7	0	0	0	7.1
Seychelles (7)	28.6	71.4	0	0	0	0
Ogasawara (40)	2.5	0	95.0	0	0	2.5
Galapagos (10)	0	0	0	100	0	0
Tortuguero (8)	0	0	0	0	100	0
Guyana (3)	0	0	0	0	0	100
Cranium						
Comoros (20)	65.0	30.0	0	0	0	5.0
Seychelles (9)	33.3	66.7	0	0	0	0
Ogasawara (42)	2.5	0	95.0	0	0	2.5
Galapagos (14)	0	7.1	0	92.9	0	0
Tortuguero (9)	0	0	11.1	0	88.9	0
Guyana (7)	0	0	0	0	14.3	85.7

illa and a long jaw articulation, whereas the Comoros sample had a relatively narrow supraorbital and a relatively narrow space between squamosals. The Ogasawara sample had a relatively short mandible, a narrow orbital, a wide nasal opening and a wide preorbital compared with the other samples.

DISCUSSION

Our results indicate the presence of notable inter-sample variation in *Chelonia mydas* (including *C. agassizii*). Specimens from local samples of Comoros, Seychelles, and Guyana had larger skulls than specimens from the other three samples. Although insufficient data are available, skull and overall body sizes seem closely correlated. According to Tachikawa (1991), carapace length of mature females of *C. mydas* decreases in the order of Surinam, Ascension, Costa Rica, Sarawak, Southern Yemen, and Ogasawara. Furthermore, the mean calculated from carapace length of 43 matured female from Guyana (Pritchard, 1969) is between those from Surinam and Ascension. This is consistent with our results in that the skulls from Costa Rica (=Tortuguero) are larger than those from Ogasawara. In addition, the Guyana turtles had the largest skulls of all our samples. If this is the case, close correlation of body and skull sizes would be further strengthened.

In our results, lengths of cranium (LC1 and LC2) were larger in the samples from the southern hemisphere, containing those from Guyana (58°W, 8°N), than in the samples from the northern hemisphere or on the equator. This is in concordance with Tachikawa (1991), because Sarawak and Southern Yemen, where nesting turtles are quite small, are in the northern hemisphere, whereas Ascension, inhabited by very large turtles, is in the southern hemisphere. Therefore, *C. mydas* seems to be smaller, both in carapace and skull lengths, in the northern hemisphere than in the southern hemisphere. Skull length, however, was not found to be affected by climatic factors. On the other hand, our results indicated that the local samples were not divided by the skull width (WC) into two geographic groups, but exhibited a climatic cline; skull width tended to increase with an increase in annual average sea surface temperature. In this way, the pattern of geographic variation in the size of *C. mydas* is complex and the key factor causing the size difference found between the two hemispheres is not clear at present. Probably complex ecological, such as kind of food and distance of reproductive migration, and genetic factors, which are unknown at present, are involved.

Results of our morphometric analyses indicated the presence of five geographic groups in *C. mydas*. The sample from the Galapagos was especially distinct from the other local samples in the skull morphometry. Thus, our results confirm the distinctiveness of the eastern Pacific population of *C. mydas*.

From nDNA haplotype frequencies among populations of *C. mydas*, Karl et al. (1992) showed close associations between the following populations: (a) Ascension, eastern Africa, and Brazil, (b) Florida, Venezuela, Costa Rica (=Tortuguero), Surinam, and Atlantic coast of Mexico, (c) Pacific coast of Mexico and Galapagos, (d) Japan (Ogasawara) and Hawaii, and (e) Oman and Australia. Also, the phenogram presented by Karl et al. (1992) indicated that the cluster containing the Pacific coast of Mexico and Galapagos (c) is fairly remote from the other clusters. These results from nDNA haplotype fre-

TABLE 5. Ratios of skull measurements to LC2 (%) in the six local samples of *Chelonia mydas*. Medians followed by ranges (N in parentheses).

Variable	Comoros	Seychelles	Ogasawara	Galapagos	Tortuguero	Guyana
RLC1	(23) 158.4	(13) 157.1	(42) 156.5	(17) 157.6	(11) 159.1	(11) 153.5
	149.6–168.8	143.2–176.8	163.2–163.6	147.8–169.9	149.2–167.6	138.1–165.0
RLUJ	(28) 53.6	(20) 54.8	(43) 54.8	(81) 53.0	(15) 53.0	(14) 53.4
	49.6–59.1	50.0–57.9	48.8–59.0	50.0–60.3	50.6–55.8	42.0–56.6
RHC	(28) 80.0	(20) 80.0	(43) 82.2	(18) 77.7	(15) 82.5	(13) 81.9
	72.3–85.8	72.4–84.1	78.1–89.0	73.0–82.2	73.1–87.6	70.5–91.7
RWPTO	(28) 74.7	(20) 74.4	(43) 74.8	(18) 77.4	(15) 77.6	(17) 76.5
	71.0–77.9	69.5–79.9	68.4–80.9	69.0–86.5	69.5–94.9	72.3–85.0
RWC	(28) 88.9	(18) 85.7	(43) 90.3	(17) 85.8	(15) 91.9	(12) 93.7
	82.8–96.8	76.0–92.7	83.8–94.7	80.4–93.0	78.5–98.0	82.9–102.5
RWEO	(28) 40.2	(13) 38.6	(43) 39.3	(17) 40.7	(12) 40.5	(15) 40.3
	36.1–45.5	31.5–43.7	34.2–44.8	35.5–44.1	36.0–43.9	34.8–42.8
RWCM	(28) 19.0	(20) 18.9	(43) 19.6	(17) 16.9	(14) 20.2	(13) 21.6
	17.3–21.0	17.2–20.1	18.2–22.3	15.4–18.9	17.2–22.9	18.0–23.7
RMWP	(28) 18.7	(20) 19.0	(43) 20.1	(17) 19.8	(15) 19.4	(17) 20.1
	15.6–21.2	17.0–22.9	17.0–23.4	15.9–22.4	15.5–22.1	17.3–22.9
RLSP	(28) 40.8	(19) 39.5	(43) 40.2	(18) 39.2	(15) 40.3	(17) 40.3
	38.6–43.5	36.0–44.7	36.1–43.3	36.7–42.2	37.0–43.0	36.1–43.1
RDO	(28) 51.8	(20) 50.5	(43) 49.5	(18) 49.7	(15) 52.3	(17) 51.4
	48.6–55.6	47.2–55.8	45.1–52.7	46.7–54.4	48.6–54.9	47.6–59.6
RHO	(28) 38.1	(20) 37.9	(43) 37.0	(18) 36.6	(15) 37.7	(17) 37.2
	35.2–41.1	34.6–42.2	33.7–39.7	31.6–41.7	36.1–40.8	33.5–43.6
RHN	(28) 16.8	(18) 16.5	(43) 16.1	(18) 18.8	(15) 15.3	(17) 15.4
	14.1–20.2	14.0–20.0	12.2–19.2	15.0–20.2	12.6–17.6	14.2–18.3
RWN	(28) 20.5	(20) 20.1	(43) 20.9	(18) 21.7	(15) 19.6	(17) 20.0
	17.9–22.3	18.4–24.1	19.1–23.8	20.3–24.0	17.1–22.5	16.2–23.0
RHPM	(28) 19.1	(18) 19.0	(43) 21.7	(19) 18.8	(15) 19.0	(13) 20.2
	16.6–22.5	15.9–22.4	17.0–25.1	14.6–23.5	16.4–20.9	16.2–22.2
RMDON	(28) 9.6	(20) 10.7	(43) 10.5	(18) 10.9	(15) 9.9	(17) 9.7
	8.2–11.2	8.9–11.8	7.8–12.6	9.8–11.6	8.6–11.4	8.7–11.5
RWSO	(26) 45.6	(20) 47.9	(43) 47.2	(18) 45.2	(15) 46.1	(17) 48.7
	40.1–49.3	38.9–55.7	40.1–58.1	40.1–52.1	38.6–52.8	41.6–55.8
RWPO	(28) 33.0	(20) 33.4	(43) 35.2	(18) 35.4	(15) 33.2	(17) 33.3
	30.2–35.4	30.0–38.3	32.1–39.1	32.1–38.3	29.6–38.0	29.9–37.3
RWZ	(27) 95.4	(20) 95.9	(43) 99.0	(18) 95.3	(15) 98.1	(17) 99.9
	87.7–101.0	88.4–103.3	90.2–105.9	88.3–110.4	85.6–104.5	92.9–112.8
RWSM	(27) 100.6	(20) 104.5	(43) 104.3	(18) 103.0	(14) 106.7	(14) 106.0
	91.8–109.0	92.3–111.3	96.2–111.8	92.3–113.4	92.5–112.5	95.7–115.9
RHM	(20) 27.7	(9) 27.5	(42) 27.7	(14) 27.6	(13) 28.0	(4) 28.6
	24.4–29.8	25.1–30.5	25.4–30.7	24.3–31.7	25.9–29.0	26.1–29.0
RLJA	(20) 21.5	(9) 19.9	(42) 21.5	(14) 20.5	(13) 22.0	(4) 20.6
	19.4–23.0	17.8–24.5	18.9–23.8	18.9–23.2	19.7–23.7	17.9–21.8
RWM	(19) 86.2	(9) 83.8	(41) 88.4	(13) 82.9	(13) 88.4	(4) 88.3
	82.2–93.2	74.4–89.8	81.7–94.2	76.6–90.6	83.6–95.2	83.3–91.5
RLM	(20) 104.4	(8) 104.2	(42) 103.8	(11) 101.1	(13) 103.4	(3) 101.3
	98.6–108.8	94.0–107.5	100.0–110.5	93.3–109.1	117.5–134.1	100.5–104.2

quencies appear, at least in essential points, to be concordant with our results, because our samples from Ogasawara, Galapagos, Tortuguero, and Guyana are regarded as corresponding to the groups (d), (c), (b), and (a), respectively, classified by Karl et al. (1992).

Conversely, populations of *C. mydas* were grouped into two assemblages that correspond exactly to major oceanic basins, i.e., the Atlantic Ocean and Mediterranean Sea, and the Indian and Pacific oceans, by mtDNA haplotypes (Bowen et al., 1992). According to the phenogram shown by Bowen et al. (1992), the sample from the Galapagos was included in a group that contained samples from such globally scattered localities as Mexico (Michoacán), Hawaii, and Oman.

Analyses of mtDNA might be valuable in confirming the natal homing hypothesis (Meylan et al., 1990) or elucidating local genetic relationships among rookeries (Bowen et al., 1992) of *C. mydas*, but phylogenetic relationships obtained from these analyses are matriarchal ones and not always in concordance with those obtained from nDNA analyses that are based on male-mediated gene flow (Karl et al., 1992). Recent studies on other vertebrates have also indicated that molecular differences tend to be concordant with zoogeographic boundaries (Avise, 1989), and are not always consistent with the phylogenetic relationships among the taxa in question (Meyer et al., 1990).

It is well-known that the population of *C. mydas* from the eastern Pacific, where the Galapagos are located, has morphological features that are different from other populations, such as dark dorsal pigmentation, gray plastron, higher and more steep-sided carapace, and smaller adult size (Pritchard and Trebbau, 1984). The present study clarified that the Galapagos sample is also the most distinct among the six studied samples in skull morphometry. It seems that the population of the eastern Pacific ocean is isolated from the other populations and has developed its unique morphological features not only externally, but also osteologically. It is arguable to classify an apparently distinct, allopatric population as a species or subspecies. The characters that were significantly different between the Galapagos sample and the others were relative values of WCM and HN (Fig. 4). That is, although the skull of the Galapagos sample is distinct on the basis of the canonical discriminant analyses, there is no single skull character that perfectly distinguishes the Galapagos sample from the others. From this result, we think it problematic to regard the population from the eastern Pacific as a full species. However, the uniqueness of the Galapagos sample is also clear from skull morphology. Therefore, we think it better to regard the eastern Pacific population of *C. mydas*, including the Galapagos sample, as the subspecies *C. m. agassizii*, as proposed by Carr (1952).

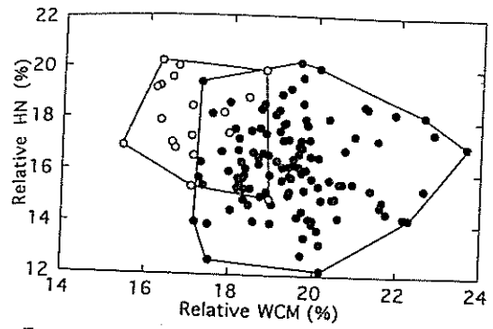

FIG. 4. Relationships between relative WCM and relative HN in samples from the Galapagos (open circles) and the other samples (closed circles).

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APPENDIX I

Specimens Examined.—USNM: United States National Museum of Natural History; UF-FSU: Florida Museum of Natural History; PCHP: Dr. P. Pritchard's Private Collection; KPC: Kamezaki's Private Collection. Comoros: USNM 231572–231578, 231578, 231587–231593, 231598–231603, 231605, 231606, 231609–231612, 251582, 1 specimen unnumbered. Seychelles: PCHP 2613–2615; USNM 220773–220776, 235855, 235868–235870, 235872, 235886, 235893–235897, 269986, 269988–269990. Ogasawara: KPC 80, 82, 84, 86, 91, 95, 98, 133, 136, 141, 143, 147, 148, 150, 153, 155, 157, 158, 161, 164, 168, 182, 183, 186, 187, 194, 199, 234, 237, 244, 247, 282, 287, 290–292, 294, 326, 1111–1113, 1223, 881215. Galapagos: PCHP 72, 178, 814, 926–929, 931, 932, 934–938, 1130, 2493; UF-FSU 47674, 47675, 57975. Tortuguero: PCHP 2026, 2699, 2700; UF-FSU 10589, 43794–43804. Guyana: PCHP 920, 921, 923, 2461, 2462, 2469, 2504, 2505, 3370, 3372–3375, 3378, 3379, 3382; UF-FSU 25698, 1 specimen unnumbered.