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Geographic Variation in the Neotropical Turtle, *Platemys platycephala*

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ABSTRACT.—**Difference in carapacial and bridge patterns, and in mensural and meristic data indicates that the populations of *Platemys platycephala* from the ríos Cenepa and Santiago, Perú and the ríos Napa and Curaray, Ecuador represent an undescribed dark subspecies. The Quaternary rainforest refuge theory is discussed in view of the origin and subsequent zoogeography of the new subspecies.**

The Neotropical sideneck turtle, *Platemys platycephala*, has an extensive range in northern South America. It occurs throughout most of the Amazon basin and its headwaters in northern Bolivia, northern Perú, eastern Ecuador and southern Colombia. It also inhabits the Caribbean drainages of eastern Venezuela, Guyana, Surinam and French Guiana. Although Schneider (1792) gave the type locality of the species as "Ost-Indien" his specimens were probably from the Guianas or eastern Brazil, since *P. platycephala* does not occur naturally on any East or West Indian islands and exploration of the Upper Amazon had not yet begun. Despite such a large distribution, no geographic variation has been described. This paper presents the results of a study of geographic variation within *Platemys platycephala*. Shell scute designations are those of Zangerl (1969).

METHODS AND MATERIALS

Specimens from 34 localities in northern South America were examined (Fig. 1). Each specimen was sexed, and straight-line measurements were taken with dial calipers (accurate to 0.1 mm) of the greatest carapace length (CL), carapace width (CW) and depth (D) at the level of the seam between vertebrals 2 and 3, marginal width (the differences between the carapacial width and the width across the pleurals taken between the points of juncture of the marginals and pleurals at the level of the seam between vertebrals 2 and 3), greatest plastron length (PL), width of the anterior plastral lobe (APW), width of the posterior plastral lobe (PPW), greatest bridge length (BL), greatest width and length of all five vertebrals and of the second right pleural scute, the medial seam length (or medial length of the intergular scute) and the greatest width of all plastral scutes, the length of the dark pigmental bar on the bridge (BP), and the lengths of the intergular-humeral seam (IGH seam) and the gular-humeral seam.

The number of rows of large scales at the lateral edge of the antebrachium between the claw of digit V and the first horizontal skin fold proximal to the elbow was recorded, as also were the number of postorbital scales (PO) and the number of scales separating the tympanum and orbit (T–O).

The carapacial pattern was carefully drawn and the colors recorded.

All data were entered into a computer, and simple statistical tests including Chi-square tests, analysis of variance (ANOVA) and cluster analyses were performed using the Statistical Analysis System (SAS) (Hellwig and Council, 1979). The mensural data were also scaled by either carapace length (CL), carapace width (CW), plastron length (PL), plastral forelobe width (APW), or

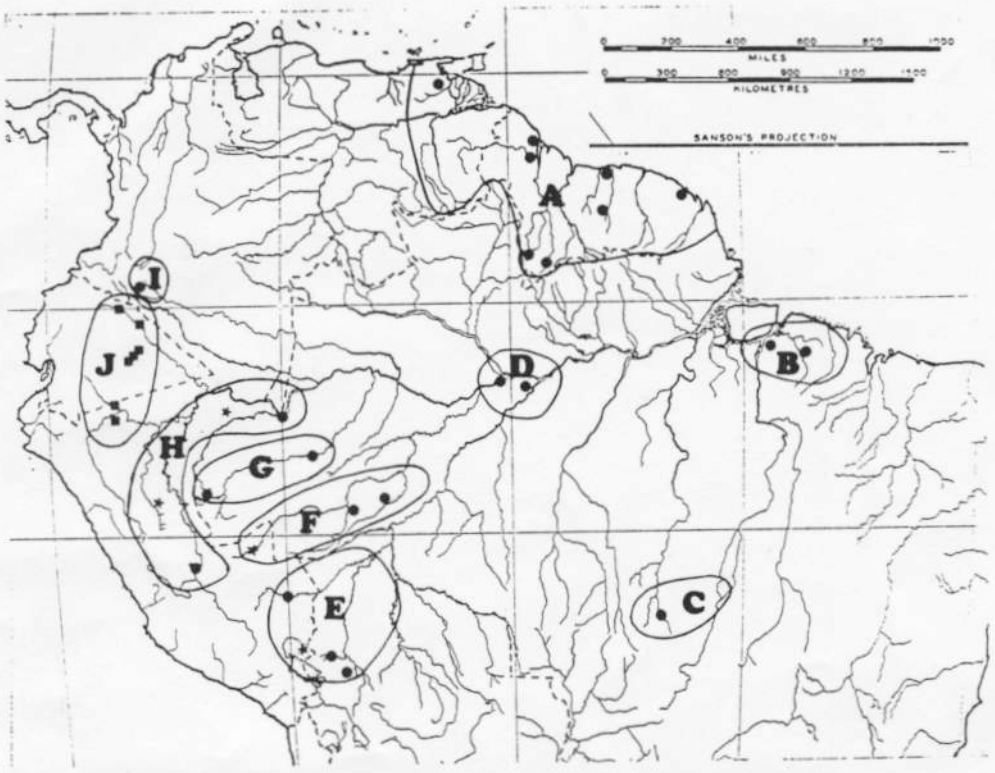

FIG. 1. Distribution of carapacial patterns in *Platemys platycephala*. Dots indicate populations with predominantly yellow carapaces; squares, populations with predominantly black carapaces; and stars, populations showing intermediate carapacial patterns. A–J indicate regions discussed in the text.

plastral hindlobe width (PPW), to reduce size bias, and subjected to univariate analyses, such as Student's *t*-test.

Specimens from the following collections were examined: American Museum of Natural History (AMNH); Field Museum of Natural History (FMNH); Los Angeles County Museum (LACM); Louisiana State University, Museum of Zoology (LSU); Museum of Comparative Zoology, Harvard University (MCZ); Museum National d'Histoire Naturelle, Paris (MNHP); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museu do Zoologia, Universidade de Sao Paulo (MZUSP); Naturhistorisches Museum Wien, Vienna (NHMW); Peter C. H. Pritchard, personal collection (PCHP); Texas Cooperative Wildlife Collection, Texas A & M University (TCWC); University of Illinois Natural History Museum (UIMNH); University of Kansas Museum of Natural History (KU); University of Michigan, Museum of Zoology (UMMZ); National Museum of Natural History, Smithsonian Institution (USNM); Zoologisches Sammlung des Bayerischen Staates, Munchen (ZSM).

RESULTS

Since many of the 34 localities sampled were represented by only a few specimens, the localities were combined into ten regions according to major drainage patterns (Fig. 1): A, the Caribbean drainages of Venezuela, Guyana, Surinam and French Guiana (23

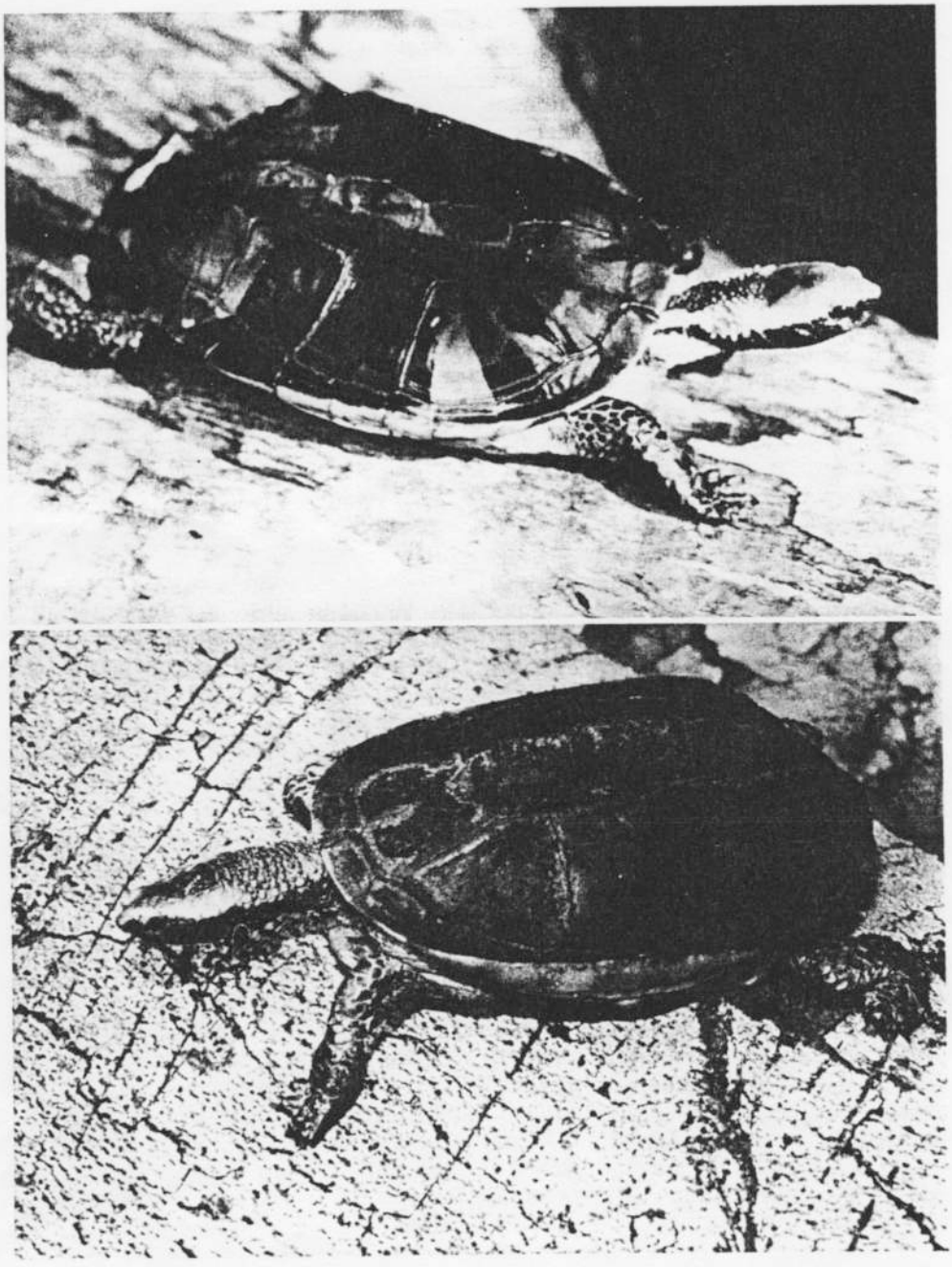

FIG. 2. Upper, *Platemys platycephala platycephala* photographed at the United States National Zoological Park. Lower, *Platemys platycephala melanonota* subsp. nov., photographed at the Baltimore Zoo. Photographs by Roger W. Barbour.

individuals); B, Río Tocantins-Río Para drainages near Belem, Brazil (5); C, Río Culvene, Mato Grosso, Brazil (1); D, Río Amazon lower Río Madeira drainages near Manaus, Brazil (4); E, Río Mamorê drainage, Bolivia, and Río Madre de Dios drainage, Perú (5); F, Río Purús drainage, Brazil and Perú (11); G, Río Jurúa drainage, Brazil (3); H, Río Yavari drainage, Brazil, Río Ucayali drainage, Perú (14); I, Río Putumayo drainage, Colombia (3); J, ríos Cenepa and Santiago drainages Perú, and ríos Napa and Curaray drainages, Ecuador (44).

Examination of the carapacial and bridge patterns revealed major differences between the populations of *P. platycephala* in region A, the Caribbean drainages of Venezuela and the Guianas, and those turtles from region J, the ríos Cenepa and Santiago drainages of Perú and the ríos Napa and Curaray drainages of Ecuador. The Caribbean drainage turtles have a mostly yellow carapacial pattern with dark pigment extending along the seams between the first and second vertebrals and the first and second pleurals on each side, and downward to the marginals on the second and third pleurals on each side. This dark color forms an incomplete band across the center of the carapace. The medial portion of the first four vertebrals, the first and fourth pleurals, and the fifth vertebral lack dark pigment and remain yellow (Fig. 2, Upper). However, turtles from northern Perú and Ecuador have very dark carapaces with little or no yellow pigment on the first pleurals, and the yellow pigment is also reduced on the fourth pleural. In many, the only yellow present is a narrow medial stripe extending along the vertebral groove (Fig. 2, Lower). That this dark pigmentation is not the result of age or sex related melanism is shown by its occurrence in both sexes and in juveniles with carapace lengths of 50 and 51 mm. Turtles from other Amazonian regions have predominantly the lighter carapacial pattern (Fig. 1). Only in the headwaters in western Brazil and eastern Perú (regions E, F, H) do the turtles show increasing dark pigmentation. Those from the ríos Curanja and Ucayali, and the Raul de Los ríos of Perú, and the Río Yavari, Brazil, appear intergrade. The distribution of the light and dark patterns, and those considered intermediate, are given in Table 1.

TABLE 1. Types of carapacial patterns of *Platemys platycephala* by regions.

		Carapacial pattern					
		Light		Intermediate		Dark	
Region	N	N	%	N	%	N	%
A	23	23	100				
B	5	5	100				
C	1	1	100				
D	4	4	100				
E	5	2	40	2	40	1	20
F	11	3	27	3	27	5	45
G	3	3	100				
H	14	11	79	2	14	1	7
I	3	3	100				
J	44			3	7	41	93

The bridge pattern in *P. platycephala* consists of a dark bar of varying length (range, 29–100% of bridge length). The extent of the dark bar was calculated as a percentage of the entire length of the bridge and coded as 1 if below 80%, 2 if between 81 and 99%, and 3 if 100% (Table 2). In the Caribbean populations (A) this bar covers less than 76% (29–75%) of the length of the bridge. In the turtles from northern Perú and Ecuador (J), the dark bar occupies 75–100% of the bridge length, with most individuals (72%) having the dark bar completely crossing the bridge. Table 2 indicates that the dark bar tends to increase in length in the Amazonian headwater populations. It is possible this character is clinal, increasing in length from east to west, in the Amazon drainage, but it is much less extensive in the Caribbean populations (A). A cluster analysis of this character clearly separated the Caribbean turtles from those of northern Perú and Ecuador. *P. platycephala* from

TABLE 2. Bridge patterns of *Platemys platycephala* by regions.

					Pattern					
		% Length			1 (0–80%)		2 (81–99%)		3 (100%)	
Region	N	$\bar{x}$	SD	Range	N	%	N	%	N	%
A	23	64	13	29–75	23	100				
B	5	78	8	67–90	4	80	1	20		
C	1	100							1	100
D	3	67	33	33–100	2	67			1	33
E	6	89	9	80–100	1	17	3	50	2	33
F	11	89	24	20–100	2	18	1	9	8	73
G	4	84	11	75–100	3	75			1	25
H	14	91	12	75–100	5	36	1	7	8	57
I	3	62	20	43–83	2	67	1	33		
J	44	96	7	75–100	2	4	10	23	32	73

the Lower Amazon populations generally clustered with the Caribbean turtles, while those in the headwaters clustered with the northern Perú and Ecuadorian populations (J).

An ANOVA was performed on the various mensural characters, and none were found to differ significantly. However, Student's *t*-tests revealed significant differences ($P < 0.05$) between the Caribbean population (A) and those from northern Perú and Ecuador (J) in the ratios of the intergular width/anterior plastral width (IGW/APW) and of the intergular-humeral seam length/anterior plastral width (IGH seam/APW) (Table 3). The intergular was wider in the Caribbean drainages (A) and narrower in northern Perú and Ecuador (J). However, when the other Amazonian populations are considered, these characters again appear to be clinal.

The number of foreleg scale rows was not significantly different between the Caribbean populations (A) and those from northern Perú and Ecuador (J), but the number of postorbital scales (PO) and the number of scales lying between the tympanum and orbit (T–O) were (ANOVA, $P < 0.05$). The number of postorbitals was greater in turtles from the Caribbean drainages (A) and decreased in the western Amazonian population (J) (Table 4). The lesser number of postorbital scales in most individuals in northern Perú and Ecuador (J) was due to a fusion of two or three scales to produce a single larger scale. Such fusion was not observed in the Caribbean turtles. The number of scales lying between the tympanum and the orbit

TABLE 3. Comparison of IGW/APW and IGH seam/APW of *Platemys platycephala* by regions.

		IGW/APW			IGH seam/APW		
Region	N	$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
A	23	27.2	2.5	22.8–32.6	21.7	2.8	16.2–27.5
B	5	26.1	2.5	22.6–29.4	21.1	2.9	18.0–24.1
C	1	25.7			19.8		
D	3	26.5	1.1	25.2–27.4	20.5	1.9	18.6–22.5
E	6	23.5	2.8	20.5–27.0	19.1	2.6	15.0–22.8
F	11	24.5	1.2	22.7–26.7	20.2	2.9	13.4–22.9
G	4	25.6	2.8	23.3–29.5	21.6	2.2	20.2–24.9
H	14	26.3	3.7	21.4–36.1	18.6	5.2	15.2–22.4
I	3	25.1	1.6	23.3–26.6	20.7	4.5	15.6–24.3
J	41	24.2	2.3	18.0–28.3	18.8	3.6	10.7–26.2

TABLE 4. Meristic data for *Platemys platycephala* by region.

Region	N	Postorbital scales			Scales T-O		
		$\bar{x}$	SD	Range	$\bar{x}$	SD	Range
A	22	4.22	0.74	3.0–5.5	3.43	0.58	3.0–4.5
B	4	5.13	0.25	5.0–5.5	3.75	0.50	3.5–4.5
C	1	4.00			4.50		
D	2	5.25	1.06	4.5–6.0	4.50		
E	2	3.50	0.71	3.0–4.0	3.75	0.35	3.5–4.0
F	11	4.14	0.50	3.5–5.0	3.73	0.52	2.5–4.5
G	1	4.50			3.50		
H	9	3.33	0.66	3.0–5.0	3.33	0.56	2.5–4.0
I	2	4.25	1.06	3.5–5.0	4.00		
J	44	3.67	0.75	2.0–5.0	3.83	0.46	3.0–5.0

showed the opposite trend by increasing slightly in the western regions (Table 4). These two characters also appear clinal.

A cluster analysis for the total mensural and meristic characters clearly separated the Caribbean populations (A) from those of northern Perú and Ecuador (J). Individuals from the other regions clustered with either A or J, indicating intergradation. Turtles from regions E, F, and H most closely resembled those from region J; while those of B, C, D, and I clustered with A.

From the above data it is clear that geographic variation in *Platemys platycephala* occurs, and that two different subspecies are involved; a light race in the Caribbean drainage, as first described by Schneider (1792), and an undescribed dark race in the headwaters of the Amazon in northern Perú and Ecuador (Fig. 2).

Platemys platycephala platycephala (Schneider)

Testudo platycephala Schneider, 1792:261. Holotype, undesignated. Type-locality, "Ost-Indien," here restricted to Cayenne, French Guiana.

Testudo planiceps Schoepff, 1792:115. Holotype, undesignated. Type-locality, "Patria India orientalis effe dicitur," here restricted to Cayenne, French Guiana. Plate 27 shows this turtle to be *P. p. platycephala.*

Testudo martinella Daudin, 1803:344. Holotype, MNHP 8760, adult female (examined by author). Type-locality, "Cayenne," from label.

Emys discolor Schweigger, 1812:302. Holotype, undesignated. Type-locality, unknown, here restricted to Cayenne, French Guiana. Description indicates it is *P. p. platycephala.*

Emys canaliculata Spix, 1824:10. Holotype, ZSMH 3007/0, shell and skeleton. Type-locality, "fluminis Solimoens," Brazil. Plate 8 shows it to be *P. p. platycephala.*

Hydraspis constricta Gray, 1831:43. Holotype, undesignated. Type-locality, not given, here restricted to Belem, Brazil as many of the other South American chelids described in the same paper were from "Brasilia." The description is vague, so the designation as *P. p. platycephala* is arbitrary.

Diagnosis.—A light-colored subspecies of *Platemys platycephala* with the dark pigment on the yellow carapace restricted to the border of the seam separating the vertebrals from the pleurals and to an incomplete band extending on each side from the medial groove downward through the second and third pleurals to the lateral carapacial rim (the medial groove remains yellow); a dark bar crossing less than 80% of the bridge ($\bar{x}$ = 64.0%); a wide intergular scute ($\bar{x}$ = 27.2% of APW); a relatively long seam between the intergular and humeral scutes ($\bar{x}$ = 21.7% of

APW); usually more than 4 postorbital scales; and usually less than 3.5 scales separating the tympanum from the orbit.

Description (based on 23 specimens from the Caribbean drainages, A).—The elliptical carapace (to 165 mm in males and 141 mm in females) is flattened, widest at the level of marginas 7–8, and highest at the seam between vertebrals 2–3. The carapace depth averages 27.0% (22–29%) of the carapace length, and the carapace width averages 72.0% (65–81%) of the carapace length. A pronounced medial groove extends from the posterior portion of the first vertebral to the anterior portion of the fifth vertebral. In juveniles all five vertebrals are wider than long, but in large adults the third vertebral is usually longer than wide. The fourth and fifth vertebrals are the smallest. The cervical scute is usually long and narrow. The posterior marginals are flared (slightly serrated in juveniles), and the lateral marginals are upturned. The surface of the scutes of turtles less than 90 mm in carapace length usually bears numerous rounded rugosities. The ground color is yellow with dark brown or black pigment extending along the seams separating the vertebrals from the pleurals bordering the medial groove, which remains yellow, and covering all of the second and most of the third pleural on each side. The marginals are dark brown dorsally, but ventrally yellow with a dark triangular mark at the anterior seam.

The plastron length is to 153 mm (males 153, females 134), and its length averages 91.4% (86–103%) of the carapace length. It is concave in males, and slightly upturned anteriorly and notched posteriorly in both sexes. The anterior lobe is longer and slightly wider than the posterior lobe. The bridge length averages 30.2% (27–31%) of the plastron length, and the plastral formula is Intergular > Abdominal > Femoral > Anal > Gular > Humeral > Pectoral. The intergular scute is wide averaging 27.2% (23–32%) of the anterior plastral width, and the intergular-humeral seam is correspondingly long, averaging 21.7% (16–26%) of the anterior plastral width. The intergular is about half as long as the length of the anterior plastral lobe. Small axillary and inguinal scutes are present. The plastron is dark brown or black with a yellow border. The bridge is yellow with a dark bar crossing less than 80% of its length (29.0–75.0, $\bar{x} = 64.0$).

The head is small with a slightly protruding snout and an unnotched upper jaw. The dorsal surface of the head is covered with smooth, undivided skin; 1–3 rows of large scales occur on the lateral surface.

Postorbital scales usually more than four (3–6, $\bar{x} = 4.22$), and usually less than 3.5 scales (2–4, $\bar{x} = 3.43$) separating the tympanum from the orbit. Two small chin barbels are present. The head is orange to yellow-brown dorsally, but dark brown to black laterally and ventrally. The light dorsal pigment extends downward on the sides to the midpoint of the orbit and tympanum. The jaws are dark. The neck is colored much like the head, and there are numerous blunt scales and tubercles on its dorsolateral surface.

The limbs are dark gray to brown or black. There are large scales covering the forelimbs and outer surface of the hindlimbs. The thighs contain small blunt tubercles. The toes are webbed.

In comparison to females, males seem larger (carapace to 165 mm, females to 141), have concave plastra, and longer tails with the vent located beyond the carapacial rim.

Range.—Caribbean drainages of Venezuela and the Guianas, and the Amazon drainages as far upstream as the Río Purús, Juruá, Yavari, and Putumayo.

Etymology.—The generic name *Platemys* is from the Greek *platos*, flat, and *emydos*, a freshwater turtle, and refers to the depressed carapace. The name

platycephala is from the Greek *platos*, flat, and *kephale*, head, referring to the flat crown.

Specimens Examined (47).—*Venezuela* (1): AMNH 65541, Caripito. *Guyana* (7): AMNH 15145, Kartabo; AMNH 61523, 61531, head of Rupununi River; AMNH 61528–29, Shudi-kar-wau River; UMMZ 46160, Dunoon, Demerara River; AMNH 61533, Guyana. *Surinam* (13): NHMW 23502:1–7, Paramaribo; PCHP 155, Pininika, Upper Commewijae River; NHMW 23503:2–3, MCZ 1886–87, MNHP 2098, Surinam. *French Guiana* (2): MNHP 8753, 8760, Cayenne. *Brazil* (17) MZUSP 2689–92, Aldeia Aracu, Igarape Gurupi-Una; MZUSP 2693, Igarape, Belem; UMMZ 115654, Mato Grosso, Río Culvene; NHMW 23503:1, Moura, Amazonas; AMNH 89782, Maues Amazonas; MCZ 2628, Río Madeira, Manes; ZSM 3007/0, Río Solimoens; MZUSP 2038, Alto Parus; MZUSP 2819, Río Assua, Mucuim; MZUSP 13, 19, Río Jurúa; MZUSP 2694, Benjamin Constant; MNHP 2099, USNM 65663, Brazil. *Colombia* (3): KU 124942, Cuqueta, Río Hacha, Florencia; UMMZ 121013, Río Amazon; USNM 224130, Santa Rosa de las Cofanes, Putumayo. *South America* (4): MCZ 58127–28; USNM 86654, 89409.

Platemys platycephala melanonota
Subsp. Nov.

Holotype.—USNM 224136, adult male; vicinity of Galilea, on the Río Santiago, Amazonas, Perú (4°1'S, 77°47'W) collected 1 February 1980 by Roy W. McDiarmid.

Paratypes.—Río Santiago drainage Amazonas, Perú: LACM 134414 (adult male); MVZ 158995 (adult female), 175379 (juvenile); USNM 224137–38 (adult males), 224139 (juvenile). Río Cenepa drainage, Amazonas, Perú: LACM 134406–07 (adult females), 134408 (adult male), 134409–10 (adult females), 134411–12 (juveniles), 134413 (adult female); MVZ 163036 (adult female), 163037–38 (adult males), 163039 (adult female), 163040 (adult male), 163041 (adult female), 163042 (adult male); USNM 224132 (juvenile), 224133 (adult female), 224134 (adult male), 224135 (adult female).

Diagnosis.—A dark-colored subspecies of *Platemys platycephala* with the light pigment on the brown carapace restricted to the vertebral groove, in some on the extreme anterior portion of the first pleurals, and on the posterior portion of the fourth pleurals; a dark bar crossing more than 90%, and usually 100% of the bridge ($\bar{x}$ = 96.1%); a narrow intergular scute ($\bar{x}$ = 24.2% of APW); a relatively short seam between the intergular and humeral scutes ($\bar{x}$ = 18.8% of APW); usually less than 4 postorbital scales; and usually more than 3.6 scales separating the tympanum from the orbit.

Description (based on 44 specimens from northern Perú and Ecuador, J).—The elliptical carapace (to 168 mm in males and 167 in females) is flattened, widest at the level of marginals 7–8, and highest at the seam between vertebrals 2–3. The carapace depth averages 28.0% (23–31%) of the carapace length, and the carapace width averages 68.0% (60–77%) of the carapace length. A pronounced medial groove extends from the posterior portion of the first vertebral to the anterior portion of the fifth vertebral. In juveniles all five vertebrals are wider than long, but in large adults the third vertebral is usually longer than wide. The fourth and fifth vertebrals are the smallest. The cervical scute is usually long and narrow. The posterior marginals are flared (slightly serrated in juveniles) and the lateral marginals are upturned. The surface of the scutes of turtles less than 90 mm carapace length is usually roughened with numerous rounded rugosities. The ground color is dark brown or black with yellow pigment occurring only along the center of the vertebral groove, sometimes on the extreme anterior portion of the first pleural, and on posterior portion of the

fourth pleural, and the accompanying marginals. Undersides of marginals yellow with a dark triangular mark at the anterior seam.

The plastron length is to 157 mm (males 155, females 157) and its length averages 91.4% (85–98%) of the carapace length. It is concave in males, and slightly upturned anteriorly and notched posteriorly in both sexes. The anterior lobe is longer and slightly wider than the posterior lobe. The bridge length averages 29.6% (25–32%) of the plastron length, the plastral formula is Intergular > Abdominal > Femoral > Anal > Gular > Humeral > Pectoral. The intergular scute is narrow, averaging 24.2% (18–28%) of the anterior plastral width, and the intergular-humeral seam is correspondingly short, averaging 18.8% (11–26%) of the anterior plastral width. The intergular scute is over half as long as the length of the plastral forelobe. Small axillary and inguinal scutes are present. The plastron is dark brown or black with a yellow border. The bridge has a dark bar crossing more than 90% of its length (75.0–100.0, $\bar{x}$ = 96.1), with most (72%) having the bar completely across the bridge.

The small head has a slightly protruding snout and an unnotched upper jaw. The dorsal surface of the head is covered with smooth, undivided skin; 1–3 rows of large scales occur on the lateral surface. There are usually less than four postorbital scales (2–5, $\bar{x}$ = 3.67), the reduction is apparently caused by the fusion of two or three scales to form a single larger postorbital; usually more than 3.6 scales (3–4, $\bar{x}$ = 3.83) separate the tympanum from the orbit. Two small chin barbels are present. The head is orange to yellow-brown dorsally, but dark brown to black laterally and ventrally. The light dorsal pigment extends downward on the sides to the midpoint of the orbit and tympanum. The jaws are dark. The neck is colored much like the head, and there are numerous blunt scales and tubercles on its dorsolateral surface.

The limbs are dark gray to brown or black. There are large scales covering the forelimbs and outer surface of the hindlimbs. The thighs contain small blunt tubercles. The toes are webbed.

In comparison to females, males are about the same length (carapace to 168 mm, females to 167), have a concave plastron, and longer tail with the vent located beyond the carapacial rim.

Range.—Restricted to the Upper Amazon drainages of the ríos Santiago and Cenepa in Perú and the ríos Napa and Curaray in Ecuador. It intergrades with *P. p. platycephala* in the Río Mamorê drainage, Bolivia; and the ríos Madre de Dios, Purús, and Ucayali of Perú.

Etymology.—The name *melanonota* is from the Greek *melania*, blackness, and *notos* pertaining to the back, and refers to the dark carapace of this subspecies.

Specimens Examined (53).—Bolivia (1): USNM 65098, Rurrenabaque, Amazon. *Ecuador* (18): AMNH 113636–37, Cusuime, Río Cusuime; UIMNH 62406, Macuma, Zamora Prov.; KU 105439–40, 126676–77, 148411, 152362, 158538, Santa Cecilia, Napo Prov.; KU 121351, Puerto Napo, Napo Prov.; KU 175263, Limoncocha Prov.; USNM 204060, Loreto, Napo Prov.; USNM 204061, Río Pindo, Pastaza Prov.; USNM 204062–63, region of Río Bobonaza, Pastaza Prov.; USNM 204064, Sarayacu, Río Bobonaza, Pastaza Prov.; USNM 204065, Alto Río Curaray, Oriente, Pastaza Prov.; USNM 204066, Montalvo, Pastaza Prov. *Perú* (including type specimens listed above, 34): FMNH 45658, 45660, Yarinococha, Ucayali, Dept. Loreto; LSU 26748–49, 26753, Río Curanja, Dept. Loreto; USNM 166953, Tingo Maria, Río Huallaga, Dept. Huanuco; USNM 222369, Río Tambopata, Dept. Madre de Dios; USNM 224131, Ancaya, nr. Iquitos, Centro Union, Dept. Loreto. *Intergrade P. p. platycephala* × *P. p. melanonota* (20): *Brazil* (3): MZUSP 310, Río Jurúa, MZUSP 2799, Seringal Uniao, Río Acre; MZUSP 3002, Río Moa. *Bolivia* (1): KU 135215, Cochabamba, 6.5 km N. Chiripi. *Perú* (16): AMNH 71175–76, Raul de los

ríos; FMNH 45661–64, 56194–95, Yarinococh, Ucayali, Dept. Loreto; FMNH 168077, Avispas, nr. Inambari, Dept. Madre de Dios; LSU 14588, Balta, Río Curanja, Dept. Loreto; LSU 26750–52, 26754, Río Curanja, Dept. Loreto; TCWC 41802–04, Centro Union, Dept. Loreto.

Discussion

The Quaternary forest refuge theory (see summary in Haffer, 1979) presents a plausible explanation for the process of subspeciation in *Platemys platycephala*. Region J, which includes the subspecies *P. p. melanonota*, has been previously proposed as a possible Quaternary rainforest refuge for fruitflies (Winge, 1973), butterflies (Brown, 1976, 1977*a*, *b*; Brown et al., 1974), anurans (Duellman, 1982), lizards (Vanzolini, 1970, 1973; Vanzolini and Williams, 1970), birds (Haffer, 1967, 1969, 1970, 1974, 1975), vertebrates in general (Müller, 1972, 1973), and trees (Prance, 1973). During the Quaternary, significant climatic changes occurred in the equatorial regions due to the periods of glaciation in the temperate zones. These climatic changes resulted in constriction of the lowland rainforests in northern South America during dry (glacial) periods, followed by alternating wet (interglacial) periods during which the rainforests expanded again. This alternation between drier and wetter periods was reflected in spreading and retreat of the large areas of rainforest and of the complementary open formations, probably either xerophytic caatingas or very degraded cerrados or a patchy distribution of both types (Vanzolini, 1973). During the drier periods the open formations made great inroads into the Amazonian rainforest, which was reduced to isolated patches in areas where conditions remained relatively more humid. Populations of forest animals and plants isolated in the rainforest refuges during the dry periods either became extinct, survived with little change, or, more often, differentiated to the level of subspecies or species before they came into secondary contact with previously conspecific populations from other refugia during a favorable expansive period (Haffer, 1979).

Platemys platycephala is an inhabitant of shallow rainforest streams, and frequently wanders about on the forest floor. Prior to the Pleistocene the populations of *P. platycephala* were probably continuous through the Amazon basin. A population of *P. platycephala* isolated in northern Perú and Ecuador (J) during a dry period could have undergone enough change to produce the new subspecies, *melanonota*. During subsequent wet periods either *melanonota* spread downstream in the Amazon basin or *platycephala* migrated upstream, following reforestation, where they met and intergraded in western Brazil, and eastern Perú (E, F, H). Populations of *P. p. platycephala* from the Caribbean drainages (A) were isolated by the Guiana Shield, and genetic exchange between *melanonota* and the Lower Amazon populations (B, C, D, I) of *P. p. platycephala* has not occurred.

Bull and Legler (1980) reported that two *P. platycephala* they examined had unusual triploid karyotypes, 96 chromosomes, instead of the normal diploid 64. The locality of these specimens was listed only as "South America," and they were not described, but it would be interesting to compare them with *P. p. melanonota*.

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